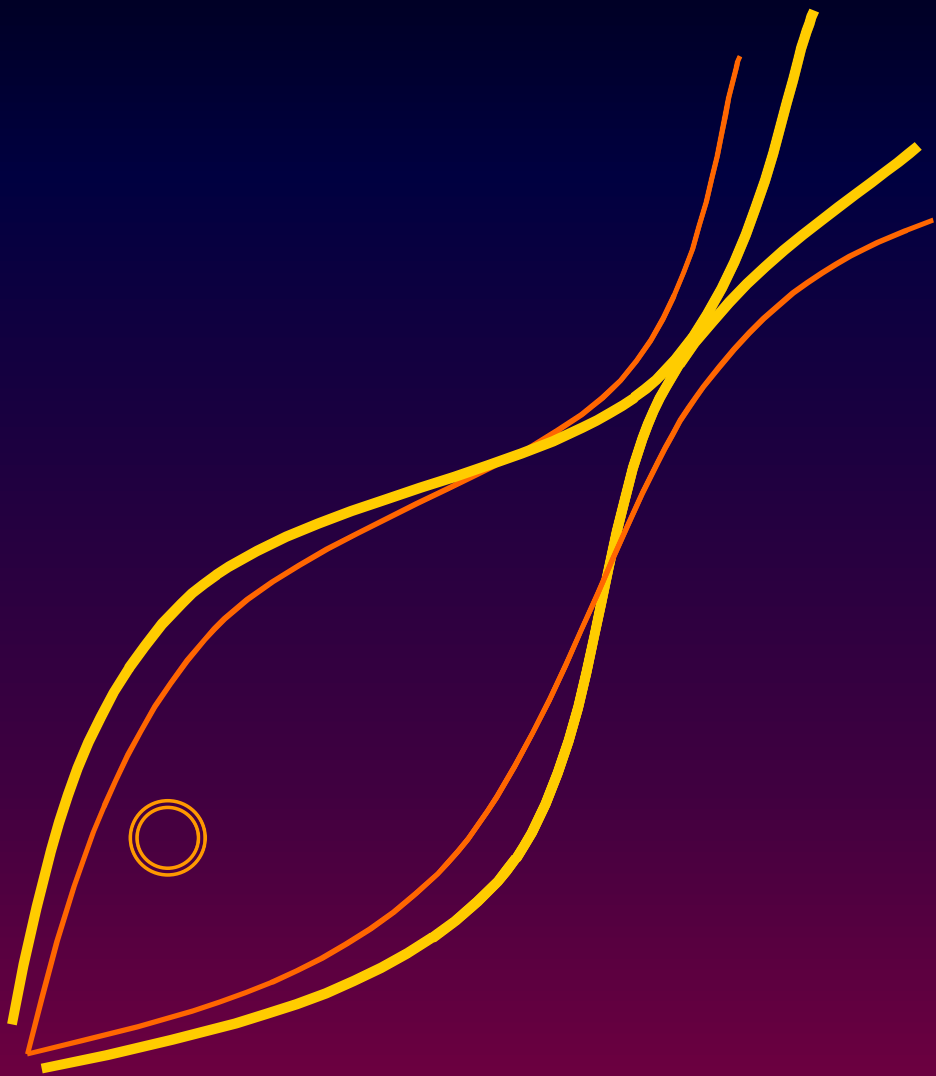

European Fisheries Ecosystem Plan

The North Sea significant web

European Fisheries Ecosystem Plan:

The North Sea significant web

EU Project number: Q5RS-2001-016585

DELIVERABLE THREE

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Preface

This report describes the selection of the species and habitats which form the 'significant web' in the North Sea as a contribution to the development of a European Fisheries Ecosystem Plan (EFEP) (EU Project number Q5RS-2001-01685). The aim of the EFEP project is to develop an ecosystem-based management plan for the fisheries of the North Sea.

Over the last few decades, there is a growing understanding that harvesting natural resources can influence the structure and functioning of marine ecosystems. For that reason, there is an increased interest for an ecosystem-based approach to management. For an ecosystem-based management to be fully operational, it is important to identify those *key* species and habitats which are the major drivers in the functioning of the ecosystem, as it is not practical, or even possible, to manage the whole system. However, while it is clear that some species and habitats are not such drivers, they may as well be important to society in other ways. For example, predation pressure on fish by guillemot (*Uria aalge*), which is an abundant seabird species, is greater than that of the much rarer roseate tern (*Sterna dougallii*). Removal of all guillemots from the North Sea could lead indirectly to changes in fish community structure as a result of predatory release, while removal of roseate terns would not. However, the roseate tern is an uncommon breeding bird within the North Sea, and protected by the EU Birds' Directive (1979) and considered of societal value. In other words, there is a societal demand to protect roseate tern in order to maintain biodiversity.

An important part of the EFEP project is to develop a suite of models under which several management scenarios can be run in order to examine their effect on ecosystem components and determine whether the outcomes of these are acceptable to both the public and scientists. One step to achieve that goal is to identify those species and habitats which are the key drivers in structuring the North Sea ecosystem and construct the North Sea 'significant web'.

With growing knowledge on the effects of fishing activities on the ecosystem, there is greater interest in conserving ecosystem integrity rather than focussing on individual species. In this report, the importance of species and habitats found in the North Sea were evaluated and those which were selected, constituted as part of the significant web. Such information is of vital importance for modelling work which, furthermore, will advance the development of ecosystem-based management plans for fishing activities within the North Sea.

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EXECUTIVE SUMMARY

There is a growing understanding that fishing activities can exert impacts which are detectable at the ecosystem level. This has prompted management initiatives by the FAO and EU to move away from approaches which involve the management of single species to consider the ecosystem as a whole. For application of ecosystem-based management it is necessary to focus on those species and habitats which are the major drivers in the ecosystem as it is not practical, or possible, to manage every ecosystem component.

1. Introduction

This report is one of seven project deliverables from the *European Fisheries Ecosystem Plan* (EFEP), a European Commission Research and Technological Development Project (no. QLRT-CT-2000-01685), which aims to develop a Fisheries Ecosystem Plan (FEP) for the North Sea. This report details work on selection of the North Sea 'significant web' which involves identification of those species and habitats found among each of the main ecosystem components, seabirds, marine mammals, fish, zooplankton and benthos and habitats, which are the major drivers in ecosystem functioning and in structuring the North Sea foodweb and/or importance to humans. Finally, application of metrics (tools to measure the state and the health of the ecosystem) was reviewed.

2. Selection of key species and habitats in the 'significant web'.

Key species and habitats in each of the six ecosystem components were selected on the basis of four criteria:

Economic importance: Species and habitats which provide profit to humans.

Societal importance: Species and habitats which are of conservation importance, many of which are protected by national and international legislation.

Ecological importance: Species and habitats which play important roles in the trophic web of the North Sea.

Functional importance: Species and habitats which provide physico-chemical service to the ecosystem.

Ecosystem components

Seabirds

The majority of seabird species found in the North Sea are protected under the EC Birds Directive 1979 (74/409/CEE) and therefore have high societal value. Some bird species such as the fulmar and the various gull species were found to be of indirect economic importance as they compete with the fishery for the same food resources. Most seabird species are important as predators and for that reason have high ecological importance. In this report, information on food consumption by seabirds and population trends are reviewed. Supplementary information on distribution, densities and mortalities can be found in Appendix 1 and in the file ‘seabirds.xls’ (diskette attached with the report).

Cetaceans

Among cetaceans, the harbour porpoise (*Phocoena phocoena*) is by far the most abundant. All cetaceans are protected under the Annex IIa and IVa of the EU Habitats and Species Directive (1992) (EU directive 92/43/EEC) and are therefore of high societal value. Cetaceans are of economic importance both indirectly as they compete with the fishing industry for food resources, and directly as they provide income from whale watching. Cetaceans are important predators of fish and zooplankton and are therefore of high ecological importance. In the report, distribution and abundances within subareas is reviewed. Information on the distribution, abundance, mortality and diets is given in the file ‘cetaceans.xls’. In the file ‘SAC marine mammals.xls’, distribution of special areas of conservation (SAC) for marine mammals is shown.

Pinnipeds

The dominant seal species within the North Sea are the common seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*). Both of these species are listed under Annex II of the EU Habitats and Species Directive (1992) and are therefore of societal importance. They are of high ecological importance and economic importance as they are important fish predators and compete with fisheries for food resources. Information on population trends, production, distribution and population size is given in the report and in the data file ‘seals.xls’.

Zooplankton

In general, zooplankton is of high ecological importance due to their importance in diets of fish, invertebrates and cetaceans. Further information on zooplankton can be found on the data file ‘zooplankton.xls’.

Fish

In this report, the biology, distribution, reproduction, life history, feeding ecology, natural mortality and landings of 45 fish species found in the North Sea is reviewed. Cod, haddock, whiting and saithe, which are heavily targeted, can make up to 80% of the total biomass of the demersal piscivore predator guild. Some of the non-target species were found to be of ecological importance. Several fish species have been identified of conservation value, and are for example, found on the OSPAR list of threatened and/or declining species. These include cod (*Gadus morhua*) and several elasmobranch species (sharks, rays and skates). Some fish species are of high ecological importance as they are both important as prey and predators. Commercial fish species selected in the significant food web were categorised into age classes while non-target species were divided into size classes due to limitations with the data.

Benthos and habitats

In total, 59 benthic invertebrate families and 4 habitat types were evaluated for the inclusion in the North Sea significant web, and out of these, 27 benthic families and one habitat type were selected. Relatively few benthic species are harvested within the North Sea but species of high economic importance were Norway lobsters (*Nephrops norvegicus*), brown shrimps (*Crangon crangon*), cockles (*Cerastoderma edule*), mussels (*Mytilus edulis*) and scallops (*Pecten maximus*). Benthos is a very important prey item for a large number of predators. However, data on benthos in diets is often at very coarse taxonomic resolution. Most of the benthic families and habitats which were evaluated of high functional importance were generally habitat formers and/or important bioturbators. The former includes habitat forming epibenthic bivalves such as mussels (Mytilidae) and reef-building polychaetes (Sabellariidae). An example of bioturbators are the megafaunal crustacean species belonging to Callianassidae, but the amount of sediment reworked annually by *Callianassa subterranea* populations in the North Sea has been estimated to be 15.5 kg dry wt m^{-2} y^{-1}. There are very few benthic species and habitats that are protected by legislation and are therefore of societal value. In Appendix 6, the biology and ecology of benthic families which were evaluated for the inclusion in the significant North Sea web is reviewed.

3. Conservation measures and actions

This chapter reviews conservation measures and legislation instruments for the protection of the North See fauna. This includes a review of various regional and global conventions, agreements and legislations. Protected areas and habitats in the UK, Belgium, Netherlands, Denmark and Germany are presented. Around the UK, several areas important for seabirds and marine mammals have been identified as 'Special Protection Areas' (SPAs) and 'Special Areas of Conservation' (SAC). Closed areas to protect fish stocks are reviewed. Within the North Sea, no single area has been permanently closed for fishing: the plaice box is open for fishing at certain times of the year, while the sandeel box (inshore waters from eastern Scotland to NE England) is closed if breeding success of kittiwakes fall below certain levels. Relatively few benthic species and habitats are regarded as of conservation importance.

4. Metrics

Metrics which have been developed to measure the state/health of the ecosystem were reviewed for each component for the ecosystem. Most metrics have been developed to measure changes in fish populations. These include metrics to detect changes in population size, community structure and population traits or life history structure. For other ecosystem components, fewer metrics have been proposed. For example, variation in zooplankton biomass and species composition can be used as an indicator of changes in environmental conditions. Among metrics proposed for benthos, these include indicator species and changes in species composition. For marine mammals, metrics include mainly population size and distribution. For seabirds, metrics have been developed within the framework of EcoQOs and include levels of contamination in eggs and feathers, and seabird population trends as an index of seabird community health. Finally, for each component the data requirements and applicability for each metric is reviewed.

CHAPTER ONE
Introduction

The ecological interactions within the North Sea foodweb are complex due to the high number of species it comprises, changes in diet preferences of animals with age and size and an overall lack of ecological specialists. For these reasons, the number of trophic levels in the North Sea is high, whilst there are probably relatively few species and habitats which play important role in structuring the North Sea web. These include species with strong controlling interactions between predator and prey (e.g. Raffaelli and Hall, 1992) and species or habitats which modify their biological or physical environment. However, an attempt to identify the key species and key habitats in the ecosystem allows us to construct a subset of the North Sea web, which can be termed as the 'significant web'.

Recently, there has been an increased focus on the development of approaches to ecosystem management and monitoring. These include work on identifying species and habitat at risk from human activities (e.g. Biodiversity Action Plans, OSPAR Biodiversity Committee), and identification of general patterns of fishing activities on benthic communities (e.g. Collie *et al.*, 2000) which has facilitated the development of 'Ecological Quality Objectives' (EcoQOs) within ICES and OSPAR. To our knowledge however, there have been only limited attempts to identify which species and habitats are the important drivers for ecosystem functioning. For the ecosystem-based approach to become operational, it is important to identify these drivers to conserve ecosystem integrity/health. Traditionally, conservation initiatives have been directed to protect those species and habitats which have a charismatic status (e.g. Roff and Evans, 2002). For the North Sea, this involves predominately marine mammals and birds species and some benthic habitat types. However, for the majority of the North Sea fauna found on lower trophic levels (benthos and zooplankton), there is less societal motivation for conservation measures. Benthos and zooplankton is very important in the diet of commercial fish species and these therefore need to be taken into account in ecosystem-based management plans in order to preserve ecosystem integrity, such as of trophic interactions. Their removal or alterations in their relative composition (e.g. through habitat loss or fishing disturbance) can have cascading effects at higher trophic levels. However, species of charismatic status within the North Sea, such as the coldwater coral *Lophelia pertusa* and the bottlenose dolphin *Tursiops truncates* are only found in few locations within the North Sea. Although there is a clear need to protect these in order to maintain biodiversity, they may only have very localised influence on ecosystem functioning.

The goal of this workpackage was to identify those species and habitats which are important, either because they are important to humans (harvested, tourist industry, conservation value) or because they are an essential for the ecosystem health and integrity. Four criteria were developed (see Methods chapter) to aid selection of species and habitats. This involved evaluating the importance of species and habitats in predator-prey relationships (ecological importance), in providing important functions to the ecosystem (functional importance), the amount of profit they provide to humans (economic importance) and finally the conservation value (societal importance). These criteria were applied to the following components of the ecosystem: marine mammals, birds, zooplankton, fish, benthos and habitats. To our knowledge, such evaluation has not been carried out for the North Sea or any other marine ecosystem and for that reason we consider this approach innovative. The North Sea ecosystem components evaluated were inherently different and for that reason, their evaluation approaches not always the same. For example, the benthos is by far the most species-rich component and provides a greater variety of functions compared to other components. Furthermore, there is a large gap in the knowledge of the key relationships and biology among components. Not surprisingly, species of societal importance (mainly marine mammals, birds and charismatic habitats) and of those of commercial value (mainly fish) have been better studied than benthos and zooplankton. There is for example limited understanding of the role of benthos in the North Sea ecosystem and relatively few studies have attempted to include these in models.

Over the last few years, a large number of metrics have been developed to measure the state and health of the ecosystem (e.g. Rice, 2000). In this report, we reviewed and compared various metrics, assessed availability of data and applicability of selected metrics for each of the North Sea ecosystem components.

CHAPTER TWO

Methodology

1. Categories of importance

The identification of the 'significant web' which supports the fisheries within the North Sea ecosystem is an important step in the establishment of an ecosystem model which will be used for management purposes. The inherent complexity of relationships within an ecosystem means that it is not possible to model with any accuracy, nor is it particularly useful to model, all the species within an ecosystem as many species may be of minor importance to the functioning of the system. It is more useful to instead focus on those species and components of an ecosystem which are either important from a human oriented view, such as those of economic or conservation interest, to those which are considered important to the functioning and 'health' of the ecosystem.

By reducing the number of ecosystem components examined, by choosing those which have been shown to be important, we can examine those processes we do know and use only those which form the important linkages within the ecosystem. Four categories of importance were chosen:

Species and habitats of economic importance

This category includes those species and habitats which have a monetary value. Many species of marine fauna are harvested and provide employment and profit to humans. This category may also include habitats.

Species and habitats of societal importance

This category includes species of conservation importance which are considered important by human society. Some of these species and habitats will be protected by national and international legislation, but this category also includes some charismatic species which may not be protected by law.

Species of ecological importance

To avoid overlap and confusion with the next category (species of functional importance), a decision was taken to restrict species of ecological importance to those which are considered important in the trophic relationships.

However, we recognise that species of ecological importance may also perform important functions in the ecosystem.

Species and habitats of functional importance

Within the literature, there is much disagreement about the definition of an ecosystem function, so the authors decided to define functionally important species as those which provided a physico-chemical service to the ecosystem.

2. Selection of species and habitats

Six ecosystem components were investigated. These were seabirds, marine mammals, zooplankton, fish, benthos and habitats.

2.1 Seabirds

Seabirds of economic importance

Some bird species may be considered of economic importance to recreation and tourism and generate revenue since members of society are prepared to pay for to observe and preserve them. However, this economic aspect is better addressed as societal importance in the significant food web.

Seabirds are also in competition with fishers for marine resources. The biomass of commercially important fish consumed per annum by birds in the North Sea was acquired from literature, where available. Species were scored based on the biomass consumed per annum (in tonnes):

200,000–50,000	⇒	rating: 1
49,999–10,000	⇒	rating: 0.5
10,000 and under	⇒	rating: 0

Seabirds of societal importance

Many seabirds are considered charismatic by several governmental and European legislative acts, e.g. EC Birds Directive 1979 (Council Directive

79/409/EEC of 2 April 1979 on the conservation of wild birds) with reference to the ORNIS database (http://www.kbinirsnb.be/cb/ornis/index.htm).

Under the EC Birds Directive 1979:

Annex I bird species require special conservation measures to be taken. There is a need to classify their most suitable territories in number and size as Special Protection Areas (SPAs).

Annex I species are:

species in danger of extinction;

species vulnerable to specific changes in their habitat;

species considered rare because of small populations or restricted local distribution;

other species requiring particular attention for reasons of the specific nature of habitat.

Annex II bird species may be hunted under national legislation but Member States are to ensure that hunting does not jeopardise conservation efforts. The practice of hunting must comply with the principles of wise use and ecologically balanced control of the species of birds concerned. For example, species which may be hunted, are not hunted during the various stages of the breeding season, including the period during which the young birds are still dependent on the adults.

Those species which were not identified in legislation but are identified by bird groups (e.g. the Royal Society for the Protection of Birds (RSPB), which is Europe's largest wildlife conservation charity with more than a million members) as charismatic are also included. Bird watching tourist sites were identified on the internet and species consistently identified as 'of interest' on the sites were given a 0.5 rating.

Seabirds of ecological importance

As apical predators, birds are considered to play a role in controlling the density of prey species (Pimm and Hyman, 1987). However, marine food webs are complex and determining the effect of their removal from the ecosystem is complicated (Bax, 1998; Link, 2002a). Ecological importance was linked to abundance as an index of biomass (i.e. significant contribution to the total biomass of seabirds in the North Sea) therefore offering an indication of birds' total predation in the system on fish and other species (rather than assessing their impact only on commercially important fish stocks). The types (e.g. population during different seasons), and most recently recorded abundance of bird species found in the North Sea were obtained from the literature (e.g. Skov *et al*., 1995; OSPAR, 2000). Species were scored on the basis of abundance of breeding population as this is the most robust type of data (Gill, 1995) and during breeding season, populations are relatively sedentary; the biomass of the individual species was also taken into consideration, to give an estimate of the birds' total pressure on the system:

Ψ: Breeding population (pairs)

>100,000 ⇒ score: 1

100,000–25,000 ⇒ score: 0.5

<25,000 ⇒ score: 0

Φ: Individual biomass (g)

>1,000 ⇒ score: 1

1,000–500 ⇒ score: 0.5

<500 ⇒ score: 0

The individual scores were summed, (Ψ + Φ), then ranked to determine ecological importance:

≥ 1.5 ⇒ major importance (1)

1.0 ⇒ moderate importance (0.5)

≤ 0.5 ⇒ minor importance (0)

Diet data were also acquired from scientific literature to determine trophic interactions and favoured prey items.

Seabirds of functional importance

Functionally important species are those which provided a physico-chemical service to the ecosystem. Birds' main physico-chemical role in marine and terrestrial ecosystems is the transfer of organic matter from one system to another e.g. diminution of nutrients in one area and increase of nutrients in another e.g. breeding and/or roosting grounds (Fischer *et al*., 1997). This information was extracted from the literature where available.

Inclusion in the significant web

Birds, which were considered as having societal importance as dictated by the Birds' Directive, were included in the significant web. Those which were not protected by legislation, but are considered charismatic and provide important ecological and economic roles in the ecosystem were also included.

2.2 Marine mammals

Populations of marine mammals (cetaceans and pinnipeds) in the North Sea were identified from the scientific literature. Those marine mammals were subsequently rated/marked as abundant or as rare, transient species.

Marine mammals of economic importance

Marine mammals may also be considered of economic importance to recreation and tourism and generate revenue since members of society are prepared to pay for to observe and preserve them. However, this economic aspect is better addressed as societal importance in the significant web.

Marine mammals are also in competition with fishers for marine resources. Where possible, assessments of the biomass of prey consumed were calculated and offset against fisheries landings. Annual consumption or daily intake of prey was obtained from literature for species where data was available. Where the latter was found, abundances of cetaceans in the North Sea were obtained from literature to calculate annual consumption by the populations. While this is accepted as a crude method, which does not take into account pod age structure or the foraging success of animals, it is the only one available, prior to modelling, which offers an assessment of annual intake. The abundance of the species was also considered to determine their ecological importance in the marine ecosystem.

Marine mammals of societal importance

All marine mammals included in the species list were cross-referenced with protective legislation, e.g. identified as:

(1) Vulnerable by the EC Habitats Directive 1992 (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora), further identified as

Annex II species:

Animal and plant species of community interest whose conservation requires the designation of special areas of conservation (SAC)

and/or

Annex IV species:

Animal and plant species of community interest in need of strict protection;

(2) Recognised as vulnerable by the IUCN criteria, which assesses the conservation status of species, subspecies, varieties and even selected subpopulations on a global scale in order to highlight taxa threatened with extinction, and to promote their conservation (the IUCN have produced a 'Red list' that identifies threatened species: http://www.redlist.org/info/categories_criteria1994.html#categories);

(3) Species being subject to the Bonn Convention. The Convention on the Conservation of Migratory Species of Wild Animals (CMS) 1979 concerns species of birds, mammals, reptiles and fish. The contracting parties recognise that the effective conservation of these species requires the concerted action of all States within which these species spend any part of their life cycle. Immediate protection is to be provided for migratory species threatened with extinction. Contracting parties must also pay special attention to migratory species with an unfavourable conservation status and, individually or in co-operation, take appropriate and necessary steps to conserve such species and their habitats. In addition, the concluding of international agreements for the conservation and management of such species is encouraged. The Bonn Convention has now been

signed and ratified by over 60 states, including the Federal Republic of Germany, and by the European Union;

(4) And finally, species being subject to the Bern Convention, the Convention on the Conservation of European Wildlife and Natural Habitats 1979. This is based on the principle that wild flora and fauna constitute a natural heritage, which plays a vital role in maintaining biological balances. The contracting parties recognise the importance of conserving wild flora and fauna and their natural habitats, especially those species and habitats whose conservation requires the co-operation of several States. Particular attention has to be given to endangered and vulnerable species. The European Union and all Member States are contracting parties.

Another regional convention exists, which is the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS). This was established under the Bonn Convention and applies to odontocete cetaceans (except the sperm whale) within the area of the Agreement. Under the Agreement, provision is made for the protection of specific areas, monitoring, research, information exchange, pollution control and heightening public awareness of marine mammals. Measures cover the monitoring of fisheries interactions and disturbance, resolutions for the reduction of by-catches in fishing operations, and recommendations for the establishment of specific protected areas for cetaceans.

Marine mammals of ecological importance

Information on diet of marine mammals was extracted from literature to determine trophic relationships.

Marine mammals of functional importance

Functionally important species are those which provided a physico-chemical service to the ecosystem. Marine mammals' main physico-chemical role in marine, and on shore terrestrial, ecosystems, is that they sequester nutrients in the physical bodies to be released at death. This data was extracted from literature as available.

2.3 Zooplankton

Research into the diet of predators of zooplankton rarely specifies which zooplankton species are important and often cluster zooplankton at the genus or order level. To create a tractable significant web, the significance of species in this section is determined by their biomass and abundance in the North Sea. Species and groups include copepods, e.g. for the genus *Calanus*, euphausiids (krills) and oithonids (e.g. Johns and Reid, 2001). Details of the importance of zooplankton to some commercial species were obtained from the literature.

2.4 Fish

For the purpose of the study a number of fish species were selected that are considered to be of importance in the ecosystem as well as those that are commercially exploited. The list of fish species that are of commercial value can be found in annual reports of the ICES Advisory Committee on Fishery Management. These routinely assessed fish stocks are also among the most abundant or important in terms of biomass. The ecological importance was evaluated mainly based on information on feeding habits of the different species or trophic categories in the food web. In addition, other characteristics were evaluated, such as growth rate, life span, fecundity, natural and fishing mortalities, species resiliance, Red List Status, and, more generally, stock health.

Explanation of used terms

Predators diet:

- present: observed but not quantified
- rare: occurrence between 0 and 5 % of the total diet (can be either in number or mass depending on the available data)
- frequent: occurrence between 5 and 25 % of the total diet
- common: occurrence between 25 and 50 % of the total diet
- staple: occurrence more than 50 % of the diet

If more than one term is used (e.g. rare-frequent), the importance in the diet can be both and in between (e.g. rare-common; the species has been found to be a rare, frequent and common food item).

K = the von Bertalanffy growth parameter ($year^{-1}$)

tm = age at first maturity (years)

tmax = approximate maximum age (years)

rm = intrinsic rate of population growth ($year^{-1}$)

fec = fecundity

se = standard error

For many species the population resilience is not known and is calculated using the parameters in brackets.

The Red List categories are explained on
http://www.redlist.org/info/categories_criteria2001.html

2.5 Benthos and habitats

A large number of benthic species have been recorded within the North Sea. Over 1000 species were recorded in the 1986 ICES North Sea Benthos Survey (Craeymeersch *et al.*, 1997), whilst 456 species were recorded in an epibenthic survey conducted in 2000 (Callaway *et al.*, 2002). A three-step approach was used to select those organisms which comprise the 'significant web'. First, the species list was reduced by aggregating the species from the surveys to family, which yielded about 200 families in total. We considered that the biology, ecology and functions amongst species at this taxonomic resolution was sufficiently similar to justify such an aggregation, and other studies have argued that the loss of information caused by aggregation to a coarser taxonomic level than species or genus is generally minor (e.g. Karakassis and Hatziyanni, 2000). The second step involved removing those families which were uncommon, little known, or which were clearly not important, leaving us with 59 families and 4 habitats. The third step involved collating information on these families such as distribution, life history characteristics, mortalities, densities and substrate types, which formed the basis for the further evaluation on their importance in ecosystem functioning. The evaluation procedure involved designing a scheme where various attributes of each criterion were scored according to a set of economic, societal, ecological and functional importance (Table 2.1).

The **economic** importance of the habitat or family was ranked (0–3) according its monetary value:

0 = no economic importance,

1 = low commercial importance,

2 = monetary value of harvesting ranges between £5–20 million

3 = monetary value of harvesting exceeds £20 million.

The **societal** importance of a habitat or family was ranked (0–2) according to its conservation status:

0 = no societal importance,

1 = limited conservation importance and is not protected by legislation,

2 = protected by legislation, including species listed under the 1992 EC Habitat Directive, CITES I and II, UK Biodiversity Action plan and habitats designated as Ramsar sites, protected under the Bern Convention or found within marine SACs or SPAs.

The **functional** importance of families and habitats was determined by two sub-criteria. The importance of a family in modifying (1) the biogeochemical environment ('biogeochemical functions') and/or (2) the physical and biological environment ('biological activity and habitat functions'), was evaluated. The first category refers to those families which influence the nutrient dynamics, such as enhancing the flux of nutrients as a result of bioturbation, or improve water quality by filtering out toxins. The second category, the 'biological activity and habitat functions' refers to families which modify their physical and/or the biological environment. This includes families which contain habitat forming species i.e. they increase habitat complexity and provide refugia, or destabilise sediments through bioturbation. Habitats and families were categorised depending on whether they enhanced (I) or decreased (D) species diversity, richness and abundances of associated fauna. Finally, organisms which influence the associated fauna through disturbance or other interactions, either positive or negative, were categorised as well. Examples of this interaction include the impacts of bioturbation on other organisms, or on the competition for space among habitat forming species.

The **ecological** importance of a family or a habitat was ranked (0–2) according to its importance in trophic relationships. Importance as prey was ranked on the basis of its importance in the diet of fish (f), bird (b) and invertebrate (i) predators. Those families which are important in the diets yielded a score of two whilst those which have been recorded, but sporadically or in low quantities, scored one. The importance of predators was also ranked. If there was evidence that a predator was capable of affecting densities of their prey, it received a score of two. Families which received a score of two (or three for economic importance) for *any* of the four categories of importance were included in the significant web. Some benthic families found in the intertidal were removed from the significant web list even though these were evaluated of high importance (see conclusions).

Table 2.1 Overview of the scoring system which was used to rank the importance of families by criteria. For further explanation, see the text above.

Criteria	Subcriteria	Attributes	Score
Economic importance			0–3
Societal importance			0–2
Functional importance	Biogeochemical functions	Nutrient recycling Bioaccumulates Improves water quality	0–2 0–1 0–2
	Biological activity and habitat functions	Habitat complexity Alteration of hydrodynamics Provision of refugia Diversity Interactions/disturbance Biostabilisation Bio-destabilisation	0–2 0–2 0–2 I/D 0–2 0–2 0–2
Ecological importance		Important prey for birds (b), fish (f) and invertebrates (i) Important predator	0–2 0–2

Functional groups

Feeding guilds were determined on the basis of their feeding mode, feeding apparatus and mobility. This information was extracted from the literature where feeding guilds have been determined (Fauchald and Jumars, 1979; Swift, 1993; Dauwe *et al.*, 1998; Bonsdorff and Pearson, 1999).

CHAPTER THREE

Results

1. Seabirds

The bird component of the North Sea ecosystem contains both seabirds and migratory waders. Their importance is illustrated below (Table 3.1).

Table 3.1 The importance of seabird and migratory waders in the North Sea. Key: 0 = minor importance; 0.5 = some importance; 1 = important and ? = unknown.

Species	Ecosystem importance			Societal importance
	Ecological	Economic	Functional	Birds Directive 79/409/CEE
Northern fulmar *Fulmarus glacialis*	1	1	0.5	0.5
Manx shearwater *Puffinus puffinus*	0	0	0.5	0.5
European storm petrel *Hydrobates pelagicus*	0	0	0.5	Annex I
Leach's storm-petrel *Oceanodroma leucorhoa*	0	0	0.5	Annex I
Northern gannet *Morus bassanus*	1	0	0.5	0.5
Great cormorant *Phalacrocorax carbo*	0.5	?	0.5	Annex I
European shag *P. aristotelis*	0.5	0	0.5	0.5
Great skua *Stercorarius skua*	0.5	?	0.5	0.5
Black-headed gull *Larus ridibundus*	0.5	?	0.5	Annex II
Lesser black-backed gull *L. fuscus*	1	?	0.5	Annex II
Herring gull *L. argentatus*	1	0.5	0.5	Annex II
Great black-backed gull *L. marinus*	1	0.5	0.5	Annex II
Black-legged kittiwake *Rissa tridactyla*	1	0.5	0.5	0.5
Sandwich tern *Sterna sandvicensis*	0	?	0.5	Annex I
Roseate tern *S. dougallii*	0	0	0.5	Annex I
Common tern *S. hirundo*	0	?	0.5	Annex I
Arctic tern *S. paradisaea*	0	?	0.5	Annex I
Little tern *S. albifrons*	0	?	0.5	Annex I
Common guillemot *Uria aalge*	1	1	0.5	0.5
Razorbill *Alca torda*	1	0	0.5	0.5
Black guillemot *Cepphus grylle*	0	?	0.5	0.5
Atlantic puffin *Fratercula arctica*	0.5	?	0.5	0.5
Eider *Somateria mollissima*	1	1	0.5	Annex II
Oystercatcher *Haematopus ostralegus*	1	1	0.5	Annex II

1.1 Economic importance

Bird species are considered of economic importance when society is prepared to pay both for their conservation and for access to view them. Revenue may be generated for access to, and maintenance of, bird watching areas. The Royal Society for the Protection of Birds (RSPB) is Europe's largest wildlife conservation charity, and recently purchased the Mull of Oa (1800 ha) and Revack Forest (800 ha) as bird reserves. However, the economics of the tourism of charismatic species are not considered in detail as the bird species are assessed on the basis of their charismatic status.

Seabirds compete with fishers for fish and may therefore have an economic impact on fishers. To put this into perspective, it was estimated that the biomass of fish consumed by seabirds in the North Sea was in the range of 0–2 t km^{-2} annually, compared to the 1.4–6.1 t km^{-2} of fish removed by all fisheries (Bax, 1991). In more recent studies, the total food consumed by breeding seabirds in the North Sea was estimated to be approximately 600,000 tonnes per annum (5NSC, 1997; ICES, 2002a) which is equivalent to 10% of the estimated total landing in the EU in 1999 (EC, 2001). Calculations of the consumed biomass of commercially important species were used (e.g. Tasker and Furness, 1996) to assign ratings of the economic importance of the bird species in the marine ecosystem (Table 3.1).

A more detailed breakdown of the consumption of prey items by seabirds is in the file (‘seabirds.xls’).

1.2 Societal importance

Many bird species are protected by international legislation. Within the context of the North Sea, the primary bird conservation legislation is the Birds Directive 1979 (79/409/EEC). All birds listed in Annex I or II of this directive are considered of societal importance and included in the significant food web (Table 3.1).

From an examination of bird watching literature, including the internet, several species which are not protected by legislation, e.g. the fulmar, kittiwake and puffin, were identified as of importance to ornithologists and bird watchers (Table 3.1).

1.3 Ecological importance

Seabirds consume a variety of pelagic and benthic organisms, and in many food webs they are apex predators. Some seabirds also predate on other seabirds.

As birds often occur at high densities, and since the vast majority are predators, their potential impact on their prey populations in the intertidal zone and inshore waters can be considerable. Some populations of seabird species demonstrate a close dependency on the abundance of prey species, especially when their foraging range is limited during the breeding season. Assessing each local population of birds is impossible and, therefore, total abundance of breeding populations and individual biomass were used as a proxy to determining ecological importance in the North Sea ecosystem (Table 3.2).

Table 3.2 Breeding population and biomass of seabirds in the North Sea as a proxy for ecological importance (data from Gill, 1995; Skov *et al.*, 1995; Zwarts *et al.*, 1996; ICES, JNCC and OSPAR websites).

Species	Breeding population (pairs)	Score	Individual biomass (g)	Score	Total score (• + •)	Impor-tance ranking
Northern fulmar *Fulmarus glacialis*	310,000	1	700–900	0.5	1.5	1
Manx shearwater *Puffinus puffinus*	250	0	450	0	0	0
European storm petrel *Hydrobates pelagicus*	1,000	0	25	0	0	0
Leach's storm-petrel *Oceanodroma leucorhoa*	100	0	40	0	0	0
Northern gannet *Morus bassanus*	45,000	0.5	2,800–3200	1	1.5	1
Great cormorant *Phalacrocorax carbo*	6,700	0	1,800	1	1	0.5
European shag *P. aristotelis*	22,500	0	1,810	1	1	0.5
Great skua *Stercorarius skua*	14,000	0	1,300–1,800	1	1	0.5
Black-headed gull *Larus ridbundus*	129,000	1	250	0	1	0.5
Lesser black-backed gull *L. fuscus*	130,000	1	700–900	0.5	1.5	1
Herring gull *L. argentatus*	300,000	1	800–1,200	1	2	1
Great black-backed gull *L. marinus*	25,000	0.5	1,100–2,000	1	1.5	1
Black-legged kittiwake *Rissa tridactyla*	415,000	1	300–500	0.5	1.5	1
Sandwich tern *Sterna sandvicensis*	48,000	0.5	235	0	0.5	0
Roseate tern *S. dougallii*	36	0	100–120	0	0	0
Common tern *S. hirundo*	65,000	0.5	120	0	0.5	0
Arctic tern *S. paradisaea*	75,000	0.5	100	0	0.5	0
Little tern *S. albifrons*	2,500	0	50	0	0	0
Common guillemot *Uria aalge*	>1 million	1	1,000	1	2	1
Razorbill *Alca torda*	183,000	1	620	0.5	1.5	1
Black guillemot *Cepphus grylle*	24,000 (ind.)	0	410	0	0	0
Atlantic puffin *Fratercula arctica*	225,000 (ind.)	1	375–400	0	1	0.5
Eider *Somateria mollissima*	100,000	1	1,630	1	2	1
Oystercatcher *Haematopus ostralegus*	350,000	1	500–600	0.5	1.5	1

Food consumption by seabirds in the North Sea

Table 3.3 provides a brief summary of the total consumption of fish by seabirds in the North Sea. The most important fish prey of seabirds in the North Sea are sandeels, sprats and herrings, especially during the breeding season (a more detailed breakdown is available on the database file). The quality of dietary data is known to be highly variable and the majority of dietary information relates to consumption during the breeding season as species are easier to observe when they aggregate (ICES, 2003a).

Table 3.3 Estimated quantities of food consumed by seabirds (tonnes) in each quarter of the year in each ICES statistical rectangle of the North Sea (Tasker and Furness, 1996)

Area in North Sea	Metric tonnes consumed
IV a west	227 017
IV a east	56 478
IV b west	99 623
IV b centre	54 250
IV b east	20 824
IV c	19 146
Total	**477 338**

Food consumption by oystercatchers and eiders in the North Sea

Oystercatchers and eider ducks are reported as feeding extensively on *M. edulis* (Seed and Suchanek, 1992). There is evidence of prey switching (Dare and Mercer, 1973), but there appears to be a preference for mussels. In the southern North Sea and the Wadden Sea some bird species, e.g. the oystercatcher and eider, are especially dependent on shellfish as prey. The most important shellfish for birds in these areas are bivalve molluscs (*Mytilus edulis*, cockles and *Spisula* spp.). In the Wadden Sea, the consumption of bivalves by birds is of the same order of magnitude as that taken by the fisheries (5NSC, 1997). In Morecambe Bay, UK, Dare (1976) identified oystercatchers, herring gulls and eider ducks as major predators of *Mytilus edulis*.

Mussel consumption

Different birds prefer specific size ranges of *M. edulis*; herring gulls prey on *M. edulis* of 3–20 mm length; oystercatchers and eiders at larger sizes (Nagarajan *et al.*, 2002). In contrast, Raffaelli *et al.* (1990) reported that eiders preferred *M. edulis* of 10–25 mm in the Ythan estuary. For other size classes preferred by oystercatchers and eiders see the file (‘seabirds.xls’).

Baird and Milne (1981) reported that in the Ythan estuary, 4,000 birds consumed 72% of the annual *M. edulis* production. Eider consumed 42% and oystercatchers with herring gulls cumulatively consumed 15% of the annual production of *M. edulis*. In the east Scheldt, Holland, 40% of the annual mussel production was consumed by oystercatchers (Meire and Ervynck, 1986), and mussel production was presumed to be the major limiting factor for density of overwintering flocks (Craeymeersch *et al.*, 1986). In Conway, North Wales, oystercatchers were found to consume up to 574 mussels (average length 25.7 mm) or 186 mussels (average 37.5 mm) each during a low tide (Drinnan, 1958). Mussels which are barnacle encrusted, thick shelled or otherwise difficult to open are avoided by oystercatchers (Leopold *et al.*, 1989; Meire and Ervynck, 1986).

Hilgerloh (1997) evaluated the predation by birds on mussel beds on the tidal flats of the East Frisian island Spiekeroog (Lower Saxony, Germany) in 1991 and 1994. In May 1991, *M. edulis* beds covered an area of 5.2 km^2 and a total biomass of 311 t AFDW/1290 t was available in the study area. In May 1994, the *M. edulis* beds covered an area of only 2.3 km^2, and the total biomass available was reduced to 48 t AFDW/550 t. The annual consumption of mussels by birds in the intertidal flats was estimated at 165 t AFDW. The highest proportion of total consumption was by oystercatchers (54%), while eiders consumed 39% and herring gulls 7%. Consumption by all three species amounted to 32 g AFDW per m^2 of mussel bed in 1991 and to 71 g AFDW per m^2 in 1994.

Considerations regarding diet: prey items available to seabirds

The quality of the food is important. For example, adult puffins, *Fratercula arctica*, supply their young mainly with sandeel, sprat, whiting and rockling rather than other fish species. Adult puffins display size selectivity taking sprats and sandeels over whiting for their young (Harris and Hislop, 1978). Presumably, this is due to calorific value and proportion of protein with respect to body weight in different fishes. Sprats are 14.1–15.3% protein and sandeels are 17.8% protein whilst whiting have a lower proportion of protein. Young puffins fed exclusively on whiting die. In Harris and Hislop’s study (1978), the best season was 1975 when chicks attained significantly heavier peak weight during their growth. Their diet was dominated by sprats rather than sandeels. See the bird database file for other diets.

1.4 Functional importance

The functional importance of birds in the North Sea could not be assessed due to limitations in the scientific literature. However, seabird and migratory waterfowl are presumed to be important sources as nutrient vectors, enriching nutrient concentration in plants and affecting abundance and behaviour of several benthic species (Anderson and Polis, 1999; Fischer *et al.*, 1997; Palomo *et al.*, 1999; Post *et al*., 1998; Wainright *et al.*, 1998). The functional importance of birds was given a generic 0.5 rating.

The list of species that are considered important is shown in Table 3.4.

Table 3.4 List of bird species considered important.

Family	Species	Economic importance	Social importance	Ecological importance
Procellariidae	Northern fulmar (*Fulmarus glacialis*)	Major relative to other species. Annual consumption of commercial fish species has been estimated to be 166 480 metric tonnes (Tasker and Furness, 1996). It is a scavenger and predator of commercially important fish stocks.	Important to ornithologists and bird watchers.	Important as an apex predator. Large population of birds in the North Sea.
	Manx shearwater (*Puffinus puffinus*)	Minor.	Important to ornithologists and bird watchers.	Minor importance; there is only a small population in the North Sea.
Hydrobatidae	European storm petrel (*Hydrobates pelagicus*)	Minor.	Birds' directive Annex I species.	Minor importance; there is only a small population in the North Sea.
	Leach's storm-petrel (*Oceanodroma leucorhoa*)	Minor.	Birds' directive Annex I species.	Minor importance; there is only a small population in the North Sea.
Sulidae	Northern gannet (*Morus bassanus*)	Minor.	Important to ornithologists and bird watchers. In addition, the British Isles hold over 70% of the world population.	Of some importance, there is a fairly substantial population of birds in the North Sea.
Phalacrocoracidae	Great cormorant (*Phalacrocorax carbo*)	Unknown.	Birds' directive Annex I species.	Of some importance, the breeding population has been estimated at 6,700 pairs in the North Sea.
	European shag (*P. aristotelis*)	Minor, a relatively small biomass of commercially important species is consumed in the North Sea per annum.	Important to ornithologists and bird watchers.	Of some importance, there is a fairly substantial population of birds in the North Sea.
Stercorariidae	Great skua (*Stercorarius skua*)	Unknown. But the species is primarily a scavenger and utilises discards rather than targeting commercially important stocks. It is though mainly kleptoparasitic.	Important to ornithologists and bird watchers.	Of some importance, the breeding population has been estimated at 14,000 pairs in the North Sea.
Laridae	Black-headed gull (*Larus ridbundus*)	No assessment found, but the species is an opportunistic feeder, and forages on terrestrial rubbish in addition to taking invertebrate prey and commercial fish species.	Birds' directive Annex II species.	Major importance. There is a large population in the North Sea (129,000 breeding pairs). The species targets a variety of prey items from invertebrates to commercially important species such as sandeels.

Table 3.4 Continued.

Family	Species	Economic importance	Social importance	Ecological importance
	Lesser black-backed gull (*L. fuscus*)	Unknown.	Birds' directive Annex II species.	Major importance. The species is abundant in the North Sea. It targets both fish and discards.
	Herring gull (*L. argentatus*)	Of moderate importance. It has been calculated that the bird consumes approximately 33 180 metric tonnes of commercially important fish per annum.	Birds' directive Annex II species.	Of major importance. The species is abundant in the North Sea (circa 300,000 breeding pairs). As an opportunistic feeder, it takes a variety of prey items from marine invertebrates to fish in addition to scavenging terrestrial rubbish.
	Great black-backed gull (*L. marinus*)	Of moderate importance. It has been calculated that the bird consumes approximately 41,909 metric tonnes of commercially important fish per annum.	Birds' directive Annex II species.	This gull is not as abundant as other gull species in the North Sea (circa 25,000 breeding pairs), but as it is somewhat larger, it consumes significant amounts of fish species in addition to taking a range of prey items from invertebrates, rubbish and predating other seabirds.
	Black-legged kittiwake (*Rissa tridactyla*)	Of moderate importance. It has been calculated that the bird consumes approximately 41,663 metric tonnes of commercially important fish per annum in the North Sea.	Important to ornithologists and bird watchers.	The breeding population numbers 400,000 pairs, which is greater than any other seabird in the North Sea apart from the guillemot. The kittiwake often specialises on pelagic fish, notably sandeels.
	Sandwich tern (*Sterna sandvicensis*)	Unknown, no assessments found.	Birds' directive Annex I species.	Minor importance. The sandwich tern often specialises on pelagic fish, notably sandeels and sprats.
	Roseate tern (*S. dougallii*)	Unknown but presumed to be negligible given the small number of roseate terns in the North Sea.	Birds' directive Annex I species.	Minor. There is an extremely small population in the North Sea.
	Common tern (*S. hirundo*)	Unknown.	Birds' directive Annex I species.	Minor-moderate, there is a reasonably large population in the North Sea. During migration, abundances in the North Sea are between 40,000–80,000 (Skov *et al.*, 1995). Feeding predominantly in the inshore zone, local impacts on fish and invertebrates may be great.

Table 3.4 Continued.

Family	Species	Economic importance	Social importance	Ecological importance
	Arctic tern (*S. paradisaea*)	Unknown.	Birds' directive Annex I species.	Minor-moderate, there is a reasonably large population in the North Sea. Juveniles targeted mainly sandeels, small herrings and sprats.
	Little tern (*S. albifrons*)	Unknown.	Birds' directive Annex I species.	Minor, given that there is a very small population in the North Sea.
Alcidae	Common guillemot (*Uria aalge*)	Major – relative to other species. Annual consumption of commercial fish species is circa 166,549 metric tones (Tasker and Furness, 1996). It is a predator of commercially important fish stocks, mainly targeting pelagic species.	Important to ornithologists and bird watchers.	Major. Important as an apex predator. There is a very large population of these large birds in the North Sea.
	Razorbill (*Alca torda*)	Presumably of minor importance based on the biomass of commercially important species consumed per annum.	Important to ornithologists and bird watchers.	Major. Important as an apex predator. There is a large population of birds in the North Sea, preying on both fish and invertebrates.
	Black guillemot (*Cepphus grylle*)	Unknown.	Important to ornithologists and bird watchers.	Minor. Relatively small population in the North Sea.
	Atlantic puffin (*Fratercula arctica*)	Unknown.	Important to ornithologists and bird watchers.	Relatively large population in the North Sea targeting a variety of prey species, mainly pelagic fish.
Anatidae	Eider (*Somateria mollissima*)	Large populations feeding on commercially important invertebrates in inshore fishing zones.	Birds' directive Annex I species.	Major. Feeding predominantly in the inshore zone, local impacts on populations of invertebrates may be especially significant.
Haematopodidae	Oystercatcher (*Haematopus ostralegus*)	Large populations feeding on commercially important invertebrates in inshore fishing zones.	Birds' directive Annex I species.	Major. Feeding predominantly in the inshore zone, local impacts on populations of invertebrates may be especially significant.

1.5 General seabird population trends

Guillemots (family Alcidae) show an increase in abundance in contrast to the terns (family Sternidae) over the last decade (ICES, 2001a). Guillemots are large, deep diving seabirds that are able to prolong their period of foraging, whereas the terns are smaller birds, feed at the surface of the water column and their foraging behaviour is energetically expensive (Cramp *et al.*, 1974). Thus the guillemots are able to hunt over a larger area over a greater amount of time in the search for food.

The populations of kittiwakes (family Laridae) have been declining in the last fifteen years, although the breeding population includes 400,000 pairs, which is greater than any other seabird in the North Sea. The success of this species is closely linked to sandeel abundance and they show little ability to prey switch (Lewis *et al.*, 2001; Rindorf *et al.*, 2000). Kittiwake abundance and breeding success responds rapidly to increases in sandeels on a local scale (Lewis *et al.*, 2001). However, whilst decreasing in number overall, they are evidently more successful than other members of the family Laridae and terns. This may be due to their ability to utilise discards at the surface of the water column, like the larger gulls. Observed trends in the population figures for seabirds in the North Sea (Table 3.5) shows that the seabirds that scavenge, e.g. gulls, fulmars and gannets, and are likely to supplement their diet with discards and offal, show increased abundance.

1.6 Abundances throughout the North Sea

For a breakdown of abundances in separate regions of the North Sea (and adjacent waters) see the bird database table (‘seabirds.xls’).

Table 3.5 Population trends for seabirds on North Sea coasts. Key: ↑ increasing numbers (general trend), ↓ decreasing numbers (general trend), ~ some local variation in numbers, = stable, ? unknown (Cramp *et al*., 1974; ICES, 2001a).

Species	Feeding strategy	Trend
Northern fulmar *Fulmarus glacialis*	Scavenger, opportunistic	↑
European storm petrel *Hydrobates pelagicus*	Pelagic fish, zooplankton	?
Northern gannet *Morus bassanus*	Scavenger, fish (target stocks)	↑
Great cormorant *Phalacrocorax carbo*	Fish (target stocks)	↑ ~
European shag *P. aristotelis*	Pelagic fish	~
Great skua *Stercorarius skua*	Scavenger, discards	↑
Black-headed gull *Larus ridbundus*	Generalist incl. rubbish	~
Lesser black-backed gull *L. fuscus*	Fish, discards	↑ ~
Herring gull *L. argentatus*	Opportunistic	~
Great black-backed gull *L. marinus*	Discards	↑
Black-legged kittiwake *Rissa tridactyla*	Pelagic fish, zooplankton, some discards	↓
Sandwich tern *Sterna sandvicensis*	Pelagic fish	=
Common tern *S. hirundo*	Pelagic fish, invertebrates	↓ ~
Arctic tern *S. paradisaea*	Pelagic fish, invertebrates	=
Little tern *S. albifrons*	Crustaceans, annelids	↑
Common guillemot *Uria aalge*	Pelagic fish, invertebrates	↑
Razorbill *Alca torda*	Pelagic fish, invertebrates	↑
Black guillemot *Cepphus grylle*	Pelagic fish, invertebrates	=
Atlantic puffin *Fratercula arctica*	Pelagic fish	↑

2. Marine mammals

2.1 Cetaceans in the North Sea

The most abundant cetacean in the North Sea is the harbour porpoise (*Phocoena phocoena*). The white-beaked dolphin (*Lagenorhynchus albirostris*), white-sided dolphin (*L. acutus*), killer whale *(Orcinus orca*) and the minke whale (*Balaenoptera acutorostrata)* are relatively common in the North Sea.

Bottlenose dolphins (*Tursiops truncates*) are not abundant but there is an identified breeding ground (Moray Firth off east coast of Scotland), which is of international importance in the North Sea.

Long-finned pilot whale (*Globicephala melaena*), false killer whale (*Pseudorca crassidens*), fin whale (*Balaenoptera physalus*), common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*) and sperm whale *(Physeter catodon*) are not common in the North Sea.

2.2 Pinnipeds in the North Sea

The grey seal *(Halichoerus grypus*) and the common seal (or harbour seal) (*Phoca vitulina*) are abundant in the North Sea. The ringed seal (*P. hispida*), harp seal (*P. groenlandica*), hooded seal (*Cystophora crista*) and the bearded seal *(Erignathus barbatus*) are rare winter visitors.

2.3 Individual summaries of cetaceans

2.3.1 Harbour porpoise *Phocoena phocoena*

Economic importance

Cetaceans are known to compete with fishers for fish (Silva *et al*., 2002; Yano and Dahlheim, 1995). Given the high abundance of harbour porpoises in the North Sea (341,366 individuals) (coefficient of variation, CV = 0.14; 95% confidence interval, CI = 260,000–449,000) (Hammond *et al*., 2002), and that daily food consumption is 3.5–4.5 kg (Lockyer *et al.*, 2001), the total annual fish consumption is (crudely) in excess of 500,000 tonnes in the North Sea. This is broadly equivalent to the reported landings (mass in tonnes) of fish in the Netherlands in 1999 (EC, 2001) and could be considered of significant economic importance. Santos (1998 cited in Santos and Pierce, 2003) estimated consumption per annum of various commercial fish species in the North Sea. Consumption of whiting by porpoises could surpass the landings of this species for human consumption in the North Sea. Harbour porpoises off Scotland and the east coast of England (SCANS blocks C, D and J – see section 3.2.4) could consume around 14,640 t of whiting, 13,800 t of sandeels and 1,000 t of herring per year. Off the Danish coast (SCANS blocks I and L), harbour porpoises could eat around 2880 t of herring, 6,660 t of cod and 6,230 t of viviparous blenny. Off the Dutch coast and west coast of Germany (SCANS blocks H and Y), Santos (1998) estimated that porpoises could eat around 1,800 t of whiting, 650 t of cod and 300 t of sandeels (assuming porpoises off the east coast of Germany to have a diet similar to the combined diet of Danish and Dutch porpoises). Finally, using combined dietary data for Scotland, Denmark and Holland, in the central North

Sea it was calculated that harbour porpoises could eat around 3,900 t of herring, 33,400 t of whiting and 14,000 t of sandeels. This is approximately 100,000 t per annum; however, Santos (1998) notes that the confidence limits on all these estimates are low.

Regarding tourism, there are insufficient data to consider the economic benefits of cetaceans on an individual species basis. Generically, tourism has been increasing since the 1950s, such that it surpasses the growth rates of most other sectors (Gormsen, 1997). The growth rate for tourism in Europe is 3.7% per year and was expected to continue through 2000 (EC, 1995). The section of tourism which relates to watching marine mammals is ecotourism and it is on the increase worldwide and is thought to continue to increase as long as global economies improve and leisure time increases (Burger, 2000). In the North Sea, specifically the UK sector, the numbers of tourist and destinations have increased in value (Table 3.6).

Table 3.6 Summary of the growing worldwide value of whale watching (adapted from Hoyt, 1992; Hoyt, 1995b; Hoyt, 2000 – from Woods-Ballard, 2000).

Year	Direct spend £ UK	Indirect spend £ UK	No. of tourists
1991	25,000	850,000	400+
1994	850,000	6,500,000	15,000+
1998	1,170,000	5,140,000	121,125+

Despite the figures in Table 3.6, there is some evidence that the growth of the marine mammal watching industry in the UK is slowing (Woods-Ballard, 2000). While indisputably, there is an economic gain in ecotourism, this aspect is better treated as one of societal importance.

Societal importance

Marine mammals are protected by the EU Habitats and Species Directive (92/43/EEC annexes IIa and IVa). There is one candidate SAC in the Moray Firth protecting a resident harbour porpoise population. They are also covered by the Bern and Bonn Conventions. Conservation, management and research action is being undertaken and planned under ASCOBANS.

Ecological importance

Harbour porpoises are important predators on fish in the North Sea. Börjesson *et al*. (2003) analysed the diet of juvenile and adult harbour porpoises in the Kattegat and Skagerrak and showed that the porpoise preyed on a variety of species. The Atlantic herring (*Clupea harengus*) was dominant and the Atlantic hagfish may be important for adult porpoises. On the Scottish coast, sandeels and gadoids have been reported as the main food items in stomachs of harbour porpoises (Santos *et al*., 1994; Santos *et al*., 1995). The SEA 2 assessment reports that harbour porpoises' diet has changed over the past 40 years from one composed mainly of herring to a diet currently dominated by whiting (SEA 3, 2002). Santos and Pierce (2003) consider that there is evidence of a long term shift from predation on clupeids (mainly the herring) to predation on sandeels and gadoids in the Northeast Atlantic region which is possibly due to the decline in herring stocks since the mid-1960s.

Functional importance

Cetaceans are thought to have an important functional role as they tie up large amount of nutrients and are able to buffer short term fluctuation in resource availability (Bowen, 1997). Given the abundance of harbour porpoises in the North Sea, and their longevity (14–15 years, IWDG, 2003) this is presumed to be one functional role of harbour porpoises with respect to the other cetaceans in the ecosystem. Some researchers have speculated that cetaceans may have a role in recycling nutrients by feeding in the demersal zone and defecating in the euphotic zone (Kanwisher and Ridgway, 1988 cited in Bowen, 1997) but this has yet to be proven (Bowen, 1997).

2.3.2 White-beaked dolphin *Lagenorhynchus albirostris*

Relatively common in the North Sea.

Economic importance

Lack of data prevents estimation.

Societal importance

EU Habitats and Species Directive (92/43/EEC IVa). They are also covered by the Bern and Bonn Conventions.

Ecological importance

White-beaked dolphin stomachs examined by Santos *et al.* (1994, 1995) contained mainly gadids, especially the whiting *Merlangius merlangus*, but the octopus *Eledone cirrhosa* was also recorded as a prey item. In the North Atlantic, herring and gadoid fishes also appear in the diet (Reeves *et al.*, 1999a).

Functional importance

The abundance white-beaked dolphin is in the North Sea is not high, and therefore the species may not play large role in the ecosystem functioning of the North Sea.

2.3.3 White-sided dolphin *Lagenorhynchus acutus*

Relatively common in the North Sea.

Economic importance

Lack of data prevents estimation.

Societal importance

EU Habitats and Species Directive (92/43/EEC IVa). They are also covered by the Bern and Bonn Conventions.

Ecological importance

Atlantic white-sided dolphins prey on gadids but cephalopods are also important (Santos *et al.,* 1994; Santos *et al*., 1995). Reeves *et al*. (1999b) reported herring, mackerel, horse mackerel, silvery pout and squid as prey.

Functional importance

The abundance of the white-sided dolphin in the North Sea is not high, and therefore the species may not play large role in the ecosystem functioning of the North Sea.

2.3.4 Killer whale *Orcinus orca*

Relatively common in the North Sea.

Economic importance

Lack of data prevents estimation.

Societal importance

EU Habitats and Species Directive (92/43/EEC IVa). They are also covered by the Bern and Bonn Conventions.

Ecological importance

The species diet in the North Sea is largely unknown, but in Norway herring is thought to be a major diet item (SEA 3, 2002). Killer whales are thought to prey to limited extent upon seals in Shetland, and possibly offshore. They are also reported to feed on mackerel around Shetland (Fisher and Brown, 2001).

Functional importance

The abundance of the killer whale in the North Sea is not high, and therefore the species may not play large role in the ecosystem functioning of the North Sea.

2.3.5 Minke whale *Balaenoptera acutorostrata*

Relatively common in the North Sea.

Economic importance

Lack of data prevents estimation.

Societal importance

EU Habitats and Species Directive (92/43/EEC IVa). They are also covered by the Bern and Bonn Conventions.

Ecological importance

Minke whale stomachs of by-caught animals mainly contain main fish remains, mostly whiting and sandeels (Santos *et al*., 1994). Olsen and Holst (2001) compared diets of minke whale in the North Sea and the Norwegian Sea. In the Norwegian Sea, the diet is almost 100% Norwegian spring-spawning herring. Minke whale diet in the North Sea was found to be more varied with sandeels (*Ammodytes* spp.) dominating the diet, followed by mackerel, whiting, herring, and Norway pout.

Functional importance

The abundance of the minke whale in the North Sea is not high, and therefore the species may not play large role in the ecosystem functioning of the North Sea.

2.3.6 Bottlenose dolphins *Tursiops truncates*

Not abundant but a breeding ground of international importance has been identified within the North Sea.

Economic importance

Given the abundance of this protected species in the North Sea, their economic importance as related to the amount of commercial species that they consume is considered to be negligible.

Societal importance

EU Habitats and Species Directive (92/43/EEC IIa and IVa). There is one candidate SAC in the Moray Firth protecting a resident population. They are also covered by the Bern and Bonn Conventions.

Ecological importance

They are predators of fish. Stomach contents of by-catch bottlenose dolphins recovered in Scotland suggest a diet that includes salmon (*Salmo salar*), cod, Norway pout and octopus (Santos *et al.*, 1994). In a similar study, Santos *et al.* (2001a) identified cod, saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*) as the main prey eaten, although, salmon, haddock (*Melanogrammus aeglefinus)* and cephalopods were identified in the stomach. Couperus (1997) assessed stomach contents of bottlenose dolphins caught along the continental shelf of the UK, and reported that the diet was dominated by mackerel and horse mackerel. Analysis of the otolith remains in the stomachs indicated a varied diet of hake, silvery pout, greater argentine, poor cod, to mackerel and horse mackerel.

Functional importance

The abundance of the bottlenose dolphin in the North Sea is very low (129 individuals, CI = 110–174) (Wilson *et al.*, 1999), and therefore the species is likely not to play any role in the ecosystem functioning of the North Sea.

2.3.7 Other species of cetaceans

Long-finned pilot whale (*Globicephala melaena*), false killer whale (*Pseudorca crassidens*), fin whale (*Balaenoptera physalus*), common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*) and sperm whale *(Physeter catodon*) are not common in the North Sea, nor are there any resident populations necessitating SAC protection. Their functional and economic status is negligible in the larger ecosystem. They are protected under the EU Habitats and Species Directive (92/43/EEC IVa).

2.4 Distribution and abundances of small cetaceans in the North Sea

In the summer of 1994, Hammond *et al.* (2002) conducted the SCANS survey (Small Cetacean Abundance in the North Sea) to assess the status of small cetaceans in the North Sea (and adjacent waters) using shipboard and aerial line transect surveys (Figure 3.1). Although the abundance estimates were calculated over a short time period, these are the best data available.

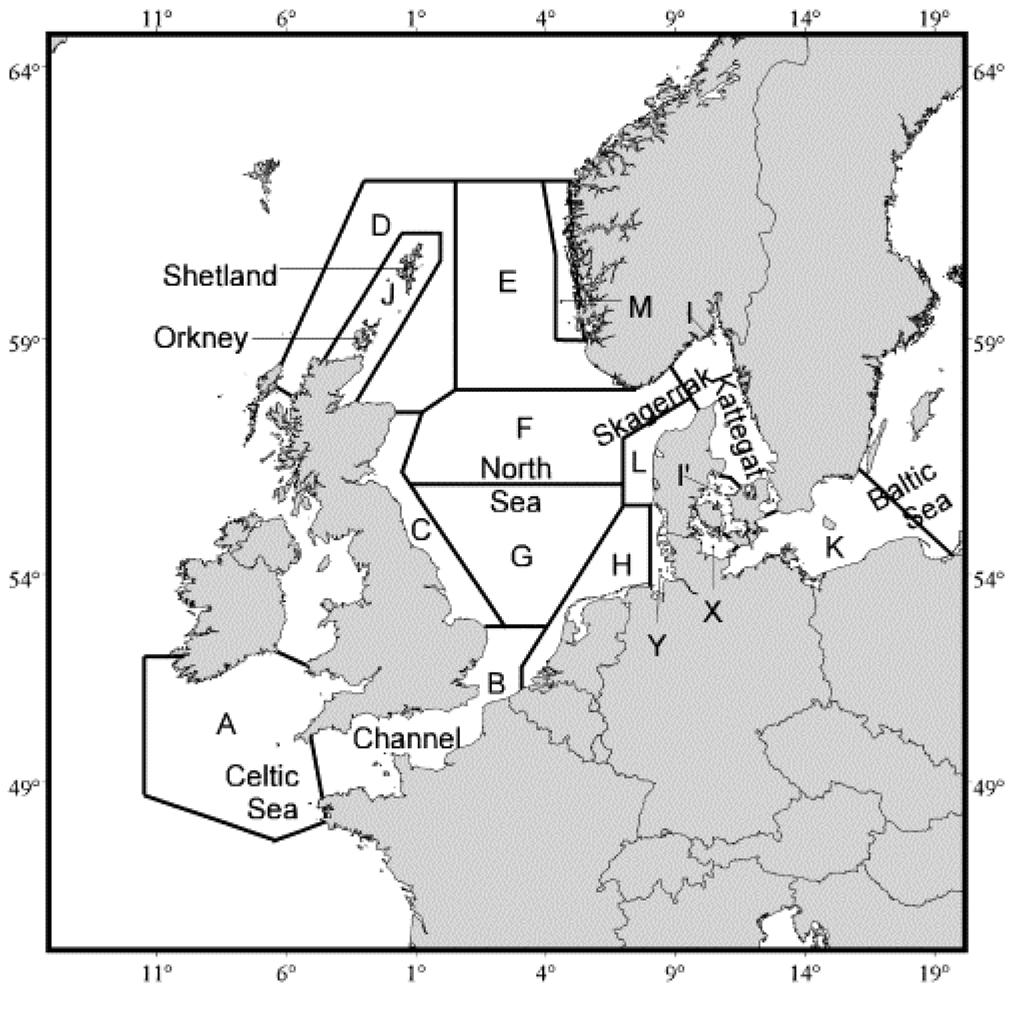


Figure 3.1 Area covered during the SCANS survey in 1994. Blocks A–I were surveyed by ship. Blocks I' (a subset of block I), J–M, X and Y were surveyed by aircraft. Blocks A–I were surveyed by nine ships for a total of seven ship months between 27 June and 26 July 1994 (Hammond *et al.*, 2002).

In summary, harbour porpoise *Phocoena phocoena* abundance for the entire survey area was estimated as 341,366 (coefficient of variation, CV = 0.14; 95% confidence interval, CI = 260,000–449,000). The estimated number of minke whale *Balaenoptera acutorostrata* was 8,445 (CV = 0.24; 95% CI = 5,000–13,500). The estimate for white-beaked dolphin *L. albirostris* based on confirmed sightings of this species was 7,856 (CV = 0.30; 95% CI = 4,000–13,000). When Atlantic white-sided dolphin *Lagenorhynchus acutus* and *Lagenorhynchus* spp. sightings were included, this estimate increased to 11,760 (CV = 0.26; 95% CI 5,900–18,500). For further detail see Figures 3.2–3.4 and Tables 3.7–3.9.

Phocoena phocoena **abundance**

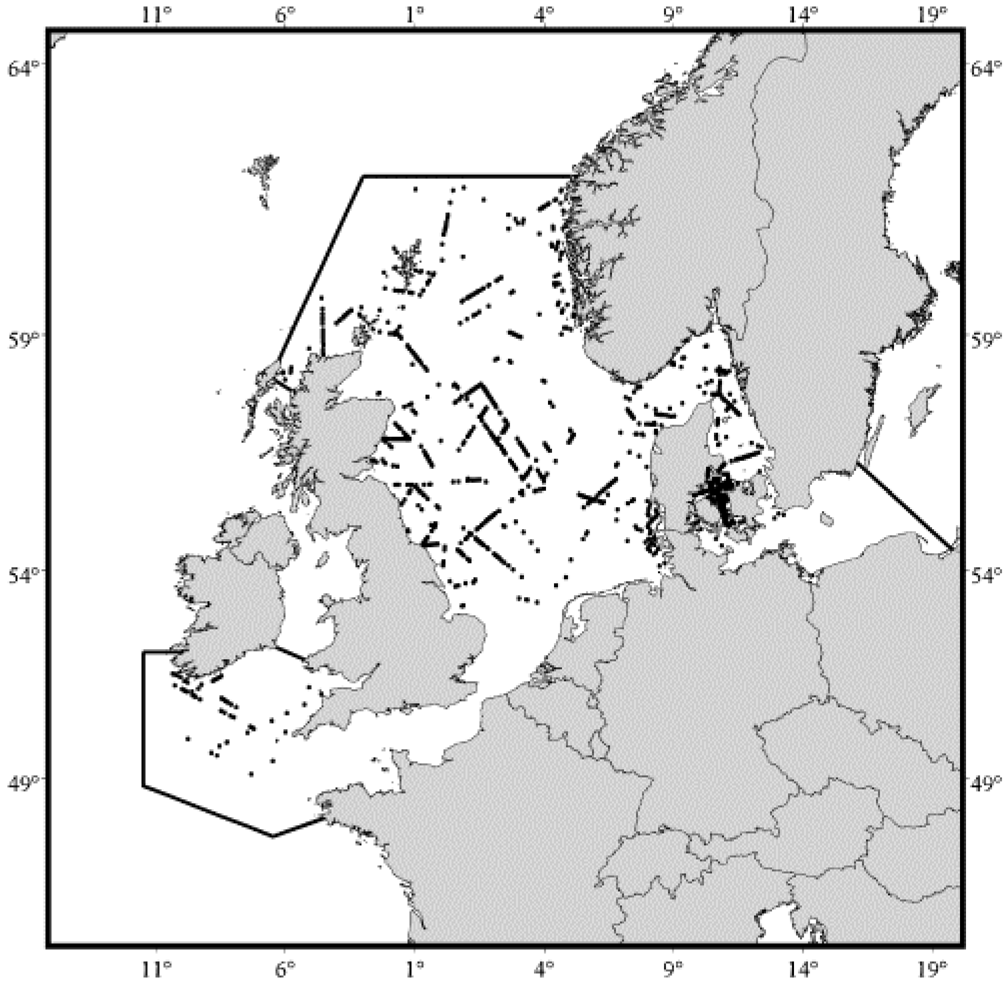


Figure 3.2 Sightings of *Phocoena phocoena* made on effort during shipboard and aerial survey (Hammond *et al.*, 2002).

Table 3.7 Estimates of school abundance, mean school size, animal abundance and animal density for *P. phocoena* (Hammond *et al.*, 2002). Figures in brackets are coefficients of variation. CVs for animal density are the same as for animal abundance.

Block	School abundance	Mean school size	Animal abundance	Animal density (ind. km^{-2})
*B	0	–	0	0
C	10 255 (0.19)	1.65 (0.07)	16 939 (0.18)	0.387
F	63 542 (0.26)	1.46 (0.04)	92 340 (0.25)	0.776
G	26 685 (0.36)	1.45 (0.10)	38 616 (0.34)	0.340
H	2 850 (0.35)	1.48 (0.14)	4 211 (0.29)	0.095
L	7 327 (0.46)	1.62 (0.08)	11 870 (0.47)	0.635

Lagenorhynchus spp. abundance

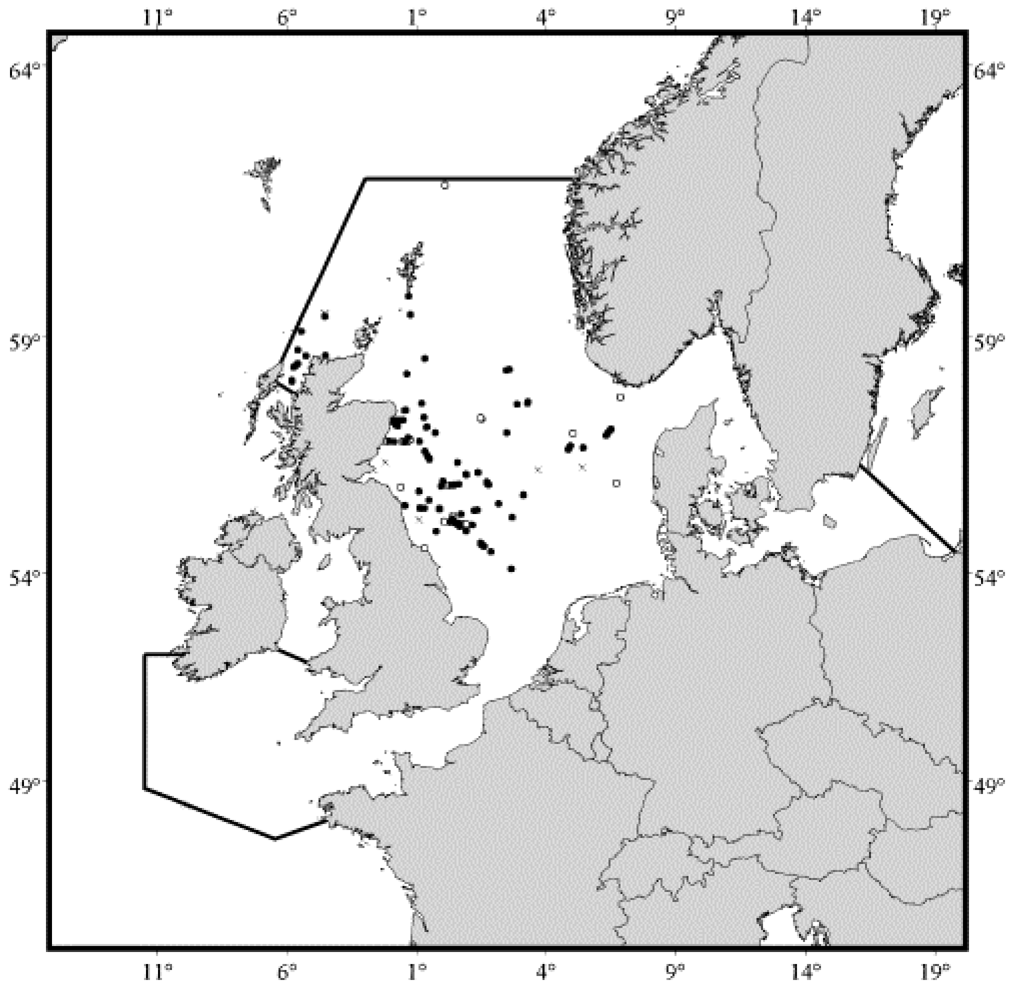


Figure 3.3 Sightings of unidentified *Lagenorhynchus* spp. (open circles), *L. albirostris* (filled circles) and *L. acutus* (crosses) made on effort during shipboard and aerial survey (Hammond *et al.*, 2002).

Table 3.8 Estimates of school abundance, mean school size, animal abundance and animal density for *L. albirostris* and *Lagenorhynchus* spp. (Hammond *et al.*, 2002). Figures in brackets are coefficients of variation. CVs for animal density are the same as for animal abundance.

Block	School abundance	Mean school size	Animal abundance	Animal density (ind. km^{-2})
L. albirostris				
B	0	–	0	0
C	526 (0.56)	4.47 (0.22)	2 351 (0.52)	0.0538
F	505 (0.36)	3.67 (0.12)	1 790 (0.42)	0.0150
G	679 (0.49)	3.56 (0.08)	2 443 (0.54)	0.0215
H	0	–	0	0
Lagenorhynchus spp.				
B	0	–	0	0
C	836 (0.51)	4.86 (0.16)	4 063 (0.50)	0.0929
F	494 (0.39)	3.92 (0.14)	1 937 (0.36)	0.0163
G	880 (0.46)	3.68 (0.08)	3 242 (0.47)	0.0285
H	0	–	0	0

Northridge *et al*. (1997) examined the data available for *L. albirostris* in the North Sea and around the British Isles and concluded that the observed distribution suggested that these animals may form a separate population from those found further north and west.

B. acutorostrata abundance

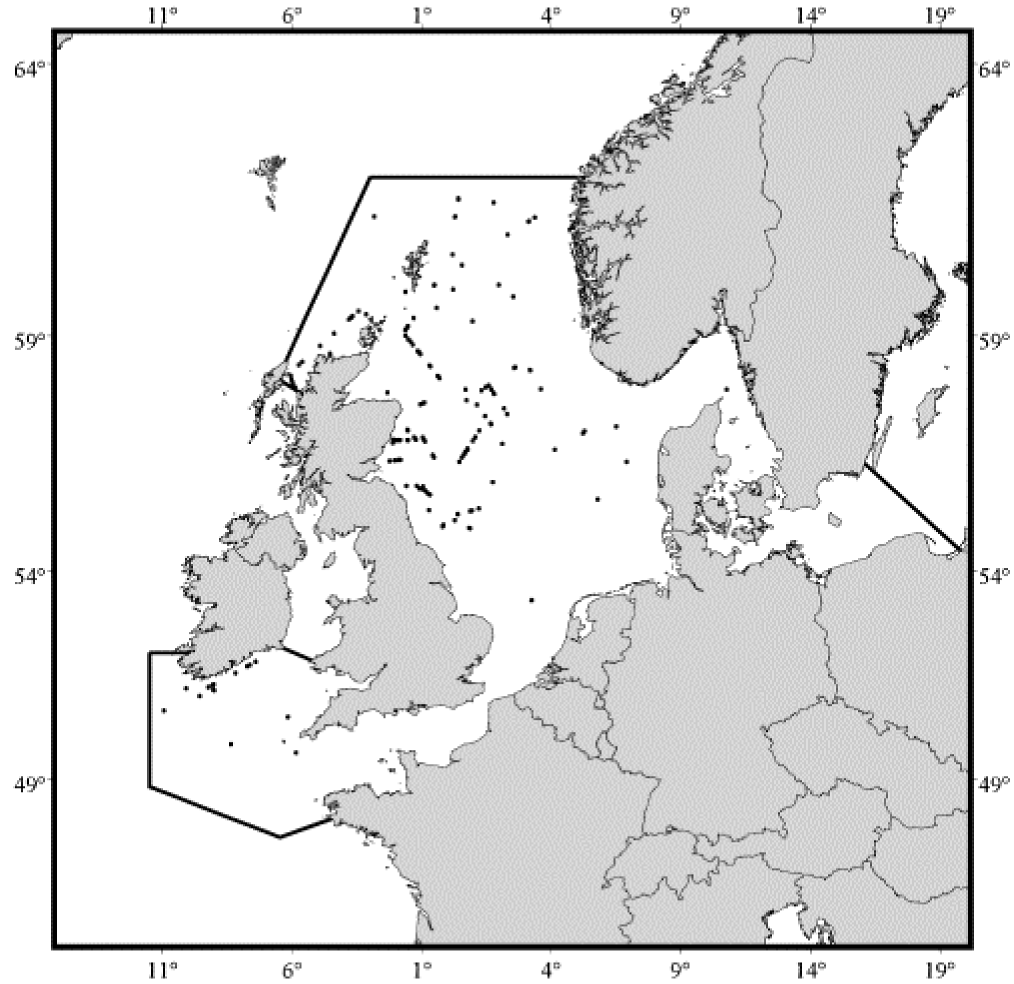


Figure 3.4 Sightings of *B. acutorostrata* during shipboard and aerial survey (Hammond *et al.*, 2002).

Table 3.9 Estimates of school abundance, mean school size, animal abundance and animal density for *B. acutorostrata* (Hammond *et al.*, 2002). Figures in brackets are coefficients of variation. CVs for animal density are the same as for animal abundance.

Block	School abundance	Mean school size	Animal abundance	Animal density (ind. km^{-2})
B	0	–	0	0
C	1 032 (0.40)	1.04 (0.03)	1 073 (0.42)	0.0245
F	1 354 (0.36)	1.00 (0.01)	1 354 (0.36)	0.0114
G	751 (0.62)	1.33 (0.14)	1 001 (0.70)	0.0088
H	0	–	0	0

Access to databases

The Scottish Marine Research Unit (SMRU) is developing a standardised cetacean distribution database for effort related cetacean sightings data for several years with the JNCC. This database is administered by the Sea Watch Foundation (http://www.seawatchfoundation.org.uk/index.htm). This database is not available currently to outside researchers, but access will be allowed in the future.

2.5 Individual summaries of pinnipeds

2.5.1 Grey seal *Halichoerus grypus*

Economic importance

Hammond and Fedak (1994) calculated the annual consumption of grey seals in the North Sea as 76, 000 tonnes, using a consumption rate of 7 kg of cod or 4 kg of sandeels per day to meet a grey seal's daily energy demands of approximately 5,500 kcal. The SMRU on behalf of SEA 2 (the DTI's Strategic Environmental Assessment) calculated the annual consumption by grey seals in 2001 at approximately 130,000 tonnes (SEA 3, 2002). The Sea Mammal Research Unit is currently carrying out a study of grey seal diet in the North Sea, Orkney, Shetland and the Hebrides. This is funded by DEFRA, SEERAD and SNH and its objectives are to repeat a study of diet carried out previously by SMRU in 1985. A wider area will be covered in 2002 than in 1985. This 3-year project began in January 2002 and the data are not yet available.

Societal importance

The grey seal is listed in Annex II of the Habitats and Species Directive (1992). A number of terrestrial candidate SACs have been established for grey seals around the coast of the UK; there are currently no marine candidate SACs. Many of these candidate SACs are shared with the harbour seal.

Ecological importance

Grey seals are particularly abundant around the UK coast and represent 40% of the world population and 95% of the EU population (JNCC, 2003). Given their abundance in the North Sea (about 300,000 individuals), they are important predators in the North Sea. Further details of the species diet in the North Sea are available on the seal database file ('seals.xls').

Functional importance

If like cetaceans, pinnipeds can have functional role in sequestering nutrients (Bowen, 1997), given the abundance and longevity (over 35 years for females and over 25 years for males, Corbet and Harris, 1991) of grey seals, this is presumed to be one functional role of the seals in the ecosystem.

2.5.2 Common seal (or harbour seal) *Phoca vitulina*

Abundant in the North Sea.

Economic importance

The SMRU calculated the annual consumption of fish by common seals to be in the region of 65,000–90,000 tonnes (SEA 3, 2002).

Societal importance

The common seal is listed in Annex II of the Habitats Directive. A number of terrestrial candidate SACs have been established for grey and common seals around the coast of the UK; there are currently no marine candidate SACs.

Ecological importance

In general, common seals are varied in their feeding habits and take a wide range of prey. The diet is composed predominantly of fish species including sandeels, whitefish (cod, haddock, whiting, ling), and flatfish (plaice, sole, flounder, dab) (Brown *et al.*, 2001; Hall *et al.*, 1998; Hammill and Stenson, 2000; Prime and Hammond, 1990). The diet has been shown to vary seasonally and from region to region (Hall *et al.*, 1998). Further details of the species diet in the North Sea are available on the seal database file ('seals.xls').

Functional importance

As for grey seals.

2.5.3 Other species of pinnipeds

The ringed seal (*P. hispida*), harp seal (*P. groenlandica*), hooded seal (*Cystophora crista*) and the bearded seal (*Erignathus barbatus*) are rarely encountered in the North Sea. There are no resident populations and they are not covered by the Habitats Directive necessitating SAC protection in the North Sea. Their ecological, functional and economic status is for all intents and purposes, negligible in the ecosystem. Their charismatic status as marine mammals garners the species a 0.5 rating of moderate importance.

2.6 Seals: European status and distribution

2.6.1 Grey seal *Halichoerus grypus*

Grey seals are among the rarest seals in the world. Their total abundance in the UK is estimated to be 300,000 individuals. The UK population represents about 40% of the world population and 95% of the EU population. Globally, there are three reproductively isolated stocks of grey seal: a west Atlantic (northern North American) stock; a Baltic stock; and an East Atlantic stock. The latter extends from Iceland and northern Norway southwards to northern France, with the majority breeding around Great Britain and Ireland.

Current status of British grey seal populations

The following text on grey seal populations derives from the document of SCOS (2002). Duck (2002) reports on the populations of common and grey seals in the North Sea for the Scottish Marine Research Unit (SMRU). Pup production is often used as an indicator of population trends. The total number of grey seal pups born in 2001 at all surveyed colonies was estimated to be 36,920 individuals.

Trends in pup production

A recent comparison of surveys in the pup production at breeding sites indicated that there were increases in some regions (Orkney) but declines in others (the Hebrides) (Table 3.10). Further analysis of data over longer periods indicates that the average annual increase in pup production at the main breeding sites between 1997 and 2001 was 2.8%. This compares with 5.2% between 1992 and 1996 and 6.2% between 1987 and 1991. The SMRU considers that there is some evidence for a slowing in pup production in recent years, despite the increase in Donna Nook.

Table 3.10 The percentage change in grey seal pup production at annually surveyed colonies, between 2000 and 2001 with the mean annual change between 1997 and 2001.

Location	Change 2000–2001	Mean change 1997–2001
Inner Hebrides	–8.8%	–0.5%
Outer Hebrides	–8.0%	+1.4%
Orkney	+9.6%	+4.4%
Isle of May + Fast Castle	–10.4%	+3.3%
Farne Islands	+6.5%	–1.7%
Donna Nook	+2.6%	+14.5%
Total	**0.0%**	**+2.8%**

Population size

The estimated size of the UK grey seal population at the start of the 2001 pupping season was about 130,000 individuals (range from less than 112,000 to as many 147,000 seals). The study was carried out at the major breeding sites including, the Hebrides, Orkneys, Isle of May/Fast Castle, Donna Nook, Farne Islands and other sites.

The majority of grey seals, approximately 91.5% (i.e. 119,000), are associated with breeding colonies in Scotland and the remainder, 8.5% (11,000), with colonies in England and Wales.

Uncertainty in estimates

There is considerable uncertainty associated with the total population estimates provided in Table 3.10. Estimates of pup production are thought to lie within a range of –14% to +13% of the values given and there are similar levels of uncertainty associated with other factors used to calculate total population size. Furthermore, the estimates of total population size assume that males have similar demography to females despite the belief that male grey seals die younger than females. Therefore, depending upon the degree to which this is true in grey seals, the estimates of total population size may be greater than the actual population size.

Overall trends in population size

The average rate of increase in the UK grey seal population associated with annually monitored sites over the past 5 years (1997–2001), is +5.6%. This does not represent a significant change in the rate of increase compared to the previous five years (1991–1996).

Distribution

McConnell *et al*. (1999) investigated the foraging movements of grey seals of the Farne islands using Satellite Relay Data Loggers (SRDLs) (Figure 3.5) and identified two distinct types of movement: long and distant travel (up to 2100 km away) and local, repeated trips from the Farnes, Abertay and other haul-out sites to discrete offshore areas. In 88% of trips to sea, individual seals returned to the same haul-out site from which they departed and 43% of the seals' time was spent within 10 km of a haul-out site. This has relevance to modelling of seal-fishery interactions.

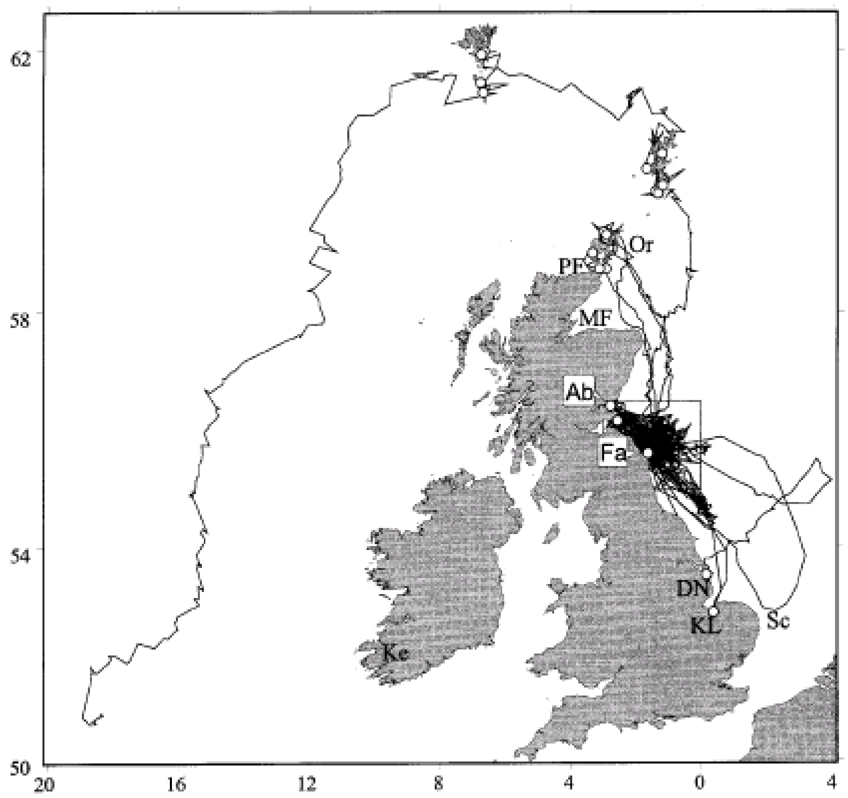


Figure 3.5 Tracks of all seals, based on primary locations, combined (McConnell *et al.*, 1999). Sites where the study seals hauled out on land are shown as circles. The limits of the Farnes Box are shown. Ab, Abertay; DN, Donna Nook; Fa, Farnes; Ke, Kerry; KL, King's Lynn; MF, Moray Firth; Or, Orkney; PF, Pentland Firth; Sc Scroby Sand.

Current status of Wadden Sea grey seal populations

The grey seal is considered indigenous in the Wadden Sea area. Two identified grey seal breeding sites exist in the Wadden Sea area. One colony is situated near the island of Vlieland in the Netherlands with about 315 animals, where at least 30 pups are born each year (Table 3.11). Three factors dominate the growth in the Vlieland colony: immigration, re-introduction (release of rehabilitated animals) and local births. The largest contribution to the increase in this population has been by immigration from other areas, e.g. the Farne Islands (TSEG-plus, 2002).

Table 3.11 Counted numbers of grey seals in the colony between Terschelling and Vlieland in the Dutch Wadden Sea between February and April.

Year	Adults	Pups
1979	2	0
1980	7	0
1981	8	0
1982	16	0
1983	31	0
1984	43	0
1985	60	2
1986	59	2
1987	66	5
1988	66	6
1989	80	6
1990	90	6
1991	120	9
1992	178	21
1993	220	25
1994	218	32
1995	275	20
1996	315	40
1997	320	–
1998	350	41
1999	550	64
2000	380	43

The other reproductive colony at Schleswig-Holstein, Germany, numbers between 30 to 40 animals (TWSP, 2003) (Table 3.12). Pup production is considered to be stable, as is the size of the colony during the breeding season. Observed increases in the number of adults during the spring/summer is attributed to influx from elsewhere in the Wadden and North Sea (TSEG-plus, 2002).

Table 3.12 Registered numbers of grey seals in the Schleswig-Holstein Wadden Sea.

Breeding season	Counted live pups; number of births	Dead pups	Adults counted during breeding season	Adults counted in spring
88/89	9	0	16	26
89/90	3	1	20	51
90/91	7	1	10	47
91/92	6	1	13	57
92/93	10	1	28	54
93/94	7	3	12	56
94/95	5	2	7	88
95/96	11	3	17	53
96/97	11	4	14	73
97/98	9	0	18	100
98/99	11	2	19	–
99/00	13	3	?	?

Neither small population of grey seals is considered viable (TSEG-plus, 2002; TWSP, 2003). Other regions in the Wadden Sea where grey seals are observed are haul-out sites, rather than reproductive colonies.

2.6.2 Common seal *Phoca vitulina*

Common seals have a near-circumpolar distribution, with at least four subspecies recognised. Only the eastern Atlantic subspecies *P. vitulina vitulina* occurs in Europe, where its range extends from Iceland and northern Norway southwards to northern France, including the Kattegat/Skagerrak and south-western Baltic.

A minimum estimate of population size for this sub-species based on counts at haul-out sites is around 70,000 individuals in the North Sea. However, counts of seals hauled out on land during the moulting season (August) represent only about 60–70% of the total population. Approximately 54% of this subspecies breeds in the North Sea (SEA 3, 2002; SMRU). According to the JNCC (2003), the UK population is circa 48,000–56,000 seals. The SMRU estimate the UK population at 34,625 (minimum estimate) and the range is 50,000–60,000 seals (see also the seal database file 'seals.xls' for previous estimates). The UK population represents about 5% of the world population of *P. vitulina*, approximately 50% of the EU population, and 45% of the European subspecies (JNCC, 2003). Table 3.13 shows the minimum estimates of population size for areas in the North Sea based on aerial surveys of animals hauled out on land during the moult or the pupping season (SEA 3, 2002).

Table 3.13 Counts of common seals in the North Sea (SEA 3, 2002).

Area	Year	Count
UK – English East coast	1999	3,700
UK – Scottish East coast	1996–97	1,500
UK – Shetland	1996–97	6,000
UK – Orkney	1996–97	8,500
Denmark	2000	2,100
Germany	2000	11,500
The Netherlands	2000	3,300
Norway, south of 62ºN	1996–98	1,200

<u>Distribution</u>

Common seal distribution at sea is constrained by the need to return periodically to land. Originally it was considered that common seals were unlikely to be found foraging more than 60 km from shore sand and that they only moved to alternate haul-out sites less than 75 km from their main site (Thompson *et al.*, 1996a). Recent SMRU studies using satellite-telemetry (Figure 3.6) have mapped the distribution of the common seal from sites in Scotland foraging widely over the North Sea.

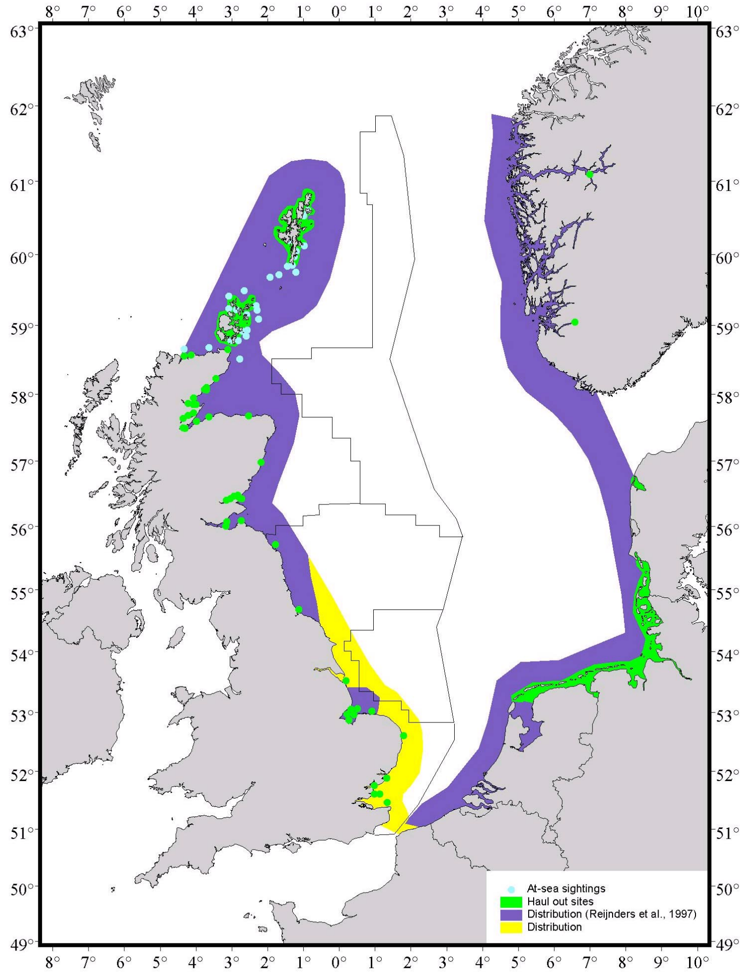


Figure 3.6 Common seal distribution around the North Sea. (SEA 3, 2002, sourced from: Reijnders *et al.*, 1997, Pollock *et al.*, 2000, SMRU, unpublished data, and Bjørge, 1991).

Overall trends in population size

Due to uncertainties in the counting methods related to the behaviour of common seals, the SMRU is unable to conclude from the data currently available, that there has been a change in the size of the common seal populations in Scotland (Orkney and Shetland) during the past 10 years. In contrast, common seal populations in the Wash and along the coast of eastern England are the highest so far recorded.

Current status of Wadden Sea common seal populations

In 2003, the maximum number of seals counted during the moult period (August) was estimated at 10,800: 1,160 seals were observed in Denmark; 4,235 in Schleswig-Holstein, 3,050 in Lower Saxony/Hamburg and 2,365 in the Netherlands. A maximum number of 2,956 pups were counted during the June whelping period: 270 in Denmark, 140 in Schleswig-Holstein, 799 in Lower Saxony/Hamburg and 480 in the Netherlands (TWSP, 2003). The recent phocine distemper virus (PDV) outbreak (2002–2003) had strong similarities in terms of its geographical origins and the chronology of infection to the outbreak in 1988, in which common seals in the southern North Sea were heavily impacted compared to those in the northern North Sea (Harding *et al.*, 2002; Jensen *et al.*, 2002; SCOS, 2002). The common seal in the Wadden Sea was impacted by the 2002–2003 PDV as a total of 20,975 seals were counted in 2002, approximately 50% more than in 2003 (TWSP, 2003). Prior to the outbreak of PDV, between 1990–1998 the overall annual growth rate of the common seal in the area was approximately +13% per annum. In 1999, there was a reduction in the observed growth rate (+5.5%) but this is considered to be an underestimate due to bad weather hampering the 1999 survey. In 2000, a population growth rate of +13% was recorded once again (TSEG-plus, 2002). Up to 2001, TSEG-plus (2002) considered that there were no real changes in the population trends in the common seal in the region.

At this time, the full effects of the recent 2002–2003 PDV outbreak on the common seal populations in the North Sea and the Wadden Sea cannot at this time be fully assessed.

3. Zooplankton

Zooplankton are an important food source for many organisms, especially the juveniles of many commercial fish species (see Table 3.14 in section 3.4.18). Zooplankton biomass in the central parts of the eastern North Sea, in the vicinity of a front, has been reported at 43 mg dry weight m^{-3} (Munk, 1993). Steele (1974) constructed the first North Sea energy flow and estimated herbivorous zooplankton production to be 175 kcal m^{-2} yr^{-1} with a biomass of 3–10 g DW m^{-2}. These are the first figures of this nature for the North Sea and have been revised and studied since this time. Other data are available on the zooplankton database file ('zooplankton.xls').

3.1 Copepods

The zooplankton communities of the central and southern North Sea regions are dominated in terms of biomass and productivity by copepods, particularly *Calanus* species (Heath *et al*., 1999; SEA3, 2002). On the Fladen grounds in the North Sea with the onset of thermal stratification coupled with the spring phytoplankton bloom, the biomass of copepods can reach as much as 80–90% of the zooplankton biomass (Fransz *et al.*, 1991). For copepods in the North Sea, Crisp (1975) reports an annual consumption and production of 60 and 18 g C m^{-2}, respectively. Christensen (1995) assumed that the biomass of copepods in the North Sea was 10 g C m^{-2}. A food conversion efficiency (production/consumption ratio) of 30% can be assumed for copepods (Christensen, 1995). Copepods are assumed to feed 95% on microplankton (evenly distributed between autotrophic and heterotrophic forms) and 5% on detritus.

However, most studies of zooplankton, and specifically copepod biomass, do not take into account the presence of copepod nauplii and small copepods (Hansen *et al.*, 1996; Melle and Skjoldal, 1998), mainly because quantification is extremely difficult and few data exist, adding to the uncertainty.

3.2 Individual summaries for zooplankton

Calanoid copepods

Economic importance

Zooplankton are not harvested in the North Sea.

Societal importance

Zooplankton are not considered as charismatic species and are not protected by legislation

Ecological importance

Calanoid copepods are primarily pelagic. Approximately 75% of the species are marine, of which a proportion are bentho-pelagic or commensal, and the other 25% are freshwater (Mauchline, 1998). Numerically, pelagic calanoid copepods dominate the organisms caught in plankton samples from most seas, representing 55–95% of the individuals caught (Mauchline, 1998). In the North Sea, *Calanus* can constitute up to 70% of the biomass of the mesozooplankton at certain times of the year, usually spring and autumn (Heath *et al*., 1999). There are two main species of *Calanus* in the North Sea: *Calanus finmarchicus* and *C. helgolandicus*. *Calanus finmarchicus* occurs mainly in northern regions (limited by the 55°N parallel in the North Sea (Planque and Fromentin, 1996) while *C. helgolandicus* is more common in the southern regions. Recent research on the biogeography of *C. finmarchicus* and *C. helgolandicus* has indicated that the distribution of these two species has changed in the last few decades (Beaugrand *et al.*, 2002; Johns and Reid, 2001). *Calanus finmarchicus* has moved north to colder waters and *C. helgolandicus* has moved northwards. This is believed to be a response to hydroclimatic conditions in the North Sea driven by the North Atlantic Oscillation (NAO) (see also Fromentin and Planque, 1996). The biomass of *C. finmarchicus* in the North Sea has also fallen recently (Figure 3.7) to levels similar to that of *C. helgolandicus*.

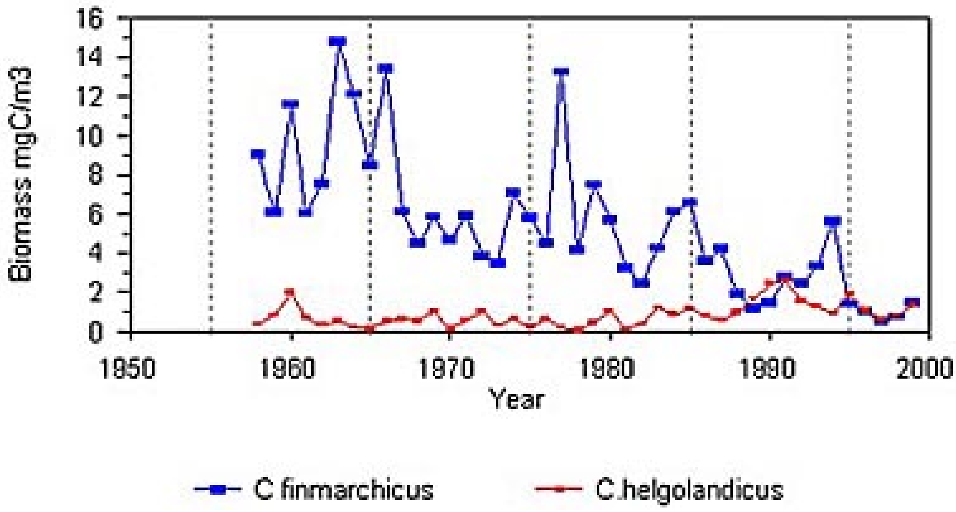


Figure 3.7 Annual average biomass of late copepodite stages of *Calanus finmarchicus* and *C. helgolandicus* in the northern North Sea. Drawn from data supplied by the Sir Alister Hardy Foundation for Ocean Science (Fisheries Research Services).

Calanus spp. are known to accumulate large reserves of lipid, almost exclusively wax esters, during their life cycles (Lee, 1974, 1975; Sargent and Henderson, 1986; Sargent *et al.*, 1987). *Calanus finmarchicus* has a one year life cycle in the North Sea/Norwegian fjords (Tande, 1982) and recruitment is closely correlated with the spring bloom. Indeed, studies on the predominantly herbivorous *C. finmarchicus* have indicated that the wax ester reserves allow the copepods to reproduce when, after a period of winter quiescence, they start to feed on the following spring bloom. *Calanus helgolandicus* is similar in size to *C. finmarchicus* but is neither as lipid rich (Lee *et al.*, 1972) nor in terms of carbon content (Harris *et al.*, 2000).

As dominant members of the plankton, and as predominantly herbivorous members of the fauna, these copepod species provide an important link between the primary producers and higher trophic levels providing a lipid-rich, high-energy diet. Hop *et al.* (1997) fed Arctic cod with a variety of diets (*Calanus* copepods, *Themisto* or capelin fillets) and the fish fed with *Calanus* spp. had the highest net growth efficiencies. Lynch *et al.* (2001) developed a conceptual model of larval fish feeding on stage-structured prey populations. *Calanus finmarchicus* alone was shown to be insufficient to support the smallest cod larvae (4 and 6 mm), but provided good growth (≥10%/day) for larger larvae (10–12 mm). Thus *Calanus* copepods are important in the diets of juvenile fish.

Sars (1879) first showed that young fish fed initially on *Calanus* and *Temora* (see below). Furthermore, the critical period of larval 'first feeding' has been shown to control interannual variability in the recruitment success of fish stocks (Hjort, 1914; Blaxter, 1974; Chambers and Trippel, 1997). In the northern North Sea, many 0-group fish (cod, haddock, whiting, saithe and Norway pout) feed mainly on copepods, especially *C. finmarchicus* (Bromley *et al.*, 1997). In the south-west part of the North Sea, along the coast of the Netherlands, 0-group whiting (*Merlangius merlangus*) and bib (*Trisopterus luscus*) fed almost exclusively on calanoid copepods during May (Hamerlynck and Hostens, 1993). In the northern North Sea, *C. finmarchicus* form an important part of the diet of small Norway pout (11 to 19 cm) (more than 10% of the percentage contribution by weight) (Albert, 1995), although the commercial species, *Pandalus* spp. contribute more than 20% by weight to the diet. This is contrast to Bromley *et al.* (1997) where Norway pout, between 2.1–6.6 cm in length, were estimated to consume up to 70% copepods (percentage wet weight). In the Skagerrak, calanoid copepods constituted 33% of the food consumed by juvenile cod (*Gadus morhua*) and 16% of the food of whiting (*Merlangius merlangus*) at one location (Fjøsne and Gjøsæter, 1996).

Acartia copepods are estuarine or neritic species and they are often dominant in coastal waters, whilst *Calanus* copepods are more oceanic (Nielsen and Munk, 1998; Heath *et al*., 1999; ICES, 2003b). At an offshore SE North Sea sampling station, Helgoland Roads (54°11'18" N, 7°54' E), plankton net samples have been taken three times a week since 1975. *Acartia clausi* form a significant fraction of the copepods in the samples (ICES, 2003b). There is some evidence that the smaller *Acartia* spp. are potentially favoured by larval fish such as whiting over the larger *Calanus* copepods (Nielsen and Munk, 1998). Arrhenius (1996) showed in the Baltic Sea that 0-group herring preferred *Acartia* spp. over *Eurytemora* > cladocerans > *Pseudocalanus minutus* >copepod nauplii (in order of preference) while sprat took *Eurytemora* > cladocerans > *Acartia* > *Pseudocalanus* > copepod nauplii (in order of preference).

Acartia spp. are not as lipid, energy-rich as *Calanus* copepods and seem to deposit protein during somatic growth rather than sequestering lipids (Thor, 2000). Thus they are potentially not as valuable in energetic terms as *Calanus* copepods, but smaller, larval fish with a smaller gape may consume them preferentially (Bremigan and Stein, 1994). Although Gaughan and Potter (1997) compared the diets and mouth sizes of five estuarine species of larval fishes and concluded that mouth width had only a small influence on prey sizes eaten and that disparate feeding patterns among larvae were likely to be due to behavioral differences. Consumption is a function of prey availability and abundance.

Temora longicornis feed on the eggs and nauplii of *Calanus finmarchicus* and *Pseudocalanus* spp. (Sell *et al.*, 2001) and in turn are prey for the euphausiid *Meganyctiphanes norvegica* (Lass *et al*., 2001). They are also important prey for larval fish, e.g. sprat and herring (Arrhenius, 1996; Sars, 1879).

Functional importance

Food web

Copepods (and other members of the zooplankton) are important in the carbon flow in the coastal and pelagic planktonic ecosystems as they provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels.

Carbon nutrient recycling

Grazing and sedimentation are the two major processes that determine the fate of a phytoplankton bloom. Sakshaug and Skjoldal (1989), argue these processes are reciprocal in that, if a large standing stock of zooplankton grazes heavily on phytoplankton, a small proportion of the phytoplankton will remain ungrazed to sink out of the upper layer. In contrast, a large fraction will sink down if zooplankton stocks and grazing pressure are low. Ungrazed organic matter will sink through the water column to the benefit of benthic processes (Denman, 1994; Lenihan and Micheli, 2001).

Faecal matter/pellets

A proportion of the phytoplanktonic/microzooplankton material which is consumed is excreted. Faecal pellets represent an ecologically important energy source for detritus feeders, benthic organisms (Smetacek, 1984) and organisms in the water column. It is difficult to state that one type of copepod (or other type of zooplankton) faecal pellets are more likely to contribute to processes in the water column or benthic processes.

Many copepods produce relatively large faecal pellets with high sinking rates (Yoon *et al*., 2001) and as they are membrane covered, they do not disintegrate as quickly as others, which increases their role in the vertical pellet flux (Pasternak *et al*., 2002). Indeed, the flux of faecal pellets to the sea floor may have a significant impact on nutrient cycling and sedimentation rates (Pasternak *et al*., 2002; Riser *et al.*, 2002, Turner *et al*., 1998). However, Turner (2002) considers that faecal pellets of small mesozooplankton and microzooplankton are mostly recycled or repackaged in the water column by microbial decomposition and coprophagy, therefore contributing more to processes in the water column than flux to the benthos. The fate of faecal pellets, and their ultimate functional role, is more likely to be related to the seasonality of surface phytoplankton and zooplankton production cycles and how these relate to productivity, biomass, size spectra and composition of communities in the water column and also the trophic interactions between various components of the plankton communities.

Cyclopoid copepods

***Oithona* spp.**

Economic importance

Zooplankton are not harvested in the North Sea.

Societal importance

Zooplankton are not protected by legislation

Ecological importance

The smaller copepods, such as *Oithona* spp. are often underestimated in terms of biomass due to inadequacies in sampling methodology e.g. inadequate mesh size. *Oithona* spp. may contribute significantly to copepod biomass and production (Nielsen and Andersen, 2002; Nielsen and Sabatini, 1996). Given the problems with sampling these smaller copepods, and that time series may have over time dramatically underestimated the abundance and biomass of these copepods, assessing the ecological importance of *Oithona* spp. is extremely difficult.

Functional importance

See calanoid copepods.

Cladocerans

Evadne spp.

Economic importance

Zooplankton are not harvested in the North Sea.

Societal importance

Zooplankton are not protected by legislation

Ecological importance

As with *Acartia* spp., *Evadne* spp. are neritic species and are preyed upon by larval whiting (Arrhenius, 1996; Nielsen and Munk, 1998) and larval turbot *Scophthalmus maximus* (Last, 1979).

Functional importance

See calanoid copepods.

Euphausiids

Economic importance

Zooplankton are not harvested in the North Sea.

Societal importance

Zooplankton are not protected by legislation

Ecological importance

The three dominant species of Euphausiacea in the North Sea are *Thysanoessa inermis, T. raschi* and *Meganyctiphanes norvegica*. Annual production for *T. inermis* and *T. raschi* in the North Sea is within the range 0.69 to 4.66 mg m^{-3}, and the ratio between production and biomass (P:B) is between 1.3 and 4.2 (Lindley, 1980). On the Fladen ground in the North Sea during

March/April, stocks of euphausiids can represent more than 90% of the zooplankton biomass (Williams and Lindley, 1980). Euphausiids take both autotrophic and smaller heterotrophic prey. They are an important link to high trophic levels. However, the herbivorous calanoid copepods produce larger lipid reserves than omnivorous euphausiids and are a more valuable, calorific resource. Other data are available on the zooplankton database file ('zooplankton.xls').

Functional importance

See calanoid copepods.

Megaplankton, Thaliacea (salps and doliolids)

Economic importance

Zooplankton are not harvested in the North Sea.

Societal importance

Zooplankton are not protected by legislation.

Ecological importance

The megaplankton, Thaliacea (salps and doliolids), are present in the North Sea and are thought to be more abundant in late summer and autumn (Johns and Reid, 2001). A wide range of fish species, including their juveniles, consume salps and doliolids (Avent *et al*., 2001). These gelatinous taxa (which also include siphonophores, ctenophores, and medusae (jellyfish) are poorly sampled in studies (e.g. North Sea CPR tows) since their bodies disintegrate on contact with the sampling equipment. Assessing the ecological importance of Thaliacea is extremely difficult due to the sampling problems, and historical data sets may be extremely inaccurate.

Functional importance

Salp faecal pellets are thought to be important in the vertical flux of organic matter as they sink quickly to the sea floor (Caron *et al*., 1989; Yoon *et al.*, 2001).

4. Fish

The North Sea is inhabited by approximately 182 native fish species (Froese and Pauly, 2003), of which only a small fraction are fished commercially. As fish make up a significant part of the marine biomass and occur at practically all trophic levels, they can be considered to be of considerable ecological and functional importance. The societal importance of non-target species has increased as the public becomes more concerned with threatened or declining fish species and aware of biodiversity issues.

The fish species described below are characterised according to their economic, ecological or societal importance. Based on this information, the components of the significant food web can be identified. In choosing the components the aim was to maintain as many of the units as possible that have specific economic, ecological or societal importance while at the same time acknowledging the limitations of data availability.

4.1 Dogfishes (Pleurotremata, Scyliorhinidae)

Lesser-spotted dogfish *Scyliorhinus canicula*

The lesser-spotted dogfish is a very common bottom-living fish that is found from Norway and the British Isles to Senegal and the Mediterranean. It is found throughout the North Sea but numbers are higher in the northwestern part. It occurs mostly on continental shelves and upper slopes, in depths of 10 to 100 m on sandy, muddy or gravel bottoms. The young live in shallower water than the adults.

The maximum length of the lesser-spotted dogfish is 100 cm. The von Bertalanffy growth parameter K is 0.13 per year. The lifespan is unknown. Maturity is reached at lengths around 60 cm and age 5.

The spawning season is probably in spring and summer, but egg-carrying females occur throughout the year. Egg laying occurs year-round, but mostly from November till July. The eggs have horny capsules and are laid on sandy bottoms below the tide level. The young hatch after 8 to 10 months when they have reached a length of 10 cm.

Lesser-spotted dogfish is an opportunistic nocturnal benthic feeder. The diet consists mostly of crustaceans (*Pagurus* spp. *Nephrops norvegicus*, *Crangon*

crangon, *Pandalus* spp.), molluscs (whelks, scallops and razor-shells), polychaetes and fish.

The only known predator of the lesser-spotted dogfish is cod *Gadus morhua* (Froese and Pauly, 2003).

Natural mortality is estimated at 0.20 (se 0.13–0.30). The population resilience is low; the minimum population doubling time is 4.5–14 years (K=0.20; tm=5; 18–20 eggs only). This species is not on the IUCN Red list. The lesser-spotted dogfish is of minor economic importance and is mostly taken as by-catch.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.2 Skates and rays (Hypotremata, Rajidae)

Starry ray *Raja radiata*

The starry ray is a fairly common fish that is found in the eastern Atlantic from the English Channel to Svalbard and Iceland, also in the northern and central North Sea. It is also found in the western Atlantic. The starry ray is a deep to very deep-water species, 20 to 1000 m deep. In the North Sea, it is mostly found at depths from 60 to 120 m. No strong preference are found for sediments; the starry ray is found on all kinds of bottoms.

Maximum size of starry ray is 100 cm, but in the North Sea specimens over 60 cm length are rare. Maximum life span is approximately 18 years (Froese and Pauly, 2003). The von Bertalanffy growth parameter K is 0.16 per year. Maturity is reached at size 40 cm and age 3 or 4.

The spawning season is probably from February to June, but females with well-developed eggs can be found the whole year round. Location of spawning grounds is not known. Fertilization of the eggs is internal and the eggs are deposited on sand or gravel seabed. The eggs measure 4 to 9 cm length (without horns) and 2 to 7 cm width. Eggs hatch after 4 months, when the young have reached a length of 10 cm.

The starry ray is probably a nocturnal feeder (Knijn *et al*., 1993). The diet consists of crustaceans, fish (mostly sandeels), polychaetes and annelids. Young starry rays feed mostly on crustaceans. From 15 cm onwards they start feeding on fish.

Starry rays are cannibals and are also predated upon by snail species belonging to Muricidae and Naticidae (Froese and Pauly, 2003).

The natural mortality of the starry ray is 0.22 (se 0.14–0.33). The resilience of the population is low; the minimum population doubling time is 4.5–14 years (K=0.17; tm=4; assuming Fec<100). The starry ray is not on the IUCN Red list.

Starry ray is mostly a by-catch species, because it is considered to be too small for consumption. Landings from 1977 to 1988 are estimated at 100,000 tonnes.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

Cuckoo ray *Raja naevus*

The bottom-living cuckoo ray is a relatively common fish, found in the eastern Atlantic, from the British Isles to Senegal and the Mediterranean. In the North Sea, it is mainly found in the western part, from the Scottish coast to the English Channel. It lives mostly in shallow to moderate depths, 20 to 120 m, but can be found in depths up to 500 m.

Maximum length of the cuckoo ray is 70 cm. Maximum reported age is 28 years (Froese and Pauly, 2003). The von Bertalanffy growth parameter K is 0.11–0.16. Maturity is reached late in life, at lengths of 55 to 60 cm and age of 7 to 9 years.

Spawning occurs throughout the year, but there seems to be a peak in the summer. The eggs are demersal and deposited on sand or gravel bottoms. The eggs measure 5 to 7 cm in length (without horns) and 3 to 4 cm in width.

Cuckoo ray feeds on fish (sandeels), crustaceans and some polychaetes and cephalopods.

There are no known predators of cuckoo ray. The natural mortality of cuckoo ray is 0.14 (se 0.09–0.21). The cuckoo ray population has a low resilience; the minimum population doubling time is estimated at 4.5–14 years (K=0.11–0.16; tm=8–9; tmax=28; Fec<100). The cuckoo ray is not on the IUCN Red list.

Cuckoo ray makes up a significant part of the landings of the Scottish commercial-fleet.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

Thornback ray *Raja clavata*

The thornback ray is the most abundant of the rays and can be found in the eastern Atlantic, from Norway and Iceland to South Africa, including the Mediterranean. It is found throughout the North Sea, but mostly along the English coast and central North Sea. It is found on various kinds of sea bottom at depths of 2 to 300 m. The juveniles live in shallower nursery areas.

Female thornback rays can reach a maximum size of 120 cm, while males reach 105 cm. Maximum reported age is 23 years (Froese and Pauly, 2003). The von Bertalanffy growth parameter K is 0.09 to 0.14 per year. Females reach maturity in the 5th year, at lengths 60 to 75 cm, while males are mature at 50 cm and age 7.

Spawning occurs in inshore waters mostly from March to September. The thornback ray is oviparous. The eggs are demersal and are deposited on sandy or gravel bottoms. Eggs measure 5 to 9 cm in length and 3 to 7 cm in width. The incubation of the eggs is 4 to 5.5 months. The young hatch when a length of 8 to 14 cm is reached.

The thornback ray preys on polychaetes, crustaceans and fish. Young feed mostly on crustaceans and amphipods.

Grey gurnard *Eutrigla gurnardus* is reported as a predator of thornback ray. Natural mortality of the thornback ray is 0.28 (se 0.18–0.42). The population resilience is low; the minimum population doubling time is 4.5–14 years (K=0.09–0.14; tm=10; tmax=23; Fec=150). Thornback ray is not on the IUCN Red list. The thornback ray is of moderate economic importance.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.3 Isopondyli, Clupeidae

Sprat *Sprattus sprattus*

The sprat is a common fish that can be found in the eastern Atlantic, from the North Sea and the Baltic to Morocco and the Mediterranean. In the North Sea, it can be found in central and southern areas and along the British coast. The sprat is a pelagic schooling fish and can be found in coastal waters from 10 to 150 m depth. The young sprat migrate and overwinter in the shallower coastal areas.

Sprats can grow to a maximum size of 17 cm. The sprat is a short-lived species, the maximum reported age is 7 years, but rarely attains an age of five years or older. Growth of the sprat is fast during the first year; the von Bertalanffy growth parameter K is 0.13 to 0.77 per year. Most sprats spawn for the first time at the age of two and length of around 10 cm, but some reach maturity at age 1.

Spawning occurs at different spawning grounds. The German Bight population spawn from May to August; peak spawning occurs in May and June. Spawning takes place at night. The eggs are pelagic and float at the surface or in midwater. The egg diameter is between 0.8 to 1.5 mm. The eggs hatch in 3 to 8 days depending on temperature. The newly hatched larvae measure 2.55 to 3.7 mm. The larvae are pelagic and drift to the inshore coastal waters. The larvae live close inshore with the first-year herring.

The sprat is a pelagic feeder and their larvae feed on planktonic copepods. After metamorphosis, copepods remain an important part of the diet, but it also preys on cladocerans, bivalve larvae, mysids and euphausiids.

The sprat is preyed upon by red-throated diver *Gavia stellata* (frequent; Durinck *et al.*, 1994; Leopold, 1997), great crested grebe *Podiceps cristatus* (rare; Doornbos, 1984), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn and Dirksen, 1993, Boudewijn *et al.*, 1994, Buckens and Raeijmaekers, 1992, Leopold and Winter, 1997, Steven, 1933), shag *P. aristotelis* (rare-common; Carss, 1993; Harris and Wanless, 1993; Steven, 1933), Mediterranean Gull *Larus melanocephalus* (rare; Goutner, 1994), common gull *L. canus* (rare; Kubetzki, 1997; Kubetzki *et al.*, 1999), black-legged kittiwake *Rissa tridactyla* (frequent-common; Harris and Wanless, 1997, Prüter, 1989, Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (frequent-common; Brenninkmeijer and Stienen, 1992, Garthe and Kubetzki, 1998), common tern *S. hirundo* (frequent-common; Niedernostheide, 1996; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Hartwig *et al.*, 1990; Monaghan *et al.*, 1989; Niedernostheide, 1996), common guillemot *Uria aalge* (rare-staple; Blake, 1983, 1984; Blake *et al.*, 1985; Camphuysen, 1995; Camphuysen and Keijl, 1991, 1994; Durinck *et al.*, 1991; Geertsma, 1992; Halley *et al.*, 1995; Harris and Wanless, 1986; Hatchwell, 1991; Hedgren, 1976; Leopold and Camphuysen, 1992; Leopold *et al.*, 1992; Lyngs and Durinck, 1998; Reinert, 1976; Salomonsen, 1935), razorbill *Alca torda* (frequent-staple; Andersson *et al.*, 1974; Blake, 1983, 1984; Leopold and Camphuysen, 1992), little auk *Alle alle* (common; Blake, 1983), Atlantic puffin *Fratercula arctica* (rare-staple; Ashcroft, 1976; Barrett *et al.*, 1987; Corkhill, 1973; Harris, 1970; Harris and Hislop, 1978; Martin, 1989), common dolphin *Delphinus delphis* (frequent; Collet *et al.*, 1981), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Bjørge *et al.*, 1991; Rae, 1965), grey seal *Halichoerus grypus* (rare-frequent; Pierce *et al.*, 1989; Pierce *et al.*, 1991a), harbour seal *Phoca vitulina* (rare-staple; Behrends, 1982; Bjørge, 1995; Bjørge *et al.*, 1993, Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Rae, 1973a; Thompson *et al.*, 1991; Tollit and Thompson, 1996; Tollit *et al.*, 1997) (see also Leopold *et al*., 2001), herring *Clupea harengus*, bottlenose dolphin *Tursiops truncates*, whiting *Merlangius merlangus*, saithe *Pollachius virens*, veined squid *Loligo forbesi*, hake *Merluccius merluccius*, hagfish *Myxine glutinosa*, Cuckoo ray *Raja naevus*, Thornback ray *Raja clavata*, spotted ray *Raja montagui*, bonito *Sarda sarda*, grey gurnard *Eutrigla gurnardus* and sprat *Sprattus sprattus* (Froese and Pauly, 2003).

Natural mortality of sprat is 1.08 (se 0.71–1.64). The population resilience of sprat is high; the minimum population doubling time is less than 15 months (rm=1.7; K=0.13–0.77; tm=1–2; tmax=6; Fec=2,000). Sprat is not on the IUCN Red List.

Sprat is an important species in the industrial offshore fishery. Yearly landings peaked in the 1970s at 700,000 tonnes. In the 1990s catches were around 100,000 tonnes per year.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

Herring *Clupea harengus*

The herring is a very common fish that can be found in the northeastern North Sea, from the Bay of Biscay to Iceland and Greenland and Spitzbergen and Novaya Zemlya, and the northwestern Atlantic. Juvenile herring can be found throughout the North Sea, but adult herring are found mostly in the western part of the North Sea. Herring is a pelagic schooling fish that can be found at depths of up to 200 m. Herring perform extensive migrations depending on the presence and density of the food organisms. At dusk the schools move to the surface and disperse, while at daylight the fish are in deeper water.

Herring can grow to a maximum of 45 cm and age up to 11 years. The von Bertalanffy growth parameter K is 0.2 to 0.6 per year. 75% of the herring reach maturity at the age of 3 and length of 25 cm.

Different spawning groups can be found in the North Sea according to season and spawning ground. There are spring and autumn spawners. The different spawning grounds are Buchan-Shetland, Dogger Bank and Southern Bight. Herring is a demersal spawner and eggs are deposited on stones and gravel. Egg diameter ranges between 0.9 and 1.5 mm. Development of the eggs is 1 to 3 weeks depending on temperature. The newly hatched larvae are pelagic and measure between 4 and 10 mm. Due to the different spawning groups, larvae can be found throughout the year. During the first 2 years of their life, herring remain in shallow water near the banks they were spawned.

The diet of herring varies considerably with time and place, but it is mostly a planktonic feeder. Copepods are the predominant prey during the early life stages. Older fish prey also on larvae of barnacles, mysids, eggs and larvae of decapods and amphipods and young fish, mostly juvenile sandeel.

Herring is an important prey fish and is preyed upon by a considerable number of predators, including red-throated diver *Gavia stellata* (frequent-staple; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (rare; Madsen, 1957), great crested grebe *Podiceps cristatus* (present-frequent; Doornbos, 1984, Madsen, 1957, Vlug, 1983), red-necked grebe *P. griseigena* (rare; Madsen, 1957), northern fulmar *Fulmarus glacialis* (present-frequent; Garthe *et al.*, 1996; Phillips *et al.*, 1999a), gannet *Sula bassana* (rare-staple; Garthe *et al.*, 1996; Martin, 1989; Zonfrillo pers. com. in Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Kieckbusch and Koop, 1996; Leopold and Winter, 1997; Steven, 1933; Warke and Day, 1995), shag *P. aristotelis* (rare-frequent; Barrett *et al.*, 1990; Carss, 1993; Harris and Wanless, 1991; Harris and Wanless, 1993; Lumsden and

Haddow, 1946; Mills, 1969a; Pearson, 1968; Swann *et al.*, 1991), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), smew *Mergus albellus* (staple; Madsen, 1957), red-breasted merganser *M. serrator* (staple; Madsen, 1957), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), common gull *Larus canus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), lesser black-backed gull *L. fuscus* (present-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Götmark, 1984; Pearson, 1968), herring gull *L. argentatus* (present-frequent; Garthe *et al.*, 1996; Nogales *et al.*, 1995), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (rare-common; Galbraith, 1983; Garthe *et al.*, 1996; Harris and Wanless, 1997; Lilliendahl and Solmundsson, 1997; Pearson, 1968; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (frequent-staple; Brenninkmeijer and Stienen, 1992; Essen *et al.*, 1998; Garthe and Kubetzki, 1998; Pearson, 1968; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (frequent-staple; Frank, 1992; Niedernostheide, 1996; Pearson, 1968; Stienen and Brenninkmeijer, 1992; Taylor, 1979; Wendeln *et al.*, 1994), arctic tern *S. paradisaea* (rare-frequent; Ewins, 1985; Hartwig *et al.*, 1990; Monaghan *et al.*, 1989; Niedernostheide, 1996; Pearson, 1968), common guillemot *Uria aalge* (rare-staple; Birkhead, 1976; Blake, 1983, 1984, Blake *et al.*, 1985; Camphuysen, 1990a; Camphuysen, 1995; Camphuysen and Keijl, 1991, 1994; Durinck *et al.*, 1991; Halley *et al.*, 1995; Harris and Wanless, 1986; Hedgren, 1976; Leopold and Camphuysen, 1992; Leopold *et al.*, 1992; Madsen, 1957; Mathews, 1983; Pearson, 1968; Reinert, 1976; Salomonsen, 1935; Swann *et al.*, 1991), Brünnich's guillemot *U. lomvia* (present-frequent; Belopol'skii, 1957; Ogi and Tsujita, 1977; Seligman and Willcox, 1940; Uspenski, 1958), razorbill *Alca torda* (rare-staple; Andersson *et al.*, 1974; Ashcroft, 1976; Belopol'skii, 1957; Bianki, 1967; Blake, 1983, 1984; Harris, 1970; Lloyd, 1976; Madsen, 1957), black guillemot *Cepphus grylle* (rare; Asbirk, 1979; Barrett and Anker-Nilssen, 1997; Bianki, 1967; Madsen, 1957; Petersen, 1981; Preston, 1968), Atlantic puffin *Fratercula arctica* (rare-staple; Anker-Nilssen and Lorentsen, 1990; Anker-Nilssen, 1987; Ashcroft, 1976, Barrett *et al.*, 1987; Belopol'skii, 1957; Bird and Bird, 1935; Blake, 1984; Corkhill, 1973; Harris and Hislop, 1978; Harris and Wanless, 1986; Lid, 1981; Lydersen *et al.*, 1989; Myrberget, 1962; Pearson, 1968; Tschanz, 1979), minke whale *Balaenoptera acutorostrata* (present; Hoelzel *et al.*, 1989), killerwhale

Orcinus orca (staple; Bloch and Lockyer, 1988, Similä *et al.*, 1996), common dolphin *Delphinus delphis* (frequent; Collet *et al.*, 1981), harbour porpoise *Phocoena phocoena* (rare-staple; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Bjørge *et al.*, 1991; Rae, 1965; Rae, 1973b; Recchia and Read, 1989; Smith and Gaskin, 1974), grey seal *Halichoerus grypus* (rare-frequent; Bjørge, 1995; Hammond *et al.*, 1994; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Prime and Hammond, 1990; Rae, 1973a; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-common; Behrends, 1982; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997, 1998; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Rae, 1973a; Sievers, 1989; Thompson *et al.*, 1991; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-common; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1990; Nilssen *et al.*, 1995; Ugland *et al.*, 1993) (see also Leopold *et al*., 2001), veined squid *Loligo forbesi*, cod *Gadus morhua*, tunas, poor cod *Trisopterus minutus*, herring *Clupea harengus*, whiting *Merlangius merlangus*, hake *Merluccius merluccius*, starry ray *Raja radiata*, thornback ray *Raja clavata*, salmon *Salmo salar*, spur-dog *Squalus acanthias*, grey gurnard *Eutrigla gurnardus*, swordfish *Xiphias gladius*, Arctic eelpout *Lycodes frigidus*, curled octopus *Eledone cirrhosa*, long rough dab *Hippoglossoides platessoides*, bullrout *Myoxocephalus scorpius*, long-tailed duck *Clangula hyemalis* and three-spined stickleback *Gasterosteus aculeatus* (Froese and Pauly, 2003). Natural mortality of herring is 0.45 (se 0.30–0.68). The resilience of the herring population is high; the minimum population doubling time is less than 15 months (rm=0.5–1.2; K=0.2–0.6; tm=2–5; tmax=25; Fec=20,000). Herring is not on the IUCN Red List.

Herring is commercially very important. In the North Sea, catches peaked in 1965 at 1,000,000 tonnes per year after which they declined until in the herring fishery was closed in 1977. In 1983 the fishery was reopened and yearly landings are now around 500,000 tonnes.

4.4 Anacanthini, Gadidae

Cod *Gadus morhua*

Cod is widely distributed in the North Sea and is an important predator in this ecosystem. It is classified as a benthopelagic species and found at depths down to 600 m (Cohen *et al.*, 1990). Smaller fish live close inshore (Wheeler, 1978). Cod is an omnivorous species, but the diet of larger fish is dominated by fish prey. The most important prey of cod in the North Sea are haddock and whiting, each making up about 9% of the cod diet (Table 3.14). Other important prey are Brachyrhyncha (e.g. *Carcinus maenas* and related crab species), Norway pout, sandeels and dab (Greenstreet, 1996).

Cod has been found in the stomachs of various predators including red-throated diver *Gavia stellata* (frequent-staple; Durinck *et al.*, 1994; Madsen, 1957), black-throated diver *G. arctica* (common; Madsen, 1957), great northern diver *G. immer* (common; Madsen, 1957), great crested grebe *Podiceps cristatus* (rare; Doornbos, 1984), red-necked grebe *P. griseigena* (frequent-common; Madsen, 1957), northern fulmar *Fulmarus glacialis* (frequent; Erikstad, 1990; Froese and Pauly, 2003; Garthe *et al.*, 1996; Harrison, 1984; Phillips *et al.*, 1999a), storm petrel *Hydrobates pelagicus* (rare-frequent; Dée and Hémery, 1998), fork-tailed storm petrel *Oceanodroma furcata* (frequent; Harrison; 1984), gannet *Sula bassana* (rare-frequent; Garthe *et al.*, 1996; Martin, 1989; Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1998; Buckens and Raeijmaekers, 1992; Härkönen, 1988; Kieckbusch and Koop, 1996; Nehls and Gienapp, 1997; Paillard, 1985; Pearson, 1968; Reinhold, 1996; Van Damme, 1994), shag *P. aristotelis* (rare-staple; Barrett *et al.*, 1990; Carss, 1993; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Mills, 1969a; Pearson, 1968; Swann *et al.*, 1991), grey heron *Ardea cinerea* (present-frequent; Carss and Marquiss, 1996), red-breasted merganser *Mergus serrator* (rare; Madsen, 1957), goosander *Mergus merganser* (frequent-staple; Madsen, 1957), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), mew gull *Larus canus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), lesser black-backed gull *L. fuscus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Pearson, 1968), herring gull *L. argentatus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999;

Götmark, 1984; Löhmer and Vauk, 1970; Nogales *et al.*, 1995), glaucous gull *L. hyperboreus* (frequent; Erikstad, 1990), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (rare-staple; Erikstad, 1990, Garthe *et al.*, 1996; Harrison, 1984; Pearson, 1968; Prüter, 1989; Swann *et al.*, 1991; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (rare-staple; Brenninkmeijer and Stienen, 1992; Fuchs, 1977; Pearson, 1968; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare-frequent; Frank, 1992; Niedernostheide, 1996; Pearson, 1968, Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Ewins, 1985; Pearson, 1968), common guillemot *Uria aalge* (rare-staple; Anker-Nilssen and Nygård, 1987; Anon., 1980; Belopol'skii, 1957; Blake, 1983; Blake *et al.*, 1985; Durinck *et al.*, 1991; Halley *et al.*, 1995; Hatchwell, 1991; Hedgren, 1976; Lyngs and Durinck, 1998; Madsen, 1957; Pearson, 1968; Swann *et al.*, 1991), Brünnich's guillemot *U. lomvia* (staple; Erikstad, 1990), razorbill *Alca torda* (frequent; Belopol'skii, 1957; Madsen, 1957), black guillemot *Cepphus grylle* (rare-frequent; Barrett and Anker-Nilssen, 1997; Madsen, 1957; Petersen, 1981; Slater and Slater, 1972), puffin *Fratercula arctica* (rare-frequent; Anker-Nilssen, 1987; Barrett *et al.*, 1987; Belopol'skii, 1957; Corkhill, 1973; Harris and Hislop, 1978; Harris and Wanless, 1986; Hartley and Fisher, 1936; Lid, 1981; Myrberget, 1962; Tschanz, 1979), cephalopods (*Eledone cirrhosa*), fish (*Gadus morhua*, *Merlangius merlangus*, *Pollachius virens*, *Trachurus trachurus*, *Molva molva*, *Raja radiata*, *Squalus acanthias*, *Hippoglossoides platessoides*, *Anarhichas lupus*, *Chelidonichthys gurnardus*), seals (*Phoca groenlandica*, *P. vitulina*), cetaceans (*Balaenoptera acutorostrata*), while cod eggs and larvae have been found in the diet of herring and sprat (Greenstreet, 1996; Froese and Pauly, 2003).

The natural mortality, initially high (2.7 for 0-age group) decreases as the fish grow, and stabilises at about 0.2 in age groups 4+ (ICES, 2003c).

Cod are targeted largely by otter trawl and gill net vessels. The fishery is year-round. Spawning stock biomass of cod in the North Sea, Skagerrak/Kattegat and eastern Channel has varied between 30,000 and 80,000 tonnes from 1990 onwards. The annual landings (in the North Sea) have varied from 41,000 to 122,000 tonnes. Fishing mortality has been high (0.7–1.2). The stock is considered as being outside safe biological limits, which resulted in the implementation of a recovery plan in 2001 (ICES, 2003c). The IUCN Red List qualifies the species as 'vulnerable' (Hilton-Taylor, 2000).

Because of its high abundance and its role in the food web, as well as because of the intensive fishing, the species is being evaluated as ecologically and economically important.

Haddock *Melanogrammus aeglefinus*

Haddock is one of the most important fish in the North Sea. By weight it is the most abundant demersal species landed (ICES, 2003c). It lives at depths of 10–450 m and feeds mainly on small bottom-living organisms (Cohen *et al.*, 1990). The most important prey of haddock in the North Sea are echinoderms (12% of diet), long rough dab (11%), pearlsides (11%), gobies (11%), annelids (10%) and euphausians (9%). Other prey include sandeels, Norway pout and bivalves (Greenstreet, 1996).

Haddock is preyed on by northern fulmar *Fulmarus glacialis* (rare-frequent; Fowler and Dye, 1987; Froese and Pauly, 2003; Garthe *et al.*, 1996; Phillips *et al.*, 1999a; Thompson *et al.*, 1995), gannet *Sula bassana* (present-frequent; Garthe *et al.*, 1996; Martin, 1989), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1998; Härkönen, 1988; Warke and Day, 1995), great skua *Stercorarius skua* (frequent-common; Andersson, 1976; Albon *et al.*, 1976; Bayes *et al.*, 1964; Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Booth, 1976; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979; Furness, 1976b; Garthe *et al.*, 1996; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Perry, 1948; Pennie, 1948; Phillips *et al.*, 1999b; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), mew gull *Larus canus* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *L. fuscus* (rare-frequent; Garthe *et al.*, 1996, Garthe *et al.*, 1999), herring gull *L. argentatus* (rare-frequent; Garthe *et al.*, 1996; Löhmer and Vauk, 1970), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (rare-frequent; Garthe *et al.*, 1996; Prüter, 1989; Vauk and Jokele, 1975), common tern *Sterna hirundo* (frequent; Stienen and Brenninkmeijer, 1992), common guillemot *Uria aalge* (rare; Blake *et al.*, 1985; Durinck *et al.*, 1991), black guillemot *Cepphus grylle* (rare; Barrett and Anker-Nilssen, 1997), puffin *Fratercula arctica* (rare-staple; Anker-Nilssen, 1987, Anker-Nilssen and Lorentsen, 1990; Barrett *et al.*, 1987; Harris and Hislop, 1978; Martin, 1989), fish (*Pollachius virens*, *Gadus morhua*, *Merlangius merlangus*, *Trachurus trachurus*, *Melanogrammus aeglefinus*, *Amblyraja radiata*, *Hippoglossoides platessoides*, *Chelidonichthys gurnardus*), seals (*Phoca groenlandica*), cetaceans (*Balaenoptera acutorostrata*) (Greenstreet, 1996; Froese and Pauly, 2003; see also Leopold *et al.*, 2001).

The natural mortality declines from 2.1 in 0-age group to about 0.2 in age groups 5+ (ICES, 2003c).

In the North Sea, haddock are caught in the mixed demersal fishery by trawlers and seiners. Smaller quantities are taken by trawlers fishing for *Nephrops norvegicus*. By-catches of haddock are also taken in industrial fisheries (ICES, 2003c). Historically, the stock size of haddock has shown large variation due to the occasional occurrence of very strong year classes. Spawning stock biomass in the North Sea and Skagerrak/Kattegat has varied since 1990 from 81,000 to 347,000 tonnes. Fishing mortality has remained high (0.8–1.2). The North Sea haddock stock is considered to be outside safe biological limits (ICES, 2003c). The IUCN Red List qualifies the species as ‘vulnerable’ (Hilton-Taylor, 2000).

Because of its high abundance, its role in the food web (important prey and an important predator of bottom fauna), and commercial value, the species is evaluated as ecologically and economically important.

Whiting *Merlangius merlangus*

Whiting is an extremely common benthopelagic fish, living in shallow inshore waters, at depths of 10–200 m (Cohen *et al.*, 1990), but rare in waters deeper than 100 m. It is found in the northeastern Atlantic, from the Mediterranean to the Barents Sea and Iceland. It is found throughout the North Sea in high numbers. Young fish are found close inshore. Whiting is mostly found over mud and gravel bottoms.

Whiting can grow up to 70 cm and 20 years, but in the North Sea specimens over 40 cm are rare. The von Bertalanffy growth parameter K is 0.1 to 0.16 per year. Maturity is reached at 2 years and a length of around 30 cm.

Spawning takes place from March to May, in the southern part of their distribution spawning starts as early as January. The eggs are shed in numerous batches over a long period. The pelagic eggs are 0.97 to 1.32 mm in diameter. Hatching takes place after 10 days. The larvae measure 3.2 to 3.5 mm at hatching and like the eggs, they are pelagic.

Adult whiting feed on small fish and young whiting eat more crustaceans than fish. The larvae prey on planktonic crustaceans, mostly copepods. The diet of whiting in the North Sea is dominated by sandeels (27%) (Table 3.14). Other important prey are euphausians, sprat and Norway pout, each of them making up 9% of the diet, and also herring, haddock, crangonids, annelids and conspecifics (Greenstreet, 1996).

Whiting is preyed on by fish (scad *Trachurus trachurus*, cod *Gadus morhua*, whiting *Merlangius merlangus*, saithe *Pollachius virens*, haddock *Melanogrammus aeglefinus*, painted ray *Raja microocellata*, thornback ray *Raja clavata*, starry ray *Raja radiata*, cuckoo ray *Raja naevus,* hake *Merluccius merluccius*, spur-dog *Squalus acanthias*, grey gurnard *Eutrigla gurnardus*), harbour porpoise *Phocoena phocoena* (rare-staple; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Bjørge *et al.*, 1991; Rae, 1965; Rae, 1973b), grey seal *Halichoerus grypus* (rare-staple; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987; Prime and Hammond, 1990; Rae, 1973a; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-staple; Behrends, 1982; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997, 1998; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Rae, 1973a; Sievers, 1989; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-frequent; Nilssen *et al.*, 1990; Nilssen *et al.*, 1995), dolphins (*Delphinus delphis* (frequent; Collet *et al.*, 1981), bottlenose dolphin *Tursiops truncates*) and seabirds: red-throated diver *Gavia stellata* (frequent; Durinck *et al.*, 1994; Leopold, 1997), great crested grebe *Podiceps cristatus* (rare; Doornbos, 1984), northern fulmar *Fulmarus glacialis* (frequent; Garthe *et al.*, 1996; Phillips *et al.*, 1999a; Thompson *et al.*, 1995), gannet *Sula bassana* (present-frequent; Garthe *et al.*, 1996; Martin, 1989; Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994, Leopold *et al.*, 1998; Reinhold, 1996), shag *P. aristotelis* (rare-frequent; Harris and Wanless, 1993), great skua *Stercorarius skua* (frequent-common; Albon *et al.*, 1976; Andersson, 1976; Bayes *et al.*, 1964; Booth, 1976, Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979; Furness, 1976b; Garthe *et al.*, 1996; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Pennie, 1948; Perry, 1948; Phillips *et al.*, 1999b; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), common gull *Larus canus* (rare-frequent; Garthe *et al.*, 1996; Kubetzki, 1997; Kubetzki *et al.*, 1999), lesser black-backed gull *L. fuscus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996; Löhmer and Vauk, 1970; Nogales *et al.*, 1995), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), kittiwake *Rissa tridactyla* (rare-common; Garthe *et al.*, 1996; Harris and Wanless, 1997; Prüter, 1989; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (rare; Brenninkmeijer and Stienen, 1992; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare-frequent; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), common guillemot *Uria aalge* (rare-common; Blake, 1983, 1984; Blake *et al.*, 1985; Camphuysen, 1990a; Camphuysen and Keijl, 1991, 1994; Durinck *et al.*, 1991; Geertsma, 1992; Halley *et al.*, 1995; Leopold and Camphuysen, 1992), razorbill *Alca torda* (frequent; Blake, 1984), Atlantic puffin *Fratercula arctica* (rare-staple; Anker-Nilssen, 1987; Barrett *et al.*, 1987; Harris and Hislop, 1978; Harris and Wanless, 1986; Martin, 1989) (Greenstreet, 1996; Froese and Pauly, 2003, see also Leopold *et al.*, 2001).

Natural mortality of whiting is 0.36 (se 0.24–0.55). Whiting in the North Sea is mainly taken in the mixed demersal fishery with trawlers and seiners. Smaller quantities are taken by trawlers targeting *Nephrops* and by beam trawlers targeting flatfish (ICES, 2003c). Spawning stock biomass of whiting in the North Sea and eastern Channel has shown smaller variation since 1990 (compared to other commercially fished gadids). It has ranged between 145,000 and 279,000 tonnes. Fishing mortality have shown a decreasing tendency from 0.9 to 0.4. The resilience of the whiting population is medium; minimum population doubling time is 1.4–4.4 years (rm=1.1–1.6; tm=2–4; tmax=20; Fec=100,000). Whiting is not on the IUCN Red list.

Bib *Trisopterus luscus*

The bib is a common fish that can be found in the shallow waters of the eastern Atlantic, from the British Isles and Skagerrak to the West African coast. In the North Sea, it is found along the coasts, from the Skagerrak to the south and around the British Isles. Bib is a demersal fish that is mostly found over sandy areas, in depths of 30 to 100 m. Juveniles are found in the shallower areas where they form schools.

Bib can grow up to a maximum of 46 cm and age 5 years, but is most common from 15 to 25 cm. Females growing to a larger size than males. Bib is a fast growing, but relatively short-lived species. The von Bertalanffy growth parameter K is 0.2 to 0.4 per year. Maturity is reached at age 2 and length 18 to 25 cm.

Spawning period is from December to August and takes place in depths from 50 to 70 m. The eggs are pelagic and have a diameter of 0.9 to 1.23 mm. The newly hatched larvae are pelagic and have a length of 3 mm. They can be found from December till August. The larvae are probably passively transported into bays and estuaries where they stay during their early life.

The diet of bib consists of crustaceans and fish. Juveniles feed on shrimp, swimming crabs and polychaetes.

Predators of bib are northern fulmar *Fulmarus glacialis* (frequent; Thompson *et al.*, 1995), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Gremillet and Argentin, 1998; Leopold *et al.*, 1998), shag *P. aristotelis* (rare-frequent; Gremillet and Argentin, 1998; Velando and Freire, 1999), lesser black-backed gull *Larus fuscus* (rare; Garthe *et al.*, 1999), black-legged kittiwake *Rissa tridactyla* (rare; Prüter, 1989; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (rare; Brenninkmeijer and Stienen, 1992), common guillemot *Uria aalge* (rare-frequent; Blake, 1983, Blake *et al.*, 1985; Camphuysen and Keijl, 1991, 1994; Leopold and Camphuysen, 1992), common dolphin *Delphinus delphis* (frequent; Collet *et al.*, 1981), grey seal *Halichoerus grypus* (rare-frequent; Prime and Hammond, 1987; Rae, 1973a), harbour seal *Phoca vitulina* (rare-frequent; Behrends, 1982; Hall *et* *al.*, 1998; Krause, 1999; Tollit and Thompson, 1996) (see also Leopold *et al*. 2001), thornback ray *Raja clavata* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of bib is 0.87 (se 0.58–1.32). The bib population has a medium resilience; the minimum population doubling time is 1.4–4.4 years (K=0.2–0.4; tm=1–2; tmax=4; Fec=200,000). Bib is not on the IUCN Red list. Bib is of marginal economic interest.

Norway pout *Trisopterus esmarkii*

Norway pout is a common fish that can be found in the northeastern Atlantic, from the English Channel to the Barents Sea and around the Faroes and Iceland. In the North Sea, it is found in the central and northern part, as well as in the Skaggerak and Kattegat. It is a benthopelagic that is mostly found offshore in depths of 40 to 450 m, but is usually found between 80 and 200 m. It can sometimes also be found in the deeper Scandinavian inshore waters.

Norway pout is a small, short-lived species that can grow to a maximum of 35 cm and age 5 years. Fish larger than 20 cm and older than 3 years are rare. Females grow faster and reach larger sizes than males. The von Bertalanffy growth parameter K is 0.36 per year. Maturity is usually reached at the age of two and size 15 cm, but some already mature at the age of 1 year.

Norway pout spawns from January to July, with the most intense spawning at the beginning of the period. Spawning takes place at the deep continental shelf spawning grounds. The pelagic eggs measure 1.0 to 1.19 mm in diameter. The newly hatched larvae are pelagic and have a length of 3.2 mm.

Norway pout is an active hyperbenthic predator that feeds mainly during daylight hours. The feeding intensity decreases during the spawning season. The diet of Norway pout consists of crustaceans, mysids, copepods, euphausiids, natantians, amphipods, and small fish, mostly Gobiidae. The juvenile diet consists of copepods and appendicularians.

Known predators of Norway pout are northern fulmar *Fulmarus glacialis* (frequent; Fowler and Dye, 1987; Garthe *et al.*, 1996; Thompson *et al.*, 1995), gannet *Sula bassana* (frequent; Garthe *et al.*, 1996), shag *Phalacrocorax aristotelis* (rare-frequent; Harris and Wanless, 1993; Velando and Freire, 1999), great skua *Stercorarius skua* (frequent-common; Albon *et al.*, 1976; Andersson, 1976; Bayes *et al.*, 1964; Booth, 1976; Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979; Furness, 1976b; Garthe *et al.*, 1996; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Pennie, 1948; Perry, 1948; Phillips *et al.*, 1999b; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), common gull *Larus canus* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *L. fuscus* (frequent; Garthe *et al.*, 1996), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (frequent; Garthe *et al.*, 1996), common guillemot *Uria aalge* (rare-common; Blake, 1983; Blake *et al.*, 1985, Halley *et al.*, 1995), razorbill *Alca torda* (frequent; Blake, 1983), Atlantic puffin *Fratercula arctica* (rare; Anker-Nilssen, 1987; Harris and Hislop, 1978; Martin, 1989), common dolphin *Delphinus delphis* (frequent; Collet *et al.*, 1981), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Bjørge *et al.*, 1991; Rae, 1965, 1973b), grey seal *Halichoerus grypus* (rare-common; Bjørge, 1995; Hammond *et al.*, 1994; Rae, 1973a), harbour seal *Phoca vitulina* (rare-common; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997; Des Clers and Prime, 1996; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Rae, 1973a), harp seal *P. groenlandica* (rare-common; Nilssen *et al.*, 1990; Ugland *et al.*, 1993) (see also Leopold *et al.*, 2001), bottlenose dolphin *Tursiops truncates*, cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, pollack *Pollachius pollachius*, saithe *P. virens*, bib *Trisopterus luscus*, blue ling *Molva dipterygia*, ling *M. molva*, hake *Merluccius merluccius*, Cuckoo ray *Raja naevus* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of Norway pout is 0.55 (se 0.36–0.83). The resilience of the Norway pout population is medium; the minimum population doubling time is 1.4–4.4 years (K=0.36; tm=1–2; tmax=5; Fec=27,000). Norway pout is not on the IUCN Red list.

Norway pout is not important as a food fish because of its size, but it is important for the industrial fishery of the northern European countries. North Sea catches peaked in the 1970s at 750,000 tonnes per year, but declined to 100,000 tonnes per year in the 1980s.

Poor cod *Trisopterus minutes*

The poor cod is a common gadoid that can be found in the eastern Atlantic from Trondheim and Faroes to Morocco and the Mediterranean. Ii is common throughout the North Sea. The poor cod is a demersal schooling fish. It can be found in small schools in depths up to 400 m, but is more common in depths from 15 to 250 m. Juveniles live closer to the shore than adults.

Maximum length of poor cod is 40 cm and maximum age is 6 years. Specimens longer than 25 cm and older than 3 years are rare. Growth is fast; the von Bertalanffy growth parameter K is 0.18 to 0.51 per year. Maturity is reached at length 15 cm and age 2.

Spawning period is from February to April, and takes place at depths of 50 to 100 m. The pelagic eggs are small, 1 mm in diameter. The newly hatched larvae are 2 to 2.5 mm long.

Poor cod is an unspecialised bottom-living fish. The diet consists of larger decapods, mysids, *Portunus* spp., *Galathea* spp., *Nephrops* spp., *Crangon* spp., a considerable amount of fish and some polychaete worms. The pelagic larvae feed on planktonic crustaceans, copepods, larval decapods and amphipods.

Known predators of poor cod are red-necked grebe *Podiceps griseigena* (rare; Madsen, 1957), northern fulmar *Fulmarus glacialis* (present-frequent; Leopold and Camphuysen, 1992; Phillips *et al.*, 1999a), storm petrel *Hydrobates pelagicus* (frequent; Dée and Hémery, 1998), cormorant *Phalacrocorax carbo* (frequent; Van Damme, 1994), shag *Phalacrocorax aristotelis* (rare-frequent; Harris and Wanless, 1993; Mills, 1969a; Steven, 1933; Velando and Freire, 1999), great skua *Stercorarius skua* (frequent; Phillips *et al.*, 1999b), herring gull *Larus argentatus* (frequent; Löhmer and Vauk, 1970), black-legged kittiwake *Rissa tridactyla* (rare-frequent; Prüter, 1989; Vauk and Jokele, 1975), common guillemot *Uria aalge* (rare-common; Blake, 1983, 1984; Blake *et al.*, 1985; Halley *et al.*, 1995; Leopold and Camphuysen, 1992), razorbill *Alca torda* (rare-frequent; Blake, 1983, 1984; Madsen, 1957), black guillemot *Cepphus grylle* (present; Gates, 1998), common dolphin *Delphinus delphis* (frequent; Collet *et al.*, 1981), harbour porpoise *Phocoena phocoena* (rare-common; Aarefjord *et al.*, 1995; Bjørge *et al.*, 1991), grey seal *Halichoerus grypus* (rare-frequent; Pierce *et al.*, 1990; Prime and Hammond, 1987, 1990; Rae, 1973a), harbour seal *Phoca vitulina* (rare-frequent; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997; Des Clers and Prime, 1996, Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Pierce *et al.*, 1990; Tollit and Thompson, 1996) (see also Leopold *et al*., 2001), whiting *Merlangius merlangus*, bib *Trisopterus luscus*, poor cod *T. minutus*, hake *Merluccius merluccius*, harp seal *Phoca groenlandica*, grey gurnard *Eutrigla gurnardus* and cod *Gadus morhua* (Froese and Pauly, 2003).

Natural mortality of poor cod is 0.35 (se 0.23–0.53). The resilience of the poor cod population is medium; the minimum population doubling time 1.4–4.4 years (K=0.18; tm=1; tmax=6). Poor cod is not on the IUCN Red list and is of no economic importance.

Saithe *Pollachius virens*

Saithe is a common species that can be found in the eastern Atlantic, from the Bay of Biscay to the Barents Sea and around Iceland, and the western Atlantic. In the North Sea it is found in the northern part throughout the year, in winter some specimens can also be found in the Skagerrak or Kattegat. Saithe sometimes form large schools and can be found in depths up to 300 m. Saithe is benthopelagic and displays daily vertical migrations, from close to the bottom to high up in the water column. Juveniles are found in coastal rocky areas.

Saithe can grow to a maximum size of 130 cm and age of 25 years. However, in the North Sea, specimens over 50 cm are rare. Growth of saithe is fast; the von Bertalanffy growth parameter K is 0.07 to 0.17 per year. Maturity is reached at age 5 or 6 years at a length of around 60 cm.

Spawning takes place from January to April in the water column between 100 and 200 m depth. The eggs are pelagic and measure 1.03 to 1.22 mm in diameter. The eggs take 9 days for development. The newly hatched larvae are pelagic and measure 3.4 to 4.2 mm. The juveniles spent the first two years of live in coastal rocky areas. In spring the juveniles recruit to the stock, but for the next two years they can be found mainly higher up in the water column.

Saithe is an epibenthic predator and the diet consists of fish, herring, sandeel, Norway pout, haddock, cod and blue whiting. Larvae feed on planktonic crustaceans, mainly copepods. The immature fish feed on benthic crustaceans and some fish.

Saithe is preyed upon by northern fulmar *Fulmarus glacialis* (rare-frequent; Camphuysen, 1990b; Fowler and Dye, 1987; Garthe *et al.*, 1996; Lydersen *et al.*, 1989), gannet *Sula bassana* (rare-frequent; Garthe *et al.*, 1996; Martin, 1989; Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Okill *et al.*, 1992), shag *P. aristotelis* (rare-staple; Barrett, 1991; Carss, 1993; Harris and Wanless, 1993; Mills, 1969a), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), common gull *Larus canus* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *L. fuscus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Götmark, 1984), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), kittiwake *Rissa tridactyla* (rare-frequent; Garthe *et al.*, 1996; Lydersen *et al.*, 1989; Prüter, 1989; Vauk and Jokele, 1975), common tern *Sterna hirundo* (frequent-staple; Stienen and Brenninkmeijer, 1992; Uttley *et al.*, 1989), arctic tern *S. paradisaea* (rare-frequent; Ewins, 1985; Monaghan *et al.*, 1989), common guillemot *Uria aalge* (rare-common; Anker-Nilssen and Nygård, 1987; Blake, 1983, 1984; Blake *et al.*, 1985; Harris and Wanless, 1986), Brünnich's guillemot *U. lomvia* (frequent; Lydersen *et al.*, 1989), black guillemot *Ceppus grylle* (rare; Lydersen *et al.*, 1989), Atlantic puffin *Fratercula arctica* (rare-staple; Anker-Nilssen, 1987; Anker-Nilssen and Lorentsen, 1990; Barrett *et al.*, 1987; Harris and Hislop, 1978; Harris and Wanless, 1986; Lid, 1981; Lydersen *et al.*, 1989; Martin, 1989; Myrberget, 1962; Tschanz, 1979), killerwhale *Orcinus orca* (rare; Similä *et al.*, 1996), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Bjørge *et al.*, 1991; Rae, 1973b; Recchia and Read, 1989; Smith and Gaskin, 1974), grey seal *Halichoerus grypus* (rare-frequent; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994; Rae, 1973a; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-common; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997, 1998; Härkönen, 1987; Härkönen and Heide-Jørgensen, 1991; Rae, 1973a; Tollit and Thompson, 1996), ringed seal *P. hispida* (frequent; Lydersen *et al.*, 1989), harp seal *P. groenlandica* (rare-staple; Nilssen *et al.*, 1990, Nilssen *et al.*, 1995; Ugland *et al.*, 1993) (see also Leopold *et al.*, 2001), sea lamprey *Petromyzon marinus*, minke whale *Balaenoptera* *acutorostrata*, bottlenose dolphin *Tursiops truncates*, ling *Molva molva*, sperm whale *Physeter catodon* and swordfish *Xiphias gladius* (Froese and Pauly, 2003).

Natural mortality of saithe is 0.24 (se 0.16–0.36). The population resilience of saithe is medium; minimum population doubling time 1.4–4.4 years (rm=0.55–0.87; K=0.07–0.17; tm=2–10; tmax=25; Fec=220,000). Saithe is not on the IUCN Red list.

Saithe is an economic important fish species in the northern countries. Catches peaked in the 1970s at 300,000 tonnes per year. The yearly landings decreased to 100,000 tonnes in 1990.

Four-bearded rockling *Enchelyopus cimbrius*

The four-bearded rockling is a deep water, bottom-living species. It is a common fish that is found in the western and eastern Atlantic, from the Barents Sea to the northern Bay of Biscay. In the North Sea it is the most common of the rocklings and is found in the deeper areas. It is found in depths ranging from 20 to 650 m on sandy or muddy substrates. It is reported to make an onshore migration in autumn.

Maximum reported length and age are 41 cm and 9 years. The von Bertalanffy growth parameter K is 0.2 to 0.25 per year. Maturity is reached at 3 years of age and a size of 15 to 25 cm.

Spawning takes mainly place in summer, but the seasons may be prolonged from May to October. The pelagic eggs have a diameter of 0.66 to 0.98 mm. The newly hatched larvae have a length of 1.6 to 2.4 mm and are found as plankton in deep water.

The diet of four-bearded rockling consists of crustaceans (amphipods, shrimps and mysids), polychaetes, molluscs and fish. The larvae feed on planktonic crustaceans such as copepods.

The larvae and early juvenile stages are heavily preyed upon by mackerel *Scomber scombrus* and bass *Dicentrarchus labrax* (Knijn *et al*., 1993). Other predators of four-bearded rockling are lesser black-backed gull *Larus fuscus* (present; Götmark, 1984), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987), harbour porpoise *Phocoena phocoena* (frequent; Bjørge *et al.*, 1991), grey seal *Halichoerus grypus* (rare-frequent: Pierce *et al.*, 1990), harbour seal *Phoca vitulina* (rare-frequent; Bjørge *et al.*, 1993; Des Clers and Prime, 1996;

Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Tollit and Thompson, 1996) (see also Leopold *et al*., 2001), poor cod *Trisopterus minutus*, bib *T. luscus*, cod *Gadus morhua* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of four-bearded rockling is 0.35 (se 0.23–0.54). The population resilience is medium; the minimum population doubling time is 1.4–4.4 years (K=0.20–0.25; tm=3; tmax=9). Four-bearded rockling is not on the IUCN Red list and has no economic value.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.5 Red mullet (Percomorphi, Mullidae)

Red mullet *Mullus surmuletus*

Red mullet is a vagrant in the North Sea. It is distributed in the eastern Atlantic, from western Norway to Senegal and the Canary Islands and the Mediterranean. Small red mullets make a migration into the Channel and southern North Sea in summer. It is found in depths of 5 to 60 m, mostly over rough grounds but can also be found in shallow waters over soft bottoms. In winter, red mullet moves to the deeper offshore waters.

Red mullet can grow to a length of 40 cm and age of 10 years. Females grow faster than males. The von Bertalanffy growth parameter K is 0.1 to 0.5 per year. Maturity is reached at age 1 to 2 and length 14 to 22 cm.

In the Channel, spawning takes place from May to July. The pelagic eggs have a diameter of 0.81 to 0.93 mm. Eggs are transported passively and can be found in the North Sea. Larvae hatch at a length of 2.83 mm and can be found in the plankton from May to August. The larvae drift to the shore were they arrive in September, having grown to 5 cm and assume a bottom-dwelling life.

Red mullet has a varied diet, which consists of benthic organisms, crustaceans, shrimps and amphipods, polychaetes, molluscs and fish. Larvae feed on larval crustaceans and copepods.

The only reported predators are all species that do not live in the North Sea. However, it has been reported that northern fulmar *Fulmarus glacialis* and black-legged kittiwake *Rissa tridactyla* take undersized red mullet when they are discarded as by-catch (Camphuysen *et al.*, 1995) (see also Leopold *et al*., 2001).

Natural mortality of red mullet is 0.91 (se 0.60–1.38). The population resilience of red mullet is medium; the minimum population doubling time is 1.4–4.4 years (K=0.1–0.4; tm=2; tmax=10). Red mullet is not on the IUCN Red list.

The red mullet is a much-valued food fish and extensively exploited in the southern part of its range. As it is becoming more common in the North Sea, its economic importance is increasing.

4.6 Sandeels (Ammodytidae)

Sandeel *Ammodytes tobianus*

The sandeel is an extremely common fish. It can be found in the northeastern Atlantic coastal zone, from Murmansk and Iceland to Spain and in the Mediterranean. In the North Sea it is found in the coastal zones. Sandeel is found in inshore waters but can also be found offshore. It can be found from the mid-tide level of sandy shores to a depth of 30 m. Sandeel is a pelagic schooling fish that lies buried in the sand at night and emerges during daylight to hunt. It is believed that sandeel hibernate in the sand in winter, but others hypothesize that the schools are more compact in winter and that spawning behaviour might negatively influence catchability (Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999, Froese and Pauly, 2003).

Sandeel can grow up to 20 cm; maximum reported age is 7 years. The von Bertalanffy growth parameter K is 0.45 to 0.77 per year. Maturity is reached at age 2 to 3 years and lengths of 11 to 15 cm.

In the Baltic two spawning periods, in spring and autumn, are recognised. In the northern part of the distribution, there is only one spawning period from February till April. The eggs are small, 0.72 to 0.97 mm diameter. The eggs are deposited in the sand and stick to the sand grains. The newly hatched larvae are 4 to 6 mm long. They are pelagic but can be found in both high up en deeper in the water column.

Sandeels feed mostly on planktonic prey, copepods and crustacean larvae, but polychaete worms, amphipods and euphausiids are also taken. The larvae feed on diatoms.

Sandeel is a major prey for many fish predators and therefore has an important part in the North Sea ecosystem. Sandeel is preyed upon by red-throated diver *Gavia stellata* (rare-frequent; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (rare-staple; Madsen, 1957), great crested grebe *Podiceps cristatus* (rare; Madsen, 1957), red-necked grebe *P. griseigena* (rare-frequent; Byrkjedal *et al.*, 1997; Madsen, 1957), northern fulmar *Fulmarus glacialis* (frequent-staple; Bourne, 1982; Phillips *et al.*, 1999a), Manx shearwater *Puffinus puffinus* (frequent; Brooke, 1990), storm petrel *Hydrobates pelagicus* (rare; Dée and Hémery, 1998), gannet *Sula bassana* (frequent-staple; Zonfrillo pers. com. in Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn *et al.*, 1994; Kieckbusch, 1993; Kirby *et al.*, 1996; Leopold and Van Damme, in prep., Leopold *et al.*, 1998; Mills, 1969b; Okill *et al.*, 1992; Paillard, 1985; Pearson, 1968), shag *P. aristotelis* (rare-staple; Barrett, 1991; Barrett *et al.*, 1990; Carss, 1993; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Mills, 1969a; Pearson, 1968; Steven, 1933; Swann *et al.*, 1991; Velando and Freire, 1999; Wanless *et al.*, 1993), white-winged scoter *Melanitta fusca* (rare; Byrkjedal *et al.*, 1997), red-breasted merganser *Mergus serrator* (frequent-staple; Madsen, 1957), goosander *M. merganser* (rare; Madsen, 1957), parasitic jaeger *Stercorarius parasiticus* (present; Bourne, 1982), great skua *Stercorarius skua* (staple; Albon *et al.*, 1976; Andersson, 1976; Bayes *et al.*, 1964; Booth, 1976; Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979; Furness, 1976b; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Pennie, 1948; Perry, 1948; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), common gull *Larus canus* (rare; Garthe *et al.*, 1999), lesser black-backed gull *L. fuscus* (present-staple; Götmark, 1984; Pearson, 1968), great black-backed gull *L. marinus* (frequent; Götmark, 1984), black-legged kittiwake *Rissa tridactyla* (frequent-staple; Bourne, 1982; Pearson, 1968; Swann *et al.*, 1991), sandwich tern *Sterna sandvicensis* (frequent-staple; Brenninkmeijer and Stienen, 1992; Essen *et al.*, 1998; Fuchs, 1977; Garthe and Kubetzki, 1998; Pearson, 1968; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare-staple; Frank, 1992; Niedernostheide, 1996; Pearson, 1968;

Stienen and Brenninkmeijer, 1992; Taylor, 1979; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (frequent-staple; Ewins, 1985; Hartwig *et al.*, 1990; Niedernostheide, 1996; Pearson, 1968), little tern *S. albifrons* (staple; Norman, 1992), common guillemot *Uria aalge* (rare-staple; Anon., 1980; Belopol'skii, 1957; Birkhead, 1976; Blake, 1983, 1984; Blake *et al.*, 1985; Bourne, 1982; Camphuysen, 1995; Camphuysen and Keijl, 1991; Camphuysen and Keijl, 1994; Durinck *et al.*, 1991; Halley *et al.*, 1995; Harris and Wanless, 1986; Hatchwell, 1991; Hedgren, 1976; Leopold and Camphuysen, 1992; Leopold *et al.*, 1992; Lyngs and Durinck, 1998; Salomonsen, 1935; Pearson, 1968; Reinert, 1976; Slater, 1980; Swann *et al.*, 1991; Uspenski, 1958), Brünnich's guillemot *Uria lomvia* (frequent; Uspenski, 1958), razorbill *Alca torda* (rare-staple; Andersson *et al.*, 1974; Ashcroft, 1976; Beja, 1989; Belopol'skii, 1957; Bianki, 1967, Blake, 1983, 1984; Bourne, 1982; Harris, 1970; Leopold and Camphuysen, 1992; Lloyd, 1976; Swann *et al.*, 1991), black guillemot *Cepphus grylle* (rare-staple; Asbirk, 1979; Bergman, 1971, 1978; Bianki, 1967; Ewins, 1987; Petersen, 1981; Slater and Slater, 1972), little auk *Alle alle* (frequent; Blake, 1983), Atlantic puffin *Fratercula arctica* (rare-staple; Ashcroft, 1976; Belopol'skii, 1957; Blake, 1984; Bourne, 1982; Corkhill, 1973; Evans, 1975; Harris, 1970, Harris and Wanless, 1986; Lid, 1981; Myrberget, 1962; Pearson, 1968; Tschanz, 1979), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Bjørge *et al.*, 1991, Rae, 1965, 1973b), grey seal *Halichoerus grypus* (rare-staple; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994, Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987, 1990; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-staple; Bjørge *et al.*, 1993; Brown and Pierce, 1997, 1998; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Sievers, 1989; Thompson *et al.*, 1991; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997) and harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1995) (see also Leopold *et al*., 2001).

Natural mortality of sandeel is 1.06 (se 0.70–1.60). The resilience of the sandeel population is high; the minimum population doubling time is less than 15 months (K=0.45–0.77; tm=1–2; tmax=7). Sandeel is not the IUCN Red List.

Sandeel is important in the industrial fishery. North Sea catches of all sandeel species together are very high and amounted to 1,000,000 tonnes per year in 1989.

Raitt's sandeel *Ammodytes marinus*

Raitt's sandeel is an extremely common fish that is found further offshore than sandeels. It is only occasionally found inshore. It can be found in the northeastern Atlantic, from Novaya Zemlya, Bear Island and the Barents Sea to the Channel Islands and western English Channel, and also around Greenland and Iceland. It can be found throughout the North Sea. Raitt's sandeel is found from 30 to 150 m water depths. Raitt's sandeel is a pelagic schooling fish that lies buried in the sand or gravel at night and emerges during daylight to hunt. It is usually territorially. It is believed that Raitt's sandeel hibernate in the sand in winter, but others hypothesize that the schools are more compact in winter and that spawning behaviour might negatively influence catchability.

Maximum size and age of Raitt's sandeel are 25 cm and 10 years. The von Bertalanffy growth parameter K is 0.16 to 0.89 per year. Maturity is reached at age 1 to 3 years and length 11 to 15 cm.

Spawning takes place in winter, November to March. The eggs are deposited in the sand and stick to the sand grains. The eggs diameter varies between 0.87 to 1.2 mm. The newly hatched larvae are pelagic and measure between 5 and 6.6 mm.

The diet of Raitt's sandeel consists of annelids, amphipods, decapod larvae, copepods and fish eggs and larvae. The diet of Raitt's sandeel is the most varied compared to other sandeel species. The larvae of Raitt's sandeel feed on diatoms and planktonic copepods.

Raitt's sandeel is a major prey for many fish predators and therefore has an important part in the North Sea ecosystem. Predators of Raitt's sandeel are red-throated diver *Gavia stellata* (rare-frequent; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (rare-staple; Madsen, 1957), great crested grebe *Podiceps cristatus* (rare; Madsen, 1957), red-necked grebe *P. griseigena* (rare frequent; Byrkjedal *et al.*, 1997; Madsen, 1957), northern fulmar *Fulmarus glacialis* (frequent-staple; Bourne, 1982; Camphuysen, 1990b; Fowler and Dye, 1987; Furness and Todd, 1984; Furness, 1990; Lilliendahl and

Solmundsson, 1997; Phillips *et al.*, 1999a; Thompson *et al.*, 1995), Manx shearwater *Puffinus puffinus* (frequent; Brooke, 1990), storm petrel *Hydrobates pelagicus* (rare; Dée and Hémery, 1998), gannet *Sula bassana* (frequent-staple; Furness, 1990; Martin, 1989; Zonfrillo pers. com. in Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn *et al.*, 1994; Gremillet and Argentin, 1998; Kirby *et al.*, 1996; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Mills, 1969b; Okill *et al.*, 1992; Paillard, 1985; Pearson, 1968), shag *Phalacrocorax aristotelis* (rare-staple; Barrett, 1991; Barrett *et al.*, 1990; Carss, 1993; Furness, 1982; Furness, 1990; Gremillet and Argentin, 1998; Gremillet *et al.*, 1996; Harris and Wanless, 1991, 1993; Lumsden and Haddow, 1946; Mills, 1969a; Pearson, 1968; Steven, 1933; Swann *et al.*, 1991; Velando and Freire, 1999; Wanless *et al.*, 1993; Wanless *et al.*, 1998), white-winged scoter *Melanitta fusca* (rare; Byrkjedal *et al.*, 1997), red-breasted merganser *Mergus serrator* (frequent-staple; Madsen, 1957), goosander *M. merganser* (rare; Madsen, 1957), parasitic jaeger *Stercorarius parasiticus* (present-staple; Bourne, 1982; Furness, 1990), great skua *S. skua* (common-staple; Albon *et al.*, 1976; Andersson, 1976; Bayes *et al.*, 1964; Booth, 1976; Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979, 1990; Furnes, 1976b; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Pennie, 1948; Perry, 1948; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), common gull *Larus canus* (rare; Garthe *et al.*, 1999), lesser black-backed gull *L. fuscus* (present-staple; Götmark, 1984; Pearson, 1968), herring gull *L. argentatus* (frequent; Furness, 1990), great black-backed gull *L. marinus* (frequent-staple; Götmark, 1984; Furness, 1990), black-legged kittiwake *Rissa tridactyla* (rare-staple; Bourne, 1982; Furness, 1982, 1990; Galbraith, 1983; Harris and Wanless, 1997; Lilliendahl and Solmundsson, 1997; Pearson, 1968; Prüter, 1989; Swann *et al.*, 1991; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (frequent-staple; Brenninkmeijer and Stienen, 1992; Essen *et al.*, 1998; Fuchs, 1977; Garthe and Kubetzki, 1998; Pearson, 1968; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare-staple; Frank, 1992; Pearson, 1968, Stienen and Brenninkmeijer, 1992; Taylor, 1979; Wendeln *et al.*, 1994), Arctic tern *S.*

paradisaea (frequent-staple; Ewins, 1985; Furness, 1982, 1990; Hartwig *et al.*, 1990; Monaghan *et al.*, 1989; Pearson, 1968; Uttley *et al.*, 1989), little tern *Sterna albifrons* (staple; Norman, 1992), common guillemot *Uria aalge* (rare-staple; Anon., 1980; Belopol'skii, 1957; Birkhead, 1976; Blake, 1983, 1984; Blake *et al.*, 1985; Bourne, 1982; Camphuysen, 1990a, 1995; Camphuysen and Keijl, 1991, 1994; Durinck *et al.*, 1991; Furness, 1982, 1990; Halley *et al.*, 1995; Harris and Wanless, 1986; Hedgren, 1976; Leopold and Camphuysen, 1992; Leopold *et al.*, 1992; Lilliendahl and Solmundsson, 1997; Lyngs and Durinck, 1998; Salomonsen, 1935; Pearson, 1968; Reinert, 1976; Slater, 1980; Swann *et al.*, 1991; Uspenski, 1958), Brünnich's guillemot *U. lomvia* (frequent-staple; Lilliendahl and Solmundsson, 1997; Uspenski, 1958), razorbill *Alca torda* (rare-staple; Andersson *et al.*, 1974; Ashcroft, 1976; Beja, 1989; Belopol'skii, 1957; Bianki, 1967; Blake, 1983, 1984; Bourne, 1982; Furness, 1982, 1990; Harris, 1970; Leopold and Camphuysen, 1992; Lilliendahl and Solmundsson, 1997; Lloyd, 1976; Swann *et al.*, 1991), black guillemot *Cepphus grylle* (rare-staple; Asbirk, 1979; Bergman, 1971, 1978; Bianki, 1967; Ewins, 1987, 1990; Furness, 1990; Petersen, 1981; Slater and Slater, 1972), little auk *Alle alle* (frequent; Blake, 1983), Atlantic puffin *Fratercula arctica* (rare-staple; Anker-Nilssen, 1987; Anker-Nilssen and Lorentsen, 1990; Ashcroft, 1976; Barrett *et al.*, 1987; Belopol'skii, 1957; Blake, 1984; Bourne, 1982; Corkhill, 1973; Evans, 1975; Furness, 1982, 1990; Harris, 1970; Harris and Hislop, 1978; Harris and Wanless, 1986; Lid, 1981; Lilliendahl and Solmundsson, 1997; Martin, 1989; Myrberget, 1962; Pearson, 1968; Tschanz, 1979), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Bjørge *et al.*, 1991; Rae, 1965, 1973b), grey seal *Halichoerus grypus* (rare-staple; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987, 1990; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-staple; Bjørge *et al.*, 1993; Brown and Pierce, 1997, 1998; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Krause, 1999; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Thompson *et al.*, 1991; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1995) (see also Leopold *et al.*, 2001), veined squid *Loligo forbesi*, starry ray *Raja radiata* and mackerel *Scomber scombrus* (Froese and Pauly, 2003).

Natural mortality of Raitt's sandeel is 0.64 (se 0.42–0.97). The population resilience of Raitt's sandeel is medium; the minimum population doubling time is 1.4–4.4 years (K=0.16–0.89; tm=1–3; tmax=10; Fec=4,000). Raitt's sandeel is not on the IUCN Red List. Raitt's sandeel is important for the industrial fishery. North Sea catches of all sandeel species together are very high and amounted to 1,000,000 tonnes per year in 1989.

Greater sandeel *Hyperoplus lanceolatus*

The greater sandeel is a common fish that can be found in the coastal zone of the northeastern Atlantic, from Spitzbergen and Iceland to Portugal. In the North Sea it is found in all inshore waters. Greater sandeel can be found from the tidemarks down to 150 m, but usually not deeper than 60 m. Greater sandeel can be found buried in the sand at night or just above sandy bottoms hunting for prey.

Greater sandeel can attain a maximum size of 40 cm. The von Bertalanffy growth parameter K is 0.36 per year. Most of the greater sandeel mature at ages 2 or 3 and length 11 to 15 cm, but some species are already mature at age 1.

The spawning period of greater sandeel is from April to September, but peak spawning occurs at the beginning of the season. Spawning takes places at depths of 20 to 100 m. The eggs are deposited on the bottom. The larvae are pelagic and are 4.5 mm long at hatching. Larvae are usually found in mid-water at 50 m depth, but can occasionally be found at 150 m.

The diet of greater sandeel is varied, it consists of decapod larvae, copepods, euphausiids and fish larvae, including sandeels, but cannibalism does not take place. Larvae feed on copepods, crustacean larvae and fish larvae and eggs.

Greater sandeel is a major prey for many fish predators and therefore has an important part in the North Sea ecosystem. Known predators of greater sandeel are red-throated diver *Gavia stellata* (rare-frequent; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (rare-staple; Madsen, 1957), great crested grebe *Podiceps cristatus* (rare; Madsen, 1957), red-necked grebe *P. griseigena* (rare frequent; Byrkjedal *et al.*, 1997; Madsen, 1957), northern fulmar *Fulmarus glacialis* (frequent-staple; Bourne, 1982; Phillips *et al.*, 1999a), Manx shearwater *Puffinus puffinus* (frequent; Brooke, 1990), storm petrel *Hydrobates pelagicus* (rare; Dée and Hémery, 1998), gannet *Sula bassana* (frequent-staple; Zonfrillo pers com. in Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn *et al.*, 1994; Gremillet and Argentin, 1998; Kirby *et al.*, 1996; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Mills, 1969b; Okill *et al.*, 1992; Paillard, 1985; Pearson, 1968; Reinhold, 1996), shag *P. aristotelis* (rare-staple; Barrett, 1991; Barrett *et al.*, 1990; Carss, 1993; Gremillet and Argentin; 1998, Lumsden and Haddow, 1946; Mills, 1969a; Pearson, 1968; Steven, 1933; Swann *et al.*, 1991; Velando and Freire, 1999), white-winged scoter *Melanitta fusca* (rare; Byrkjedal *et al.*, 1997), red-breasted merganser *Mergus serrator* (frequent-staple; Madsen, 1957), goosander *M. merganser* (rare; Madsen, 1957), parasitic jaeger *Stercorarius parasiticus* (present; Bourne, 1982), great skua *S. skua* (staple; Albon *et al.*, 1976; Andersson, 1976; Bayes *et al.*, 1964; Booth, 1976; Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979; Furness, 1976b; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Pennie, 1948; Perry, 1948; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), common gull *Larus canus* (rare; Garthe *et al.*, 1999), lesser black-backed gull *L. fuscus* (present-staple; Götmark, 1984; Pearson, 1968), great black-backed gull *L. marinus* (frequent; Götmark, 1984), black-legged kittiwake *Rissa tridactyla* (rare-staple; Bourne, 1982; Pearson, 1968; Prüter, 1989; Swann *et al.*, 1991; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (frequent-staple; Brenninkmeijer and Stienen, 1992; Essen *et al.*, 1998; Fuchs, 1977; Garthe and Kubetzki, 1998; Pearson, 1968; Stienen and Brenninkmeijer, 1998), common gull *S. hirundo* (rare-staple; Brenninkmeijer and Stienen, 1992; Frank, 1992; Pearson, 1968; Taylor, 1979; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (frequent-staple; Ewins, 1985; Hartwig *et al.*, 1990; Pearson, 1968), little tern *S. albifrons* (staple; Norman, 1992), common guillemot *Uria aalge* (rare-staple; Anon., 1980; Belopol'skii, 1957; Birkhead, 1976; Blake, 1983, 1984; Blake *et al.*, 1985; Bourne, 1982; Camphuysen, 1995; Camphuysen and Keijl, 1991, 1994; Durinck *et al.*, 1991; Halley *et al.*, 1995; Harris and Wanless, 1986; Hedgren, 1976; Leopold and Camphuysen, 1992; Leopold *et al.*, 1992; Lyngs and Durinck, 1998; Salomonsen, 1935; Pearson, 1968; Reinert, 1976; Slater, 1980; Swann *et al.*, 1991; Uspenski, 1958), Brünnich's guillemot *U. lomvia* (frequent; Uspenski, 1958), razorbill *Alca torda* (rare-staple; Andersson *et al.*, 1974; Ashcroft, 1976; Beja, 1989; Belopol'skii, 1957; Bianki, 1967; Blake, 1983, 1984; Bourne, 1982; Harris, 1970; Leopold and Camphuysen, 1992; Lloyd, 1976; Swann *et al.*, 1991), black guillemot *Cepphus grylle* (rare-staple; Asbirk, 1979; Bergman, 1971, 1978; Bianki, 1967; Ewins, 1987; Petersen, 1981; Slater and Slater, 1972), little auk *Alle alle* (frequent; Blake, 1983), Atlantic puffin *Fratercula arctica* (rare-staple; Ashcroft, 1976; Belopol'skii, 1957; Blake, 1984; Bourne, 1982; Corkhill, 1973; Evans, 1975; Harris, 1970; Harris and Wanless, 1986; Lid, 1981; Myrberget, 1962; Pearson, 1968; Tschanz, 1979), common dolphin *Delphinus delphis* (rare; Silva, 1999), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Bjørge *et al.*, 1991, Rae, 1965, 1973b), grey seal *Halichoerus grypus* (rare-staple; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987, 1990; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-staple; Bjørge *et al.*, 1993; Brown and Pierce, 1997, 1998; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Krause, 1999; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Thompson *et al.*, 1991; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1995) (see also Leopold *et al*., 2001), veined squid *Loligo forbesi* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

The resilience of the greater sandeel population is medium; the minimum population doubling time is 1.4–4.4 years (tm=2; Fec=35,000). Greater sandeel is not on the IUCN Red List. North Sea catches of all sandeel species together are very high and amounted to 1,000,000 tonnes per year in 1989.

4.7 Trachinidae

Lesser weever *Echiichthys vipera*

The lesser weever is a fairly common fish species that is found in the littoral zone. It is found in the coastal waters of the eastern Atlantic, from the

North Sea to the Mediterranean and Morocco. In the North Sea, it is found from the Danish coast to the Channel and on the coasts of the British Isles. It lives buried in clean sand between the low-tide mark and 50 m deep. In summer the lesser weever seems to migrate to the north of the distribution range and to the warmer inshore waters.

Maximum length of lesser weever is 17 cm. Growth is rather slow, in six years lesser weever reaches a length of 13 cm (Knijn *et al*., 1993).

Spawning takes place from June to August. Highest densities of eggs are found in June and July. The eggs are pelagic and 0.95 to 1.4 mm in diameter. The newly hatched larvae are 3 to 3.27 mm long.

Lesser weever is a predator that lies buried in the sand waiting for its prey. Is has also been noted that it is an active predator at night (Wheeler, 1969). The diet consists almost entirely of Gobiidae. Crustaceans, polychaetes, squid and other fish are sometimes taken.

Predators of lesser weever are cormorant *Phalacrocorax carbo* (rare; Gremillet and Argentin, 1998; Pearson, 1968), shag *P. aristotelis* (rare; Steven, 1933), sandwich tern *Sterna sandvicensis* (rare; Pearson, 1968), common tern *S. hirundo* (frequent; Pearson, 1968), Arctic tern *S. paradisaea* (frequent; Pearson, 1968), Atlantic puffin *Fratercula arctica* (frequent; Pearson, 1968) (see also Leopold *et al*., 2001), whiting *Merlangius merlangus*, spotted ray *Raja montagui* and tub gurnard *Trigla lucerna* (Froese and Pauly, 2003). The lesser weever is not on the IUCN Red list and has no economic importance.

4.8 Mackerels and tunnies (Scombridae)

Mackerel *Scomber scombrus*

Mackerel is a very common pelagic schooling fish. It is distributed in the northeastern Atlantic, from northern Norway and Iceland to the Mediterranean. It can also be found in the western Atlantic. It is found throughout the North Sea. Mackerel can be found in depths from 0 to 200 m. In winter mackerel migrates to the bottom and stops feeding.

Mackerel can grow to a maximum size of 65 cm. Maximum reported age is 17 years. Growth is rapid in the first two years but slows down afterwards; the von Bertalanffy growth parameter K is 0.23 to 0.27 per year. Maturity is reached at age 2–3 and at a length of 30 cm.

Spawning season is from May to July. The pelagic eggs are shed in approximately twenty batches (Knijn *et al*., 1993). The eggs have a diameter of 0.9 to 1.4 mm. Eggs can be found up to 60 m deep, but most can be found in the upper layers. The incubation time is 6 to 7 days. The newly hatched larvae are 2.5 to 4.2 mm long. The larvae are pelagic and can be found in the upper layers.

Mackerel stops feeding in winter and only resumes after spawning. The diet is varied and consists of planktonic prey, crustaceans (especially copepods and euphausiids) and fish.

Mackerel is preyed upon by red-throated diver *Gavia stellata* (staple; Madsen, 1957), black-throated diver *G. arctica* (rare; Madsen, 1957), northern fulmar *Fulmarus glacialis* (frequent; Garthe *et al.*, 1996), gannet *Sula bassana* (frequent-staple; Garthe *et al.*, 1996; Martin, 1989; Wanless, 1984), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn *et al.*, 1994; Goutner *et al.*, 1997; Leopold *et al.*, 1998; Mills, 1969b), shag *P. aristotelis* (rare; Velando and Freire, 1999), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), common gull *Larus canus* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *L. fuscus* (rare; Garthe *et al.*, 1996; Garthe *et al.*, 1999), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996; Nogales *et al.*, 1995), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (frequent; Garthe *et al.*, 1996), common tern *Sterna hirundo* (frequent; Stienen and Brenninkmeijer, 1992), common guillemot *Uria aalge* (rare; Leopold and Camphuysen, 1992; Madsen, 1957), Atlantic puffin *Fratercula arctica* (rare-common; Anker-Nilssen and Lorentsen, 1990; Harris and Hislop, 1978; Lid, 1981; Martin, 1989; Myrberget, 1962; Tschanz, 1979), killer whale *Orcinus orca* (present-staple; Bloch and Lockyer, 1988; Couperus, 1994; Similä *et al.*, 1996), common dolphin *Delphinus delphis* (rare-frequent; Collet *et al.*, 1981; Silva, 1999), harbour porpoise *Phocoena phocoena* (rare-staple; Aarefjord *et al.*, 1995; Rae, 1965; Recchia and Read, 1989), harbour seal *Phoca vitulina* (rare-frequent; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Pierce *et al.*, 1990; Rae, 1973a; Sievers, 1989) (see also Leopold *et al.*, 2001), sea lamprey *Petromyzon marinus*, thornback ray *Raja clavata*, whiting

Merlangius merlangus, hake *Merluccius merluccius*, spur-dog *Squalus acanthias*, scabbard-fish *Aphanopus carbo*, grey gurnard *Eutrigla gurnardus*, swordfish *Xiphias gladius* and three-spined stickleback *Gasterosteus aculeatus* (Froese and Pauly, 2003).

Natural mortality of mackerel is 0.40 (se 0.27–0.61). The resilience of the mackerel population is medium; the minimum population doubling time is 1.4–4.4 years (rm=0.33–0.56; K=0.23–0.27; tm=2–3; tmax=17; Fec=200,000). Mackerel is not on the IUCN Red list.

Mackerel has a high economic value. North Sea landings rose to a maximum of 900,000 tonnes in 1967. Today yearly landings in the North Sea vary around 300,000 tonnes.

Main ref.: Wheeler, 1969; Nijssen and De Groot 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.9 Gobiidae

Common goby *Pomatoschistus microps*

The common goby is a very abundant fish species in estuaries and intertidal areas. The common goby is distributed along the northeastern Atlantic coasts from Norway to Morocco. In the North Sea, it is common along the coasts. It is found in depths from 0 to 12 m on sandy and muddy sediments. During severe winters, common goby can migrate into deeper water.

Maximum size and lifespan of common goby is 7 cm and 1.5 years. The von Bertalanffy growth parameter K is 0.30 per year. Maturity is reached at length of 4 cm and 0.8 years.

Common goby spawns from April till September. The adults spawn several times during the summer. The eggs are laid under empty shells and are guarded by the male for 9 days. The eggs are very small, only 0.7 to 0.9 mm. The pelagic larvae hatch at a length of 3 to 4 mm. It is assumed that the larvae live close to the sea floor when they reach 11 or 12 mm.

The diet of common goby consists of amphipods, mysids, gammarids, shrimps, benthic crustaceans and polychaetes. The pelagic larvae feed on pelagic copepods.

Predators of common goby are red-throated diver *Gavia stellata* (rare-staple; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (staple; Madsen, 1957), great crested grebe *Podiceps cristatus* (staple; Doornbos, 1984; Madsen, 1957; Vlug, 1983), red-necked grebe *P. griseigena* (staple; Madsen, 1957), *P. auritus* (staple; Madsen, 1957), black-eared grebe *P. nigricollis* (rare; Madsen, 1957), storm petrel *Hydrobates pelagicus* (rare-frequent; Dée and Hémery, 1998), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn and Dirksen, 1993, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Gremillet and Argentin, 1998; Härkönen, 1988; Kieckbusch and Koop, 1996; Lekuona and Campos, 1997; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Steven, 1933), shag *P. aristotelis* (rare-frequent; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Velando and Freire, 1999), smew *Mergus albellus* (staple; Madsen, 1957), red-breasted merganser *M. serrator* (common-staple; Doornbos, 1984; Madsen, 1957), goosander *M. merganser* (frequent; Madsen, 1957), greenshank *Tringa nebularia* (common; Swennen, 1971), herring gull *Larus argentatus* (frequent; Nogales *et al.*, 1995), sandwich tern *Sterna sandvicensis* (rare; Brenninkmeijer and Stienen, 1992; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare; Stienen and Brenninkmeijer, 1992), common guillemot *Uria aalge* (rare-frequent; Blake, 1984; Blake *et al.*, 1985; Durinck *et al.*, 1991; Leopold and Camphuysen, 1992; Madsen, 1957), razorbill *Alca torda* (rare-staple; Blake, 1984; Madsen, 1957), black guillemot *Cepphus grylle* (common-staple; Bianki, 1967; Madsen, 1957), common dolphin *Delphinus delphis* (rare; Silva, 1999), harbour porpoise *Phocoena phocoena* (frequent-staple; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Bjørge *et al.*, 1991), grey seal *Halichoerus grypus* (rare-frequent; Pierce *et al.*, 1989; Pierce *et al.*, 1991a), harbour seal *Phoca vitulina* (rare-common; Behrends, 1982; Bjørge *et al.*, 1993; Härkönen, 1987, 1988; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Thompson *et al.*, 1991) (see also Leopold *et al.*, 2001), twaite shad *Alosa fallax*, five-bearded rockling *Ciliata mustela*, ruffe *Gymnocephalus cernuus*, and tub gurnard *Trigla lucerna* (Froese and Pauly, 2003).

Natural mortality of common goby is 0.64 (se 0.42–0.97). The common goby has a high population resilience; the minimum population doubling time is less than 15 months (K=0.29; tm=0.8; tmax=2.6). The common goby is not on the IUCN Red list and has no economic value.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

Sand goby *Pomatoschistus minutes*

The sand goby is an abundant fish of inshore waters. It is found in the coastal waters of the eastern Atlantic, from northern Norway to Spain and the Mediterranean. In the North Sea, it can be found along the coasts and in estuaries. The sand goby can be found from 2 to 200 m depth but is most common up to 40 m depth. It shows a preference for sandy or muddy bottoms. The sand goby makes a winter migration into deeper water.

The sand goby grows to a maximum of 11 cm and 3 years. Growth of sand goby is fast; the von Bertalanffy growth parameter K is 0.93 per year. Maturity is reached after one year.

Spawning takes place from March to September. The female discards the eggs, after which the male guards them for 10 days. The newly hatched larvae are pelagic and are 2 to 3 mm long. When they reach a length of 12 to 18 mm, the larvae assume a bottom living life. Sand gobies usually die after the first spawning, only a few live to spawn a second time.

The diet of sand goby consists mainly of crustaceans (copepods, amphipods, mysids, cumaceans and shrimps). Sometimes polychaetes and fish and mollusc larvae are taken.

The sand goby is preyed upon by red-throated diver *Gavia stellata* (rare-staple; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (staple; Madsen, 1957), great crested grebe *Podiceps cristatus* (common-staple; Doornbos, 1984; Madsen, 1957; Vlug, 1983), red-necked grebe *P. griseigena* (rare-staple; Madsen, 1957), horned grebe *P. auritus* (staple; Madsen, 1957), black-eared grebe *P. nigricollis* (rare; Madsen, 1957), storm petrel *Hydrobates pelagicus* (rare-frequent; Dée and Hémery, 1998), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn and Dirksen, 1993, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Gremillet and Argentin, 1998; Härkönen, 1988; Kieckbusch and Koop, 1996; Lekuona and Campos, 1997; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Steven, 1933), shag *P. aristotelis* (rare-frequent; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Velando and Freire, 1999), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), smew *Mergus albellus* (staple; Madsen, 1957), red-breasted merganser *M. serrator* (frequent-staple; Doornbos, 1984; Madsen, 1957), goosander *M. merganser* (frequent; Madsen, 1957), common gull *Larus canus* (rare; Garthe *et al.*, 1999), herring gull *L. argentatus* (frequent; Nogales *et al.*, 1995), black-legged kittiwake *Rissa tridactyla* (staple; Vauk and Jokele, 1975), sandwich tern *Sterna sandvicensis* (rare; Brenninkmeijer and Stienen, 1992; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare; Stienen and Brenninkmeijer, 1992), common guillemot *Uria aalge* (rare-frequent; Blake, 1984; Blake *et al.*, 1985; Durinck *et al.*, 1991; Leopold and Camphuysen, 1992; Madsen, 1957), razorbill *Alca torda* (rare-staple; Blake, 1984; Madsen, 1957), black guillemot *Cepphus grylle* (common-staple; Bianki, 1967; Madsen, 1957), common dolphin *Delphinus delphis* (rare; Silva, 1999), harbour porpoise *Phocoena phocoena* (frequent-staple; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Bjørge *et al.*, 1991), grey seal *Halichoerus grypus* (rare-frequent; Pierce *et al.*, 1989; Pierce *et al.*, 1991a), harbour seal *Phoca vitulina* (rare-staple; Behrends, 1982; Bjørge *et al.*, 1993; Hall *et al.*, 1998; Härkönen, 1987, 1988; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Sievers, 1989; Thompson *et al.*, 1991; Tollit and Thompson, 1996) (see also Leopold *et al.*, 2001), sand goby *Pomatoschistus minutus*, twaite shad *Alosa fallax*, cod *Gadus morhua*, five-bearded rockling *Ciliata mustela*, tub gurnard *Trigla lucerna*, John dory *Zeus faber* and bull-rout *Myoxocephalus scorpius* (Froese and Pauly, 2003).

The natural mortality of sand goby is 1.50 (se 0.99–2.27). The resilience of the sand goby population is high, minimum population doubling time is less than 15 months (K=0.93; tm=0.7; tmax=2.7). This species is not on the IUCN Red list. The sand goby is not an economically important species.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al.*, 1993; Muus *et al.*, 1999, Froese and Pauly, 2003.

Lozano's goby *Pomatoschistus lozanoi*

A fairly abundant goby found in shallow waters of the eastern Atlantic, from the North Sea to northwestern Spain. Lozano's goby is a bottom-living fish that can be found in depths up to 80 m, but is most common in the shallower depths.

The Lozano's goby can grow up to 8 cm. Maximum reported age is 2 years. Maturity is reached at age 1.

Spawning takes place in shallow waters. Eggs are deposited under empty shells.

Lozano's goby is a predator on small crustaceans (mysids, amphipods, copepods) and nematodes.

Reported predators of Lozano's goby are red-throated diver *Gavia stellata* (rare-staple; Durinck *et al.*, 1994; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (staple; Madsen, 1957), great crested grebe *Podiceps cristatus* (staple; Doornbos, 1984; Madsen, 1957; Vlug, 1983), red-necked grebe *Podiceps griseigena* (staple; Madsen, 1957) horned grebe *P. auritus* (staple; Madsen, 1957), black-eared grebe *P. nigricollis* (rare; Madsen, 1957), storm petrel *Hydrobates pelagicus* (frequent; Dée and Hémery, 1998), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn and Dirksen, 1993, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Gremillet and Argentin, 1998; Härkönen, 1988; Kieckbusch and Koop, 1996; Lekuona and Campos, 1997; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Steven, 1933), shag *P. aristotelis* (rare-frequent; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Velando and Freire, 1999), smew *Mergus albellus* (staple; Madsen, 1957), red-breasted merganser *M. serrator* (common-staple; Doornbos, 1984; Madsen, 1957), goosander *M. merganser* (frequent; Madsen, 1957), herring gull *Larus argentatus* (frequent; Nogales *et al.*, 1995), sandwich tern *Sterna sandvicensis* (rare; Brenninkmeijer and Stienen, 1992; Stienen and Brenninkmeijer, 1998), common tern *S. hirundo* (rare; Stienen and Brenninkmeijer, 1992), common guillemot *Uria aalge* (rare-frequent; Blake, 1984; Blake *et al.*, 1985; Durinck *et al.*, 1991; Leopold and Camphuysen, 1992; Madsen, 1957), razorbill *Alca torda* (rare-staple; Blake, 1984; Madsen, 1957), black guillemot *Cepphus grylle* (common-staple; Bianki, 1967; Madsen, 1957), common dolphin *Delphinus delphis* (rare; Silva, 1999), harbour porpoise *Phocoena phocoena* (frequent-staple; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Bjørge *et al.*, 1991), grey seal *Halichoerus grypus* (rare-frequent; Pierce *et al.*, 1989; Pierce *et al.*, 1991a), harbour seal *Phoca vitulina* (rare-common; Behrends, 1982; Bjørge *et al.*, 1993; Härkönen, 1987, 1988; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Thompson *et al.*, 1991) (see also Leopold *et al*., 2001).

The natural mortality of Lozano's goby is 1.24 (se 0.70–2.21). This goby is not on the IUCN Red list and has no economic value.

Main ref.: Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.10 Callionymidae

Dragonet *Callionymus lyra*

The dragonet is a very common bottom-living fish that is found in the shallow waters of the eastern Atlantic and the northern Mediterranean. In the North Sea it is very common along the coasts in depths from 5 to 430 m. The dragonet prefers sandy or muddy bottoms.

Maximum size of the male dragonet is 30 cm and maximum lifespan is 5 years. Females live up to 7 years and 20 cm. Therefore growth rate of males is larger than females. The von Bertalanffy growth parameter K is 0.43 per year. Male dragonets reach maturity at 13 cm and age 2.

Spawning season is from April to August. The eggs are pelagic and have a diameter of 0.7 to 0.97 mm. Newly hatched larvae are 2 mm long. Larvae are pelagic and can be found in the water column from January to September.

The diet of dragonets consists of echinoderms, worms, crustaceans, ophiurians and molluscs (Knijn *et al*., 1993, Froese and Pauly, 2003; unpublished RIVO data).

Dragonet has been found in the diet of northern fulmar *Fulmarus glacialis* (frequent; Thompson *et al.*, 1995), cormorant *Phalacrocorax carbo* (rare-frequent; Boudewijn *et al.*, 1994; Gremillet and Argentin, 1998; Leopold *et al.*, 1998; Steven, 1933; Van Damme, 1994), shag *P. aristotelis* (rare-frequent; Gremillet and Argentin, 1998; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Mills, 1969a; Steven, 1933; Velando and Freire, 1999; Wanless *et al.*, 1993), common gull *Larus canus* (frequent; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), herring gull *L. argentatus* (frequent; Nogales *et al.*, 1995), lesser black-backed gull *L. fuscus* (rare-frequent; Garthe *et al.*, 1999), common guillemot *Uria aalge* (rare; Camphuysen and Keijl, 1991, 1994; Leopold and

Camphuysen, 1992), black guillemot *Cepphus grylle* (rare; Barrett and Anker-Nilssen, 1997), common dolphin *Delphinus delphis* (rare; Silva, 1999), grey seal *Halichoerus grypus* (rare-frequent; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1990; Rae, 1973a), harbour seal *Phoca vitulina* (rare-common; Behrends, 1982; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen and Heide-Jørgensen, 1991; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Tollit and Thompson, 1996) (see also Leopold *et al*., 2001), bib *Trisopterus luscus*, small eyed ray *Raja microocellata*, thornback ray *R. clavata*, spotted ray *R. montagui*, cod *Gadus morhua*, cuckoo ray *Leucoraja naevus*, spiny dogfish *Squalus acanthias* and John dory *Zeus faber* (Froese and Pauly, 2003).

Natural mortality of dragonet is 0.69 (se 0.45–1.04). The resilience of the dragonet population is medium; the minimum population doubling time is 1.4–4.4 years (K=0.43–0.47; tmax=6). Dragonet is not on the IUCN Red list and has no economic value.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

Spotted dragonet *Callionymus maculatus*

The spotted dragonet is a less common species that is found in deeper waters of the eastern Atlantic, from Iceland and Norway to Senegal and the Mediterranean. In the North Sea, it is mainly found in the deeper waters of the coast of Norway as well as the Dutch coast. Spotted dragonet can be found in depths of 45 to 650 m on sandy bottoms.

The male spotted dragonets can grow to 16 cm, while female reach a maximum length of 13 cm. No data on age, growth and maturity have been recorded.

Spawning period is from April to June. The eggs and larvae are pelagic and larvae can be found from May to September. Newly hatched larvae have a length of 2.1 mm.

Spotted dragonet feeds on benthic crustaceans, amphipods and shrimps, polychaete worms and bivalves.

Predators of spotted dragonet are grey gurnard *Eutrigla gurnardus*, poor cod *Trisopterus minutus*, hake *Merluccius merluccius* and John dory *Zeus faber* (Froese and Pauly, 2003).

Natural mortality of spotted dragonet is 0.77 (se 0.43–1.36). The spotted dragonet has no economic value.

4.11 Scleroparei, Gurnards (Triglidae)

Grey gurnard *Eutrigla gurnardus*

The grey gurnard is a very common fish and the most abundant triglid. It is found in the eastern Atlantic, from Norway and Iceland to Morocco and the Mediterranean. It is found throughout the North Sea. It is found in depths from the shoreline to 150 m, but is most common in depths between 20 to 40 m. It is a species that can sometimes be found in small schools of the bottom, but lives mostly on sandy, or sometimes rocky and muddy grounds. The grey gurnard makes a shoreward migration during the summer months.

Grey gurnard can reach a length of 60 cm and maximum reported age is 9 years (Knijn *et al.*, 1993). The von Bertalanffy growth parameter K is 0.16 per year. Females grow faster and are more long-lived than males. Maturity is reached at length of 15 cm, age 2 or 3 for males, and 24 cm and age 4 for females.

Spawning takes place from April to August. The eggs are pelagic and have a diameter of 1.16 to 1.55 mm. The eggs hatch after 7 days when the larvae have reached a length of 3 to 4 mm. The larvae are pelagic until they reach a length of 3 cm, when they start living on the bottom.

Grey gurnard feeds predominantly on fish (i.e. whiting, sandeel, dragonet and sole). The juvenile diet consists of *Crangon crangon* and crabs.

Predators of grey gurnard are northern fulmar *Fulmarus glacialis* (frequent; Garthe *et al.*, 1996), gannet *Sula bassana* (frequent; Garthe *et al.*, 1996), cormorant *Phalacrocorax carbo* (rare-frequent; Leopold *et al.*, 1998; Steven, 1933; Warke and Day, 1995), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), common gull *Larus canus* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *L. fuscus* (frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake

Rissa tridactyla (frequent; Garthe *et al.*, 1996), Atlantic puffin *Fratercula arctica* (rare-frequent; Harris and Hislop, 1978; Martin, 1989), harbour seal *Phoca vitulina* (rare; Behrends, 1982) (see also Leopold *et al.*, 2001) and haddock *Melanogrammus aeglefinus* (Froese and Pauly, 2003).

The natural mortality of grey gurnard is 0.26 (se 0.17–0.40). The resilience of the grey gurnard population is medium; the minimum population doubling time is 1.4–4.4 years (K=0.16; tm=3–4; tmax=16; Fec=200,000). The grey gurnard is not on the IUCN Red list.

Grey gurnard is a by-catch species in the North Sea and only of minor commercial interest. Since the 1980s, yearly landings amount to 3,000 tonnes.
Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al.*, 1993; Muus *et al.*, 1999; Froese and Pauly, 2003.

Tub gurnard *Trigla lucerna*

The tub gurnard is the largest European gurnard. It is a fairly common fish that is found in the eastern Atlantic, from Norway to the West African coast and in the Mediterranean. In the North Sea, it is found along the coasts, but it is more common in the southern part compared to the central and northern North Sea. Tub gurnard is found in depths from 5 to 300 m, but is most common between 50 and 150 m. It is a bottom-living fish that inhabits sand, muddy sand or gravel bottoms. In summer it migrates to the more northern part of the distribution, into the North Sea via the Channel.

Maximum length and life span of tub gurnard are 75 cm and 15 years. The von Bertalanffy growth parameter K is 0.15 to 1.6 per year. Maturity is reached at length 23 to 26 cm and age 3.

The spawning period of tub gurnard is from May to July. The small eggs, 0.22 to 0.3 mm are pelagic. The pelagic larvae hatch at lengths of 3.7 mm. The larvae are found in shallow bays and estuaries in summer.

Fish, gobies, sprat, small flatfish and dragonets are an important part of the diet of tub gurnard. It also preys on crustaceans, shrimp, crabs, mysids and amphipods, molluscs and polychaetes.

Tub gurnard is preyed upon by cormorant *Phalacrocorax carbo* (rare-frequent; Leopold *et al.*, 1998; Steven, 1933; Warke and Day, 1995), lesser black-backed gull *Larus fuscus* (frequent; Garthe *et al.*, 1999) and Atlantic puffin

Fratercula arctica (rare-frequent; Harris and Hislop, 1978; Martin, 1989) (see also Leopold *et al*.; 2001).

The natural mortality of tub gurnard is 0.26 (se 0.17–0.39). The population resilience is low; the minimum population doubling time is 4.5–14 years (K=0.15–1.6; tmax=14). The tub gurnard is not on the IUCN Red list and has little economic importance. It is mainly a by-catch species and yearly European landings amount to 20,000 tonnes.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.12 Bullheads and sculpins (Cottidae)

Bull-rout *Myoxocephalus scorpius*

The bull-rout is a common species that can be found on the eastern Atlantic coasts, from Iceland and Spitzbergen to the Bay of Biscay. It can also be found in the western Atlantic. In the North Sea, it is very common. It shows a strong preference for rocky bottoms with sand or mud, but can also be found among seaweeds. It can be found from the shore up to 110 m depth. In the North it is found closer to the shore than in the more southern part of its distribution.

Bull-rout can grow up to 34 cm in the North Sea, maximum size in the Arctic up to 60 cm. No reports of maximum age, but bull-routs of 6 years old have been caught. The von Bertalanffy growth parameter K is 0.32 per year. Females become larger than males. Maturity is reached in the second year, around 15 cm length.

Bull-rout spawns in winter, from December to March. The eggs are deposited between rocks or amongst kelp at 3 to 15 m depth and are assiduously guarded by the male. The eggs are 1.8 to 2.5 mm in diameter. Larvae are pelagic and are 7.4 to 8.6 mm long at hatching. The pelagic larvae can be found from March to May.

The bull-rout is an opportunistic benthic predator and has a varied diet. The diet consists mainly of crustaceans, shrimp and crab and fish, as well as some bivalves and polychaetes. The juveniles feed mostly on gammarids and young shrimps.

Bull-rout is preyed upon by red-throated diver *Gavia stellata* (frequent-common; Leopold, 1997; Madsen, 1957), black-throated diver *G. arctica* (rare; Madsen, 1957), great northern diver *G. immer* (rare-staple; Madsen, 1957), red-necked grebe *Podiceps griseigena* (rare; Byrkjedal *et al.*, 1997; Madsen, 1957), cormorant *Phalacrocorax carbo* (rare-common; Barrett *et al.*, 1990; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Gremillet and Argentin, 1998; Härkönen, 1988; Kieckbusch and Koop, 1996; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Pearson, 1968; Reinhold, 1996; Steven, 1933; Van Damme, 1994; Warke and Day, 1995), shag *P. aristotelis* (rare-frequent; Barrett, 1991; Barrett *et al.*, 1990; Harris and Wanless, 1993; Lumsden and Haddow, 1946; Pearson, 1968), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), red-breasted merganser *Mergus serrator* (frequent; Madsen, 1957), common tern *Sterna hirundo* (rare; Stienen and Brenninkmeijer, 1992), common guillemot *Uria aalge* (frequent; Uspenski, 1958), black guillemot *Cepphus grylle* (rare-frequent; Barrett and Anker-Nilssen, 1997; Lydersen *et al.*, 1989; Madsen, 1957; Petersen, 1981), grey seal *Halichoerus grypus* (rare-common; Hammond and Prime, 1990; Hammond *et al.*, 1994; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1990; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-staple; Behrends, 1982; Bjørge, 1995; Bjørge *et al.*, 1993; Hall *et al.*, 1998; Havinga, 1933; Krause, 1999, Pierce *et al.*, 1990; Pierce *et al.*, 1991b; Sievers, 1989; Thompson *et al.*, 1996b; Tollit and Thompson, 1996), harp seal *P. groenlandica* (frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1995), bearded seal *Erignathus barbatus* (common; Hjelset *et al.*, 1999), otter *Lutra lutra* (rare-frequent; Heggberget, 1993; Kruuk *et al.*, 1987; Watson, 1978; Watt, 1995) (see also Leopold *et al*., 2001) and cod *Gadus morhua* (Froese and Pauly, 2003).

Natural mortality of bull-rout is 0.38 (se 0.25–0.57). The bull-rout population has a medium resilience; the minimum population doubling time is 1.4–4.4 years (tm=2; Fec=2,742). Bull-rout is not on the IUCN Red list and has no economic value.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.13 Pogges (Agonidae)

Hooknose *Agonus cataphractus*

The hooknose is an extremely common fish that is found in inshore and coastal waters. It is found in the northeastern Atlantic, from the White Sea to the English Channel and Iceland and the Faroe Islands. It is very common in the North Sea coastal waters as well as in the deeper central North Sea. Hooknose is found in depths from 5 to 500 m, but mostly up to 250 m. It is a bottom dwelling fish that is found on soft sediments. In the southern part of its distribution hooknose make a winter migration to shallower areas.

Maximum size and life span of hooknose are 21 cm and 12 years. Growth of hooknose is medium; the von Bertalanffy growth parameter K is 0.48 per year. Hooknose of 8 cm, aged 3, are considered to be mature.

Spawning takes place from February to May in shallow water. Clumps of eggs are laid attached to stalks of large algae or stones. Egg diameter is 1.7 to 2.3 mm. The period of incubation is very long. After 10 to 12 months larvae of 6 to 8 mm hatch. The larvae are pelagic and can be found in the water from December to May. In July and August when larvae have reached a length of 20 mm, they start living at the bottom.

The diet of hooknose consists mainly of crustaceans, *Crangon crangon*, amphipods, *Pandalus* spp. and cumaceans. Occasionally brittle stars, polychaetes, fish eggs and Gobiidae are taken.

Predators of hooknose are red-throated diver *Gavia stellata* (frequent; Leopold, 1997), cormorant *Phalacrocorax carbo* (rare-staple; Reinhold, 1996; Steven, 1933; Van Damme, 1994), shag *P. aristotelis* (rare-frequent; Carss, 1993; Lumsden and Haddow, 1946), lesser black-backed gull *Larus fuscus* (rare; Garthe *et al.*, 1999), herring gull *L. argentatus* (frequent; Löhmer and Vauk, 1970), black-legged kittiwake *Rissa tridactyla* (rare; Vauk and Jokele, 1975), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987), harbour seal *Phoca vitulina* (rare-frequent; Behrends, 1982; Krause, 1999; Sievers, 1989; Tollit and Thompson, 1996), bull-rout *Myoxocephalus scorpius*, grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of hooknose is 0.84 (se 0.56–1.28). The resilience of the hooknose population is high; the minimum population doubling time is less than

15 months (K=0.47; tm=3–4; tmax=3; Fec=2,400). The species is not on the IUCN Red list.

The hooknose is of no importance for the commercial fishery.

4.14 Flatfishes (Heterosomata, Scophthalmidae)

Turbot *Scophthalmus maximus*

Turbot can be found in the northeastern Atlantic coastal waters, from the Arctic Circle to the Mediterranean. In the North Sea, it is found in the shallower areas (from the shore to 80 m deep). Although it can be found on sandy and mixed bottoms, turbot shows a strong preference for gravel.

Maximum size and lifespan of turbot are 100 cm and 27 years, however males larger than 50 cm and females larger than 70 cm are rare. Females are bigger and grow faster than males. Growth is relatively rapid and the von Bertalanffy growth parameter K is 0.15 to 0.32 per year. Maturity is reached at ages 3 to 5 years and lengths of 41 to 47 cm.

Spawning period is from April to August and takes place over gravelly ground. There are some spawning grounds recognised but spawning occurs throughout the distribution area. The eggs are pelagic and are 0.91 to 1.2 mm in length. Egg developing time is 5 to 9 days. The newly hatched larvae are pelagic and measure 2.14 to 3.0 mm. The larvae drift with the currents to the nursery areas in shallow coastal waters (not in estuaries). Metamorphosis starts at length 13 to 16 mm and is completed at 25 mm. Turbot larvae assume a bottom-living life after metamorphosis.

Turbot is a voracious predator. The juveniles feed mostly on polychaetes and mysids. From a length of 20 cm the fish switch their diet to almost entirely fish, e.g. sandeels, gobies, herring, sprat, cod, whiting, haddock, Norway pout, dab, long rough dab, dragonets and lesser weever. The planktonic larvae feed on copepods.

Turbot is preyed upon by little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), cormorant *Phalacrocorax carbo* (frequent-staple; Nehls and Gienapp, 1997; Warke and Day, 1995), common gull *Larus canus* (frequent; Kubetzki, 1997; Kubetzki *et al.*, 1999), common tern *Sterna hirundo* (frequent-common; Frank, 1992), Atlantic puffin *Fratercula arctica* (present; Martin, 1989), common dolphin *Delphinus delphis* (rare; Silva, 1999), grey seal *Halichoerus grypus* (rare-frequent; Hammond and Prime, 1990; Pierce *et al.*, 1991a), harbour seal *Phoca vitulina* (rare-frequent; Brown and Pierce, 1997; Des Clers and Prime, 1996; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (frequent; Nilssen *et al.*, 1990) and otter *Lutra lutra* (rare-frequent; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al*., 2001).

Natural mortality of turbot is 0.45 (se 0.29–0.67). The population resilience of turbot is medium; the minimum population doubling time is 1.4–4.4 years (K=0.15–0.28; tm=3–5; tmax=26; Fec=5 million). Turbot is not on the IUCN Red list.

Turbot is very highly valued fish; landings fluctuate around 5,000 tonnes per year.

Brill *Scophthalmus rhombus*

Brill is a common fish that can be found in the coastal waters of the northeastern Atlantic, from 64°N to Morocco and the Mediterranean. In the North Sea it occurs mainly in the shallower areas (from 5 to 50 m) and on sandy and mixed substrate.

Brill can grow to a maximum of 75 cm and 6 years. Females become taller than males. The von Bertalanffy growth parameter K is 0.32 to 0.50 per year. Maturity is reached at 25 cm for males and 33 to 41 cm and age 3 for females.

Brill is a spring and summer spawner and spawning period is from March to August. Spawning occurs between 10 and 20 m depth. The eggs take 14 days to develop. The hatched larvae measure 3.8 to 4.0 mm. The pelagic larvae are passively transported to the coastal waters. Metamorphosis is completed at lengths of 20 to 35 mm. The larvae assume a bottom-living life after metamorphosis. Young brill live closer to the shore and can even be found in mouths of estuaries. With increasing size the fish move to deeper water.

Like turbot, brill is an active predator and feeds mostly on fish, sandeels, gadoids, gobies and clupeids. Larvae feed mostly on copepods, and decapod and mollusc larvae.

Predators of brill are little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), cormorant *Phalacrocorax carbo* (rare-staple; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Gremillet and Argentin, 1998; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Warke and Day, 1995), common gull *Larus canus* (frequent; Kubetzki, 1997; Kubetzki *et al.*, 1999), common tern *Sterna hirundo* (frequent-common; Frank, 1992), Atlantic puffin *Fratercula arctica* (present; Martin, 1989), common dolphin *Delphinus delphis* (rare; Silva, 1999), grey seal *Halichoerus grypus* (rare-frequent; Hammond and Prime, 1990; Pierce *et al.*, 1991a), harbour seal *Phoca vitulina* (rare-frequent; Brown and Pierce, 1997; Hall *et al.*, 1998; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b), harp seal *P. groenlandica* (frequent; Nilssen *et al.*, 1990) and otter *Lutra lutra* (rare-frequent; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al*., 2001).

Natural mortality of brill is 0.81 (se 0.54 to 1.23). The population resilience of brill is medium; the minimum population doubling time is 1.4–4.4 years (tm=5; tmax=6). The species is not in the IUCN Red list.

The brill has a moderate commercial value. It is mostly taken as by-catch in the beamtrawl fishery. Yearly catches amount to 1,000 tonnes.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.15 Flatfishes (Heterosomata, Bothidae)

Topknot *Zeugopterus punctatus*

The topknot is a relatively uncommon fish that is found along the coast of the North Sea. It lives mainly on rocky grounds in shallow waters. Because the topknot can cling its body to the rocks, it can even be found on the low shore. It is rarely found in waters deeper than 40 m. The young immature topknots are found on rocky shores among kelp holdfasts.

Topknot grows to a maximum size of 25 cm, most commonly 7 to 10 cm (Knijn *et al*., 1993).

Spawning takes place from February to June in the western Channel. The eggs and larvae are pelagic. Eggs are 1 mm in diameter and take three days to hatch (www.fishbase.org). From March to June post-larvae are found in the plankton. In January larvae measure 4 cm and by this time they have fully transformed to adult shape and coloration and are bottom-living.

The food of adult topknots consists of young fish and crustaceans. Larvae eat mostly copepods, *Temora*. Topknot is not on the IUCN Red list and has no economic value.

Main ref.: Wheeler, 1969; Nijssen and De Groot, 1980; Muus *et al*., 1999; Froese and Pauly, 2003.

Norwegian topknot *Phrynorhombus norvegicus*

Because of the small size, Norwegian topknot is able to escape most fishing methods. Despite the low number of sightings it is probably a common fish species. Norwegian topknot is found on rough grounds either inshore or on shallow offshore waters. It is most common between 20 and 50 m depth, but can be found up to 170 m deep. It is found in the southern North Sea and along the eastern North Sea coast, from Belgium to Norway.

The Norwegian topknot attains a maximum size of 12 cm but is mostly between 5 and 10 cm (Knijn *et al*., 1993).

Spawning takes place from March to June in the western Channel. The eggs are pelagic and are 0.7 to 0.9 mm in diameter. The eggs hatch in 6–7 days. Metamorphosis of the larvae takes place at a length of 9 to 11 mm. At 13 mm, juveniles have fully transformed to adult shape and coloration and live at the bottom.

The food of Norwegian topknot consists of young fish, worms and crustaceans. Larvae feed mostly on smaller copepod species, particularly *Pseudocalanus* and *Acartia*.

Known predators are black guillemot *Cepphus grylle* (frequent; Barrett and Anker-Nilssen, 1997) and harbour seal *Phoca vitulina* (rare; Krause, 1999; Tollit and Thompson, 1996; see also Leopold *et al*., 2001). Norwegian topknot is not on the IUCN Red list and is not important for fisheries.

Megrim *Lepidorhombus whiffiagonis*

The megrim is a common deep-water flatfish. It is found on the Atlantic coasts of northern Europe and in the deeper parts of the northern and central North Sea. It is also found in the western Mediterranean. Megrim can be found in depths between 10 and 400 m, but is most common between 50 and 300 m. It has occasionally been found at the surface and close inshore. Juveniles are mostly found in the less deep waters from 46 to 55 m. Megrim lives mostly on soft bottoms.

Megrim reaches a maximum length of 61 cm, most common are fish of 20 to 40 cm. Maximum life span is 22 years. Maturity in the Celtic Sea is reached at 25 to 28 cm, at the age 3 to 5 years. The von Bertalanffy growth parameter K is 0.13 per year.

Spawning occurs from March to June in deep water, west of Ireland and off Iceland. There are no known spawning grounds in the North Sea. The eggs are pelagic and 1.07 to 1.22 mm in diameter. The eggs hatch in 5–7 days. The pelagic larvae are found in the plankton in July and August. When larvae reach a length of 19 mm, they assume a benthic life. At this stage, transformation is almost complete.

Megrim feeds mostly on fish, flatfish (mostly deep-water scaldfishes), sprats, sandeels, dragonets, gobies and gadoids (mainly whiting). Crustaceans and squid are also an important food item. Younger fish feed mainly on crustaceans, *Crangon* spp., *Pandalus* spp., and mysids. Prey are probably caught just above the sea floor.

Megrim is preyed upon by hake *Merluccius merluccius* and John dory *Zeus faber* (Froese and Pauly, 2003). It is also a rare to frequent food item in the diet of grey seals *Halichoerus grypus* (Hammond and Prime, 1990; Hammond *et al*., 1994; see also Leopold *et al*., 2001).

Natural mortality of megrim is 0.22 (se 0.15–0.34) per year. The resilience of the megrim population is low; the minimum population doubling time is 4.5 to 14 years. The species is not on the IUCN Red list.

Megrim is of moderate economic importance as a food fish. Since 1945, yearly landings fluctuate between 500 and 1,000 tonnes.

Scaldfish *Arnoglossus laterna*

Scaldfish is a common fish that is found along the northeastern coast of the Atlantic and the North Sea coasts. It is mostly found in shallow water on soft, sandy or muddy, bottoms. Scaldfish can be taken in depths from 2 to 200 m, but is most often found between 10 to 60 m.

Scaldfish grow to a maximum size of 25 cm, but in the North Sea rarely exceeds 20 cm. Life span of scaldfish is at least 13 years (Knijn *et al*., 1993).

Sexual maturity is attained at the length of 7 to 9 cm and age 2 years. Growth of scaldfish is considered to be slow; the von Bertalanffy growth parameter K is 1.04 per year.

Spawning takes place form April to June off southern Ireland and from May to August in the North Sea. The fecundity of scaldfish is 2,078 (Knijn *et al*., 1993). The pelagic eggs are very small, 0.6 to 0.76 mm. Hatching takes place after 5 to 6 days. Larvae measure only 2.6 mm at hatching. The pelagic larvae are present in the water column from June to October. Metamorphosis takes place at lengths of 16 to 30 mm. Metamorphosis in the North Sea takes place at the smaller length range 16–20 mm.

The diet consists of mysids, amphipods, crustaceans (*Crangon* and *Pandalus*), small fish and fish larvae, polychaete worms and molluscs (Knijn *et al*., 1993; unpublished RIVO data). Juveniles eat mostly crustaceans, amphipods and polychaetes.

Scaldfish is rarely preyed upon, but has been found in the diet of cormorant *Phalacrocorax carbo* (Leopold and Van Damme, in prep.), common dolphin *Delphinus delphis* (Silva, 1999) and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003; see also Leopold *et al*., 2001).

Natural mortality of scaldfish is 1.53 (se 1.01–2.32) per year. The resilience of the population is medium; the minimum population doubling time is 1.4 to 4.4 years. The species is not on the IUCN Red list. Scaldfish has no economic value because of the small size.

4.16 Flatfishes (Heterosomata, Pleuronectidae)

Plaice *Pleuronectes platessa*

Plaice is a very abundant fish that can be found in the northeastern Atlantic from Greenland and Norway to Morocco and the Mediterranean. In the North Sea, it is found in the shallower waters. Plaice can be found in depths up to 200 m, but is most common between 10 and 50 m. The juveniles live in shallower water than adults. Plaice makes a winter migration to the spawning grounds.

Maximum size of plaice is 100 cm; maximum age is 50 years. However, due to heavy fishing, specimens larger than 50 cm and older than 15 years are rare. Growth is fast; the von Bertalanffy growth parameter K is 0.06 to 0.1 per year. Females grow faster and older than males. Males reach maturity at age 2 to 4 years and lengths of 18 to 26 cm. Females reach maturity later, at age 3 to 7 years and lengths 30 to 35 cm.

Spawning takes place from November to June at the spawning grounds in 20 to 50 m depth. The eggs are pelagic but sink gradually to the bottom as development proceeds. Egg diameter is 1.66 to 2.10 mm. The incubation of the eggs takes 10 to 21 days, after which the pelagic larvae emerge. The newly hatched larvae are 5 to 7.5 mm in size. The pelagic larvae are passively transported to the nursery grounds. Metamorphosis is completed at lengths of 10 to 13 mm. After metamorphosis, the larvae assume a bottom-living life. In winter the larvae move to deeper areas, but they return in spring. These migrations continue until 3 years of age when the juvenile plaice move to the deeper waters.

Diet of plaice consists of molluscs, crustaceans, worms (especially polychaetes), echinoderms and fish. The planktonic larvae feed on pelagic crustaceans.

Plaice is preyed upon by black-throated diver *Gavia arctica* (frequent-staple; Madsen, 1957), northern fulmar *Fulmarus glacialis* (frequent; Garthe *et al.*, 1996), little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), gannet *Sula bassana* (frequent; Garthe *et al.*, 1996), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Gremillet and Argentin, 1998; Härkönen, 1988; Kieckbusch, 1993; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Mills, 1969b; Nehls and Gienapp, 1997; Okill *et al.*, 1992; Paillard, 1985; Pearson, 1968; Steven, 1933; Van Damme, 1994; Warke and Day, 1995) (rare-frequent; Barrett *et al.*, 1990; Pearson, 1968), shag *P. aristotelis* (rare-frequent; Barrett *et al.*, 1990; Carss, 1993; Harris and Wanless, 1993; Pearson, 1968), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), red-breasted merganser *Mergus serrator* (frequent; Madsen, 1957), goosander *Mergus merganser* (rare; Madsen, 1957), great skua *Stercorarius skua* (rare-frequent; Albon *et al.*, 1976; Andersson, 1976; Bayes *et al.*, 1964; Booth, 1976; Brathay Exploration Group, 1967, 1968, 1969; Burton and Steventon, 1971; Campbell and Denzey, 1954; Collier and Stott, 1976; Collinge, 1925; Fisher and Lockley, 1954; Furness, 1974, 1976a, 1977a, 1977b, 1979; Furness, 1976b; Garthe *et al.*, 1996; Gudmundsson, 1954; Ingram, 1949; Jackson, 1966; Joensen, 1963; Lockie, 1952; Mawby, 1969, 1970, 1971, 1973; Meinertzhagen, 1941, 1959; Pennie, 1948; Perry, 1948; Pitt, 1922; Venables and Venables, 1955; Williamson, 1957; Witherby *et al.*, 1944), lesser black-backed gull *Larus fuscus* (frequent; Camphuysen, 1994; Garthe *et al.*, 1999), common gull *Larus canus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), herring gull *L. argentatus* (rare-frequent; Camphuysen, 1994; Garthe *et al.*, 1996; Löhmer and Vauk, 1970), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (frequent; Garthe *et al.*, 1996), common tern *Sterna hirundo* (rare-common; Frank, 1992; Niedernostheide, 1996; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Hartwig *et al.*, 1990; Niedernostheide, 1996; Pearson, 1968) razorbill *Alca torda* (rare; Madsen, 1957), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987; Martin, 1989), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Rae, 1965), grey seal *Halichoerus grypus* (rare-frequent; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987, 1990; Rae, 1973a; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-common; Behrends, 1982; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Rae, 1973a; Sievers, 1989; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-common; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1990), otter *Lutra lutra* (rare-frequent; Heggberget, 1993; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al.*, 2001), bull-rout *Myoxocephalus scorpius*, lumpsucker *Cyclopterus lumpus*, thornback ray *Raja clavata*, spur-dog *Squalus acanthias*, lesser weever *Echiichthys vipera*, grey gurnard *Eutrigla gurnardus*, brown shrimp *Crangon crangon*, sea gooseberry *Pleurobrachia pileus* and bottlenose dolphin *Tursiops truncates* (Froese and Pauly, 2003).

Natural mortality of plaice is 0.12 (se 0.08–0.18). The resilience of the plaice population is low; the minimum population doubling time is 4.5–14 years (K=0.08–0.1; tm=2–7; tmax=50; Fec=50,000). Plaice is not on the IUCN Red list.

Plaice is a very important fish in the European fishery. Landings rose from 90,000 tonnes in the 1960s to 200,000 in the 1980s. At present landings are around 50,000 tonnes.

Flounder *Platichthys flesus*

Flounder is an abundant fish and is the only European flatfish that can be found in fresh water. Flounder can be found along the northeastern Atlantic and North Sea coasts as well as in the western Mediterranean. It can be found in depths of 1–100 m. Flounder is a migrating fish; both juvenile and mature fish move in autumn from the inshore and estuarine feeding areas to the deeper waters. Juveniles move to the coastal areas, while mature fish move to the deeper, 20 to 50 m, spawning grounds. Flounder lives on sandy and muddy bottoms, where it can bury itself in the sand.

Maximum length of flounder is 60 cm, but specimens larger than 40 cm are rarely caught. Lifespan of the flatfish is 15 years. Males mature earlier than females. Males reach maturity at 20 to 25 cm and age 2 to 3 years, while females are mature at lengths of 25 to 30 cm and ages 3 to 4 years. Growth of flounder is fast; von Bertalanffy growth parameter K is 0.23 (Froese and Pauly, 2003).

Spawning takes place from January to June. In the southern North Sea spawning takes place from January to May at depths of 20 to 50 m. In the Baltic Sea flounder spawns from April to June at depths of 40 to 100 m. The small eggs (0.8 to 1.4 mm) are pelagic but slowly sink during development. Hatching occurs after seven days when larvae have reached a length of 2.5 to 3 mm. The pelagic larval flounder enter the nursery grounds and assume a bottom-dwelling life at 2.5 to 3 mm length. Metamorphosis takes places when larvae reach 15 to 30 mm.

Flounder stops feeding during the colder winter months. When moving to the shallower areas the fish resume feeding. The diet of flounder consists of molluscs (*Macoma*, cockles, mussels and *Mya*), polychaetes, crustaceans (shrimps, crabs, mysids and *Corophium*) and occasionally other fish. Larvae feed on copepods and diatoms. Juvenile flounder feed on molluscs and crustaceans.

Predators of flounder are red-throated diver *Gavia stellata* (rare; Durinck *et al.*, 1994), black-throated diver *G. arctica* (frequent; Madsen, 1957), common loon *G. immer* (staple; Madsen, 1957), little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990;

Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Kieckbusch, 1993; Leopold and Van Damme, in prep., Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Pearson, 1968; Steven, 1933; Van Damme, 1994; Warke and Day, 1995; rare-common; Adams, 1996; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1993, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Davies and Feltham, 1996; Härkönen, 1988; Kirby *et al.*, 1996; Lekuona and Campos, 1997; Leopold and Van Damme, in prep., Leopold *et al.*, 1998, Okill *et al.*, 1992; Pearson, 1968; Platteeuw *et al.*, 1992; Steven, 1933; Van Dam *et al.*, 1995; Veldkamp, 1994; Warke and Day, 1995), shag *P. aristotelis* (rare-frequent; Carss, 1993; Barrett *et al.*, 1990; Pearson, 1968), grey heron *Ardea cinerea* (present-frequent; Carss and Marquiss, 1996; Lekuona, 1999), lesser black-backed gull *Larus fuscus* (frequent; Garthe *et al.*, 1999), common gull *Larus canus* (rare-frequent; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), herring gull *L. argentatus* (frequent; Nogales *et al.*, 1995), common tern *Sterna hirundo* (rare-common; Frank, 1992; Niedernostheide, 1996; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Hartwig *et al.*, 1990; Niedernostheide, 1996; Pearson, 1968), razorbill *Alca torda* (rare; Madsen, 1957), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987; Martin, 1989), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Rae, 1965), grey seal *Halichoerus grypus* (rare-common; Bjørge, 1995; Hammond and Prime, 1990; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987; Rae, 1973a; Thompson *et al.*, 1996b), common seal *Phoca vitulina* (rare-staple; Behrends, 1982; Bjørge *et al.*, 1993; Bjørge, 1995; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Krause, 1999; Havinga, 1933; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Rae, 1973a; Sievers, 1989; Thompson *et al.*, 1991; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1990), otter *Lutra lutra* (rare-frequent; Heggberget, 1993; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al.*, 2001), pike *Esox lucius*, perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca*, sea gooseberry *Pleurobrachia pileus* (Froese and Pauly, 2003).

Natural mortality of flounder is 0.34 (se 0.22–0.51). Resilience of the population is medium; minimum population doubling time is 1.4–4.4 years (K=0.22–0.3; tm=2–5; tmax=15). Flounder is not on the IUCN Red list.

Flounder is of little economic importance in the North Sea, but it is important in the Baltic. Landings in the North Sea fluctuate between 1,000 and 4,000 tonnes yearly.

Dab *Limanda limanda*

The dab is a very abundant flatfish that can be found in the northeastern Atlantic, from the White Sea to the Bay of Biscay. It is found throughout the North Sea. Dab can be found at depths from 5 to 150 m, but are most common between 20 and 40 m. Dab shows a preference for sandy and muddy bottoms. Dab makes a summer migration into shallower waters.

Maximum size and lifespan of dab are 40 cm and 12 years, but fish larger than 25 cm are rare. Growth is relatively slow; the von Bertalanffy growth parameter K is 0.3 to 0.6 per year. Growth of females is slightly quicker than males. Males reach maturity at the end of their second year around 10 cm length. Females mature later, at age 3 to 5 years and a length of 20 cm.

Spawning period is from January to August in depths of 20 to 40 m. The pelagic eggs are small, 0.66 to 1.2 mm. The eggs develop in 3 to 12 days, depending on water temperature. The newly hatched larvae are pelagic and 2.6 to 4.0 mm long. Metamorphosis is completed at lengths of 12 to 20 mm. After metamorphosis larvae start a bottom dwelling live in the coastal nurseries. As the juveniles grow, they gradually move into deeper water.

Dab is an opportunistic feeder and the diet is very varied. The diet consists of crustaceans, echinoderms, molluscs, polychaetes and fish. Larvae of dab feed on copepods.

Dab is preyed upon by red-throated diver *Gavia stellata* (rare; Durinck *et al.*, 1994), black-throated diver *G. arctica* (frequent; Madsen, 1957), little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), northern fulmar *Fulmarus glacialis* (frequent; Garthe *et al.*, 1996), gannet *Sula bassana* (frequent; Garthe *et al.*, 1996), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1993, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Härkönen, 1988; Kieckbusch, 1993; Leopold and Van

Damme, in prep., Leopold *et al.*, 1998; Mills, 1969b; Nehls and Gienapp, 1997; Okill *et al.*, 1992; Paillard, 1985; Pearson, 1968; Reinhold, 1996; Steven, 1933; Van Damme, 1994; Warke and Day, 1995), shag *P. aristotelis* (rare-frequent; Barrett *et al.*, 1990; Pearson, 1968; Steven, 1933), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *Larus fuscus* (frequent; Camphuysen, 1994; Garthe *et al.*, 1996; Garthe *et al.*, 1999), common gull *L. canus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), herring gull *L. argentatus* (rare-frequent; Camphuysen, 1994, Garthe *et al.*, 1996; Löhmer and Vauk, 1970), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (frequent; Garthe *et al.*, 1996), common tern *Sterna hirundo* (rare-common; Frank, 1992; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Hartwig *et al.*, 1990; Pearson, 1968), razorbill *Alca torda* (rare; Madsen, 1957), black guillemot *Cepphus grylle* (present; Gates, 1998), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987; Martin, 1989), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Benke *et al.*, 1998; Rae, 1965), grey seal *Halichoerus grypus* (rare-common; Bjørge, 1995; Hammond and Prime, 1990; Pierce *et al.*, 1989; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987, 1990; Rae, 1973a; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-common; Behrends, 1982; Bjørge *et al.*, 1993; Bjørge, 1995; Brown and Pierce, 1997; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Rae, 1973a; Sievers, 1989; Thompson *et al.*, 1996b; Tollit and Thompson, 1996), harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1990; Nilssen *et al.*, 1995), otter *Lutra lutra* (rare-frequent; Heggberget, 1993; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al.*, 2001), bull-rout *Myoxocephalus scorpius*, cod *Gadus morhua*, whiting *Merlangius merlangus*, poor cod *Trisopterus minutus*, flounder *Platichthys flesus*, plaice *Pleuronectes platessa*, starry ray *Raja radiata*, spur-dog *Squalus acanthias* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of dab is 0.86 (se 0.57–1.31). The population resilience of dab is medium; the minimum population doubling time is 1.4–4.4 years (K=0.3–0.6; tm=2–3; tmax=12; Fec=50,000). Dab is not on the IUCN Red list.

Dab is an important commercial flatfish. It is mostly caught as by-catch when fishing for other commercial species. North Sea landings of dab rose from 5,000 tonnes in 1960s to 12,000 tonnes in 1980s.

Lemon sole *Microstomus kitt*

Lemon sole is a fairly common fish species that can be found in the northeastern Atlantic, from the Bay of Biscay to the White Sea and off Iceland. In the North Sea, it can be found on coastal banks, but it is not common inshore. It can be found from 10 to 200 m depth on various kinds of sediments, but mostly on stony bottoms.

Maximum size and life span of lemon sole are 65 cm and 23 years, however, specimens over 50 cm in length are rare. The von Bertalanffy growth parameter K is 0.17 to 0.42. Males reach maturity at ages 3 to 4, while females mature at ages 4 to 6.

Lemon sole spawns throughout the distribution area at depths of 50 to 150 m. Spawning period is from April to September. The eggs are pelagic and have a diameter of 1.13 to 1.45 mm. Incubation time of the eggs is 5 to 9 days and the eggs sink during development. The newly hatched 3.5 to 5.5 mm larvae are pelagic and can be found at 50 to 100 m depth. Metamorphosis takes place at lengths between 15 and 20 mm. The larvae start living at the bottom after metamorphosis.

Lemon sole has a specialised diet, which consists mostly of errant and sessile polychaete worms. Crustaceans, molluscs, echinoderms and coelenterates are also preyed on.

Predators of lemon sole are black-throated diver *Gavia arctica* (frequent; Madsen, 1957), little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), northern fulmar *Fulmarus glacialis* (frequent; Garthe *et al.*, 1996), gannet *Sula bassana* (frequent; Garthe *et al.*, 1996), cormorant *Phalacrocorax carbo* (rare-staple; Barrett *et al.*, 1990; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Kieckbusch, 1993; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Pearson, 1968; Reinhold, 1996; Steven, 1933; Van Damme, 1994; Warke and Day, 1995) (rare-frequent; Barrett *et al.*, 1990; Pearson, 1968), shag *P. aristotelis* (rare-frequent; Barrett *et al.*, 1990; Pearson, 1968), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *Larus fuscus* (frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999), common gull *L. canus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996), great black-backed gull *Larus marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (frequent; Garthe *et al.*, 1996), common tern *Sterna hirundo* (rare-common; Frank, 1992; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Hartwig *et al.*, 1990; Pearson, 1968), razorbill *Alca torda* (rare; Madsen, 1957), black guillemot *Cepphus grylle* (frequent; Barrett and Anker-Nilssen, 1997), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987; Martin, 1989), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Rae, 1965), grey seal *Halichoerus grypus* (rare-frequent; Bjørge, 1995; Hammond and Prime, 1990; Hammond *et al.*, 1994; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Rae, 1973a; Thompson *et al.*, 1996b), harbour seal *Phoca vitulina* (rare-common; Bjørge, 1995; Bjørge *et al.*, 1993; Brown and Pierce, 1997; Des Clers and Prime, 1996; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Rae, 1973a; Sievers, 1989; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Tollit *et al.*, 1997), harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Nilssen *et al.*, 1990), otter *Lutra lutra* (rare-frequent; Heggberget, 1993; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al.*, 2001) and whiting *Merlangius merlangus* (Froese and Pauly, 2003).

Natural mortality of lemon sole is 0.25 (se 0.17–0.38). The resilience of the lemon sole population is medium; the minimum population doubling time is 1.4–4.4 years (tm=3–6; tmax=23). Lemon sole is not on the IUCN Red list.

The lemon sole is of moderate economic importance and is usually a by-catch species. Landings vary between 5,000 and 8,000 tonnes per year.

Witch *Glyptocephalus cynoglossus*

Witch is a common flatfish that is mainly found in the deeper waters on fine muddy sand or muddy bottoms. It is most commonly found between 50 and 300 m depth, but can occasionally be found inshore and at depths up to 1460 m. Witch is distributed in the eastern Atlantic, from northern Spain to northern Norway, around Iceland and in the northern and central North Sea, and can also be found in the western Atlantic. Witch is considered to be a non-migratory fish, but it has been recorded to make a winter migration into shallower areas in Swedish waters.

Witch can grow up to a maximum of 60 cm in length and age of 25 years. It is rarely caught larger than 40 cm and older than 12 years. Maturity is reached at ages 4 to 7 and lengths of 25 to 35 cm. Males mature earlier than females. Witch grows fast; von Bertalanffy growth parameter K is 0.15 to 0.20 (Froese and Pauly, 2003).

Spawning takes place from March to September at depths of 50 to 150 m. In the Irish Sea spawning occurs from March to May. In the northern North Sea, spawning is later in the year. Although witch is not found in the southern North Sea, eggs can be found here between January and June (Knijn *et al*., 1993). Eggs are pelagic and measure 1 to 1.25 mm. After 7 to 8 days the eggs are fully incubated and larvae of 4 to 6 mm hatch. Larvae are present from March to September. Metamorphosis takes places at lengths of 4 to 5 cm. Only then larvae start living at the bottom, which is much later compared to other flatfish species.

Witch feed mostly on polychaete worms, crustaceans (amphipods, decapods, mysids), starfish and molluscs. The juveniles' diet consists of molluscs and copepods.

Predators of witch are whiting *Merlangius merlangus*, minke whales *Balaenoptera acutorostrata*, American anglerfish *Lophius americanus*, harp seal *Phoca groenlandica*, grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of witch is 0.30 (se 0.20–0.45) per year. Population resilience of witch is low; minimum population doubling time is 4.5–14 years (K=0.15–0.2; tmax=25). Witch is not on the IUCN Red list.

The economic importance of witch is moderate. North Sea catches are 1,000 tonnes per year, but in the 1980s, landings were doubled.

Long rough dab *Hippoglossoides platessoides*

Long rough dab is an arctic species that can be found in the northwestern and northeastern Atlantic, from Murmansk to the English Channel. In the North Sea it is found in the deeper areas (around 55 m and deeper). In the more northern part of its distribution it can be found from the shore to 400 m. Long rough dab lives on soft, sandy or muddy, bottoms.

Maximum size of long rough dab in European waters is 40 cm. In the Western Atlantic, it can grow up to 80 cm and 30 years. The von Bertalanffy growth parameter K is 0.06 to 0.12. Female growth is faster. Maturity is reached at 15 cm length and ages 2 or 3.

Long rough dab spawns pelagic in March and April. The eggs are pelagic but sink during development. Egg diameter varies from 1.38 to 2.64 mm. Incubation time is 11 to 14 days. The newly hatched larvae are pelagic and measure 4 to 6 mm. Metamorphosis takes place at length of between 20 to 35 mm. The young long rough dab assume a bottom-dwelling life when reaching 35 or 45 mm. The juveniles move to deeper water as they grow older.

The diet of long rough dab consists of polychaetes, crustaceans, echinoderms, molluscs, ophiurans and fish. Larvae feed on copepods, especially *Calanus finmarchicus*.

Predators of long rough dab are red-throated diver *Gavia stellata* (rare; Durinck *et al.*, 1994), black-throated diver *G. arctica* (frequent; Madsen, 1957), little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), northern fulmar *Fulmarus glacialis* (rare-frequent; Garthe *et al.*, 1996; Phillips *et al.*, 1999a), gannet *Sula bassana* (frequent; Garthe *et al.*, 1996), cormorant *Phalacrocorax carbo* (rare-staple; Barrett et *al.*, 1990; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Kieckbusch, 1993; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Pearson, 1968; Steven, 1933; Van Damme, 1994; Warke and Day, 1995) (rare-frequent; Barrett *et al.*, 1990; Pearson, 1968), shag *P. aristotelis* (rare-frequent; Barrett *et al.*, 1990; Pearson, 1968), grey heron *Ardea cinerea* (present; Carss and Marquiss, 1996), great skua *Stercorarius skua* (frequent; Garthe *et al.*, 1996), lesser black-backed gull *Larus fuscus* (frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Götmark, 1984), common gull *L. canus* (rare-frequent; Garthe *et al.*, 1996; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), herring gull *L. argentatus* (frequent; Garthe *et al.*, 1996), great black-backed gull *L. marinus* (frequent; Garthe *et al.*, 1996), black-legged kittiwake *Rissa tridactyla* (frequent; Garthe *et al.*, 1996), common tern *Sterna hirundo* (rare-common; Frank, 1992; Stienen and Brenninkmeijer, 1992; Wendeln *et al.*, 1994), Arctic tern *S. paradisaea* (rare-frequent; Hartwig *et al.*, 1990; Pearson, 1968), razorbill Alca torda (rare; Madsen, 1957), Atlantic puffin *Fratercula arctica* (present; Anker-Nilssen, 1987; Martin, 1989), harbour porpoise *Phocoena phocoena* (rare-frequent; Aarefjord *et al.*, 1995; Rae, 1965), grey seal *Halichoerus grypus* (rare-frequent; Bjørge, 1995; Hammond and Prime, 1990; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Rae, 1973a), harbour seal *Phoca vitulina* (rare-common; Bjørge, 1995; Hall *et al.*, 1998; Härkönen, 1987, 1988; Härkönen and Heide-Jørgensen, 1991; Krause, 1999; Pierce *et al.*, 1990; Pierce *et al.*, 1991a; Pierce *et al.*, 1991b; Rae, 1973a; Sievers, 1989; Tollit and Thompson, 1996), harp seal *P. groenlandica* (rare-frequent; Lindstrøm *et al.*, 1996; Lydersen *et al.*, 1991; Nilssen *et al.*, 1990; Nilssen *et al.*, 1995; Ugland *et al.*, 1993), bearded seal *Erignathus barbatus* (common; Hjelset *et al.*, 1999), otter *Lutra lutra* (rare-frequent; Heggberget, 1993; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al.*, 2001), haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, halibut *Hippoglossus hippoglossus*, long rough dab *Hippoglossoides platessoides* and bottlenose dolphin *Tursiops truncates* (Froese and Pauly, 2003).

Natural mortality of long rough dab is 0.13 (se 0.09–0.20). The population resilience of long rough dab is medium; the minimum population doubling time is 1.4–4.4 years (rm=0.43; K=0.06–0.12; tm=2–11; tmax=30; Fec=50,000). Long rough dab is not on the IUCN Red list.

Long rough dab is moderately important around Norway, Iceland and Greenland. Yearly landings are around 100,000 tonnes. In the North Sea, it has no economic value.

Halibut *Hippoglossus hippoglossus*

Halibut is a common fish in the eastern Atlantic, from the Bay of Biscay to the Barents Sea and Iceland, and western Atlantic, from Virginia USA to Greenland. However, it is a relatively rare fish in the North Sea, it can only be found in the northernmost part of the North Sea. Halibut can be found in depths ranging from 50 to 2000 m on sand, gravel or mud bottoms and occasionally on rocks. It is also sometimes found in the water column. There is a separation in the distribution of young and mature and male and female specimens. Juveniles and mature females are usually found on coastal and offshore banks at depths of 110 m, while males are mostly taken on the edge of the continental shelf.

Halibut is a strong migratory fish. Local migrations are known where mature fish migrate from the spawning grounds to the shallower more prey rich waters but young fish are also able to make long migrations between the different American, Icelandic and North Sea stocks.

Maximum length and life span are respectively 300 cm and 50 years. Females larger than 200 cm and males larger than 150 cm are rare due to heavy overfishing. Females grow faster but mature later than males. Females mature at age 7 to 18 years at lengths of 110 cm, while males mature at ages 4 or 5 and 55 cm length. Growth of halibut is slow; von Bertalanffy growth parameter K is 0.03 (Froese and Pauly, 2003).

Spawning takes place from December to April at 300 to 1000 m depth. Known spawning grounds are northern Norway and Greenland. The slopes of the continental shelf are probably also spawning grounds. The eggs are pelagic and drift slowly to the surface. Egg diameter is 3 to 4 mm. The eggs hatch after 9 to 16 days and hatched larvae are 6 to 7 mm long. Larvae are present in the water from April to August. Metamorphosis takes place at 3.5 to 4 mm. At 5 to 7 mm, larvae start living at the bottom in waters of 30 to 100 m deep. The larvae move gradually up the shore to shallow, 20 to 60 m deep, nurseries where they spend their first year.

Halibut is an active predator and large fish leave the bottom to forage for demersal prey. The diet of large halibut consists almost only of fish, especially gadids and also halibut, and some crustaceans including lobsters, molluscs and cephalopods. Juveniles feed on crustaceans, molluscs, sandeels and small flatfish.

Reported predators are spiny dogfish *Squalus acanthias* and halibut (Wheeler, 1969; Froese and Pauly, 2003).

Natural mortality of halibut is low, 0.04 (se 0.03–0.06). The population resilience is very low; the minimum population doubling time is more than 14 years (Musick *et al.*, 2000).

The halibut is endangered and on the IUCN Red list.

The halibut is an extreme valuable food fish, but due to heavy overfishing it is of minor economic importance in the North Sea. After WW II catches peaked at 4,000 tonnes a year, but decreased to 500 tonnes in the 1980s.

Main ref.: Wheeler, 1969; Knijn *et al*., 1993; Muus *et al*., 1999; Froese and Pauly, 2003.

4.17 Flatfishes (Heterosomata, Soleidae)

Sand sole *Solea lascaris*

Sand sole is a common flatfish along the coast of the eastern Atlantic and Mediterranean. In the North Sea, it is found in the southern part and the Channel. It is found on different sediments, sand, mud and gravel, in shallow inshore areas, 5 to 350 m deep. In winter, the fish move to deeper water.

Sand sole can grow up to 40 cm and maximum lifespan is 15 years. Maturity is reached at the age of 4 and a length of 22 cm. The von Bertalanffy growth parameter K is 0.38 (Froese and Pauly, 2003).

Spawning takes place from May to August, in the Channel peak spawning is in July. The eggs are pelagic and 1.2 to 1.4 mm in diameter. The hatched larvae are 2.2 to 4 mm long. Larvae are pelagic and can be found from July to October.

The diet of sand sole consists of worms, molluscs and crustaceans.

Predators are not reported. Natural mortality is 0.62 (se 0.41–0.94). Sand sole population resilience is medium; minimum population doubling time is 1.4–4.4 years (K=0.41; tm=4; tmax=15). Sand sole is not on the IUCN Red list.

In the southern areas, sand sole is of minor economic importance.

Sole *Solea vulgaris*

Sole is the most common of Solidae in the European waters. It can be found in the shallower waters of the eastern Atlantic, from Trondheim to Senegal and the Mediterranean. In the North Sea, it is found in the shallower coastal areas. Sole is found in depths from 0 to 150 m on soft, sandy or muddy, bottoms. Sole makes a winter migration into the deeper areas. In spring juveniles migrate to the shallower areas, while adults move to the spawning grounds.

Maximum reported length of sole is 70 cm and maximum age is 40 years. However, specimens larger than 50 cm and age 14 are rare. The von Bertalanffy growth parameter K is 0.39 per year. Maturity is reached at ages 3 to 5 years and lengths of 23 to 35 cm. Males mature earlier than females.

Sole spawns from March to June on spawning grounds at depths of 20 to 50 m. The eggs are pelagic and the diameter is 0.95 to 1.6 mm. Hatching takes place after 10 days of incubation. Newly hatched larvae are 2.5 to 3.7 mm long. The pelagic larvae are passively transported to the nursery areas. Metamorphosis is completed after 4 to 6 weeks at lengths of 12 to 18 mm. The larvae adopt a benthic life after metamorphosis. As the larvae grow, they move gradually into deeper waters.

Sole is a night predator. The diet consists of amphipods, polychaete worms, bivalves, gastropods, brittle stars and fish. The pelagic larvae feed on copepods and fish larvae.

Predators of sole are little grebe *Tachybaptus ruficollis* (rare; Fox, 1994), cormorant *Phalacrocorax carbo* (rare-staple; Boudewijn and Dirksen, 1998; Boudewijn *et al.*, 1994; Buckens and Raeijmaekers, 1992; Goutner, 1997; Gremillet and Argentin, 1998; Leopold and Van Damme, in prep.; Leopold *et al.*, 1998; Nehls and Gienapp, 1997; Paillard, 1985; Warke and Day, 1995), shag *P. aristotelis* (rare; Gremillet and Argentin, 1998), common gull *Larus canus* (rare-frequent; Garthe *et al.*, 1999; Kubetzki, 1997; Kubetzki *et al.*, 1999), lesser black-backed gull *L. fuscus* (frequent; Camphuysen, 1994), herring gull *L. argentatus* (frequent; Camphuysen, 1994), common tern *Sterna hirundo* (frequent-common; Frank, 1992), Atlantic puffin *Fratercula arctica* (present; Martin, 1989), harbour porpoise *Phocoena phocoena* (frequent; Benke *et al.*, 1998), grey seal *Halichoerus grypus* (rare-staple; Hammond and Prime, 1990; Pierce *et al.*, 1991a; Prime and Hammond, 1987, Prime and Hammond, 1990), harbour seal *Phoca vitulina* (rare-frequent; Behrends, 1982; Hall *et al.*, 1998; Havinga, 1933; Krause, 1999; Pierce *et al.*, 1991a; Sievers, 1989), harp seal *P. groenlandica* (frequent; Nilssen *et al.*, 1990), otter *Lutra lutra* (rare-frequent; Kruuk *et al.*, 1987; Watson, 1978) (see also Leopold *et al*., 2001), whiting *Merlangius merlangus*, cuckoo ray *Raja naevus*, blonde ray *R. brachyura*, thornback ray *R. clavata* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003).

Natural mortality of sole is 0.57 (se 0.38–0.87). The resilience of the sole population is medium; the minimum population doubling time is 1.4–4.4 years (K=0.21–0.33; tm=3–5; tmax=26; Fec=100,000). Sole is not on the IUCN Red list. Sole is a highly valued food fish. Yearly landings vary from 20,000 to 40,000 tonnes.

Solenette *Buglossidium luteum*

The solenette is a very common flatfish on the eastern Atlantic and Mediterranean coasts. In the North Sea, it is found in the southern and central part and along the British coasts. It is mostly found offshore on sandy bottoms in moderate depths, 5–450 m.

Maximum reported lengths are 18 cm. Solenette can become 15 years old. Males reach maturity at 6 to 7 cm, while females are 7 to 8 cm. Both reach maturity at age 3. Growth of solenette is medium; the von Bertalanffy growth parameter K is 0.54 (Froese and Pauly, 2003).

Spawning takes place from March to August. In the Channel, spawning activity is from March to July. The eggs are pelagic and of moderate diameter, 0.64 to 1.03 mm. Hatching takes place after 5 to 6 days and newly hatched larvae are 2 mm long. The pelagic larvae can be found from April to November. The larvae become bottom dwelling when they reach 12 mm.

The solenette is an opportunistic predator. The diet consists of amphipods, crustaceans, polychaete worms and bivalves. Also juvenile shrimp and fish are taken.

Solenette is preyed upon by cormorant *Phalacrocorax carbo* (frequent; Leopold and Van Damme, in prep.; Paillard, 1985), lesser black-backed gull *Larus fuscus* (frequent; Camphuysen, 1994), common guillemot *Uria aalge* (frequent; Leopold and Camphuysen, 1992), poor cod *Trisopterus minutus* and grey gurnard *Eutrigla gurnardus* (Froese and Pauly, 2003; see also Leopold *et al*., 2001).

The natural mortality of solenette is 1.00 (se 0.66–1.52). The resilience of the population is medium; the minimum population doubling time is 1.4–4.4 years (K=0.54–0.61; tm=3; tmax=13). Solenette is not on the IUCN Red list. Because of its small size solenette has no economic importance.

Thickback sole *Microchirus variegatus*

Thickback sole is found offshore in the northeastern Atlantic and Mediterranean. In the North Sea, it is found in small numbers along the British

Isles and the Channel. It is found in depths of 18 to 400 m, but is most common between 37 to 92 m. Thickback sole prefers sandy and muddy bottoms.

Thick back sole can grow up to 35 cm and 14 years old. Maturity is reached at 14 cm and age 3. The von Bertalanffy growth parameter K is 0.24–0.37 (Froese and Pauly, 2003).

Spawning in the Channel takes place from March to May, around Ireland the spawning season lasts until August. Thickback sole spawns in waters that are 55 to 73 m deep. The eggs are pelagic and have a diameter of 1.02 to 1.42 mm. The newly hatched larvae have a size of 2.4 to 2.9 mm. The larvae are pelagic but gradually move deeper and at 12 mm start living at the bottom. Larvae are present from March to August.

The diet of thickback sole consists of polychaete worms, eupagurids, amphipods, small gastropods, small lamellibranches, ophiuroids, bivalves and shrimps.

Only one predator has been reported, hake *Merluccius merluccius* (Froese and Pauly, 2003).

The thickback sole population has a medium resilience; the minimum population doubling time is 1.4–4.4 years (K=0.37; tm=3; tmax=14). The thickback sole is not on the IUCN Red list. Due to its low numbers in the North Sea, there is no targeted fishery on thickback sole.

4.18 Diet of commercial species

For many fish species, either qualitative or quantitative information exists on their diet (Table 3.14). Extensive quantitative information exists for the main commercial species where taxa and/or size-strata are distinguished in the diet of each species and age-group (Greenstreet, 1996; Daan, 1989; ICES, 1997).

Table 3.14 Diet composition (%) of the main predators in the North Sea (recalculated from Greenstreet, 1996). For each species, the food items that were found in the stomachs are highlighted.

>0–1% | >1%–10% | >10%–50% | >50

Prey \ Predator	Cod	Haddock	Whiting	Saithe	Plaice	Dab	Lemon sole	Mackerel	Horse mackerel	Norway pout	Herring
Phaeophyta	0.0										
Porifera	0.0		0.0								
Cnidaria (Coelenterata)	0.1	0.0	0.1	0.0			21.0	0.4			
Hydrozoa						1.9					
Ctenophora		0.0	0.0								
Nemertea (Rhynchocoela)		0.0	0.0				0.5				
Gephyrea							1.6				
Echiura	0.1	0.0	1.2								
Sipuncula	0.0										
Priapulida	0.3		0.0								
Platyhelminthes			0.0								
Annelida	5.4	10.3	3.8	0.0				0.1			
Polychaeta						9.5	57.8			0.1	
Pectinaria koreni					29.6						
Nephtys spp.					2.2						
Other Polychaeta[a]					7.3						
Mollusca							10.7				
Polyplacophora		0.0									
Gastropoda	0.6	0.5	0.5	0.0				1.2			
Bivalvia	0.8	3.2	0.0			1.1		0.0			
Abra alba					42.9						
Cultellus pellucidus					3.0						
Ensis ensis					2.3						
Scaphopoda	0.0	0.0									
Cephalopoda	1.0	0.9	2.5	2.0				1.6			
Other Mollusca[b]					2.2						
Unidentified Mollusca			0.3								
Pycnogonida	0.0	0.0									
Crustacea							4.7				
Ostracoda										0.0	0.0
Copepoda			1.6	0.0				20.8	10.7		
Calanoida		0.3								36.4	
Paracalanus parvus											0.1
Pseudocalanus elongatus											0.0
Calanus finmarchius											9.0
Centropages typicus											0.0
Temora longicaudata											1.7
Euchaeta norvegica											0.0
Paraeuchaeta norvegica										2.3	
Leptostraca		0.0									
Mysidacea	0.0	0.0	0.1								3.0
Mysidae										1.8	
Amblyops abbreviata										0.2	
Boreomysis arctica										0.0	
Boreomysis nobilis										0.0	
Pseudomma roseum										0.1	

Table 3.14 Continued.

Prey \ Predator	Cod	Haddock	Whiting	Saithe	Plaice	Dab	Lemon sole	Mackerel	Horse mackerel	Norway pout	Herring
Pseudomma affine										0.0	
Erythrops serrata										0.0	
Cumacea	0.0	0.1	0.1			1.7					
Lampropidae										0.0	
Amphipoda			0.8	0.1		9.1		0.5			
Gammaridea	0.1	1.0									0.0
Gammaridae										0.1	
Hyperiidea	0.0	1.8									4.1
Hyperiidae										0.1	
Parathemisto abyssorum										1.1	
Caprellidea		0.0									
Caprellidae										0.0	
Isopoda			0.1	0.0							
Flabellifera		0.7								0.0	
Valvifera	0.0	0.1									
Asellota		0.0									
Tanaidacea		0.0									
Euphausiacea	3.8	9.2	9.4	33.4							76.1
Euphausiidae								27.5		22.3	
Meganyctiphanes norvegica										23.7	
Thysanoessa raschii										2.1	
Decapoda						30.3			22.0		
Caridea		1.9	2.8					1.9			
Crangonidae	2.4	0.1	4.6	0.0				0.1		0.3	
Crangon crangon									0.0		0.0
Pontophilus norvegicus										0.1	
Pandalidae			0.2	0.0						1.2	
Pandalus borealis										0.7	
Pasiphaeidae										0.4	
Pasiphaea tarda										0.4	
Other Caridea[c]	1.1										
Other Caridea[d]				0.0							
Other Caridea[e]									1.5		
Nephrops norvegicus	5.2										
Macrura			0.5								
Anomura	3.6	2.1	1.0	0.0				0.0			
Galatheidae										0.0	
Munida sarsi										0.0	
Brachyura				0.0				1.9			
Oxystomata	0.0										
Oxyrhyncha	0.6	0.8									
Cancridea	3.8	0.0									
Brachyrhyncha	9.0	0.8	2.7								
Upogebia spp.					10.5						
Decapod zoëa											0.0
Unidentified Crustacea			2.2								
Echinodermata	0.8	11.7	0.5	0.0			1.8			0.0	
Ophiuroidea						46.3					
Chaetognatha	0.0	0.0	0.2					1.1		6.4	
Sagitta setosa											0.1
Urochordata	0.0	0.5	0.6	0.0				4.9			

Table 3.14 Continued.

Prey \ Predator	Cod	Haddock	Whiting	Saithe	Plaice	Dab	Lemon sole	Mackerel	Horse mackerel	Norway pout	Herring
Ascidiae							1.3				
Appendicularia			0.1								
Cephalochordata	0.0	0.0									
Fish							0.5			0.0	
Cod	3.8	0.0	0.2	0.2				0.1	7.4		
Haddock	9.5	0.1	5.0	11.4				0.0	4.3		
Whiting	9.3	0.0	3.0	0.2				0.0	27.9		
Norway Pout	7.7	6.3	8.9	32.2				7.3			
Norway pout post-larvae											0.3
Unidentified gadoids			0.2						14.7		
Hake			0.0								
Clupeidae									0.8		
Herring	4.1	0.1	6.6	0.6				3.7	8.8		
Sprat	2.1	0.3	9.4	0.4				3.2	0.4		
Clupeoid post-larvae											5.1
Unidentified Clupeoidea			0.9								
Sandeels	7.3	7.2	27.3	9.7				16.6	0.0		
Ammodytes spp.											0.0
Mackerel	1.0		0.0					0.1			
Poor cod			0.1								
Silvery pout			0.1								
Unidentified rocklings			0.1								
Wolfish			0.0								
Horse mackerel			0.0								
Norway haddock			0.0								
Lesser weever			0.0								
Stickleback			0.0								
Pipe fish									0.0		
Unidentified gurnards			0.0						0.7		
Unidentified blennies			0.0								
Pearlsides		10.7	0.0								
Argentines			0.0								
Dragonets	2.4		0.1								
Crystal goby									0.6		
Unidentified gobies	4.9	10.7	1.9								
Goby post-larvae											0.1
Plaice	0.7										
Plaice eggs											0.3
Sole	0.1		0.1								
Lemon sole	0.1		0.0								
Dab	5.7	0.0	0.0	0.1				0.0			
Witch			0.0								
Long rough dab	2.4	10.7	0.1								
Unidentified flatfish			0.0								
Flatfish larvae									0.1		
Other fish[f]				9.6							
Other fish eggs[g]											0.0
Other fish post-larvae[h]											0.1
Unidentified prey	0.0	7.8	0.1					6.7			

[a] Other than *Pectinaria koreni* and *Nephtys* spp.

[b] Other than *Abra alba*, *Cultellus pellucidus* and *Ensis ensis*.
[c] Other than Crangonidae
[d] Other than Crangonidae and Pandalidae
[e] Other than *Crangon crangon*.
[f] Other than cod, haddock, whiting, Norway pout, herring, sprat sandeels and dab.
[g] Other than plaice eggs.
[h] Other than clupeoid, Norway pout and goby post larvae.

Two large sets of quantitative diet data of the main fish predators were collected in 1981 ('the year of the stomach') and 1991. The focus was on the species cod, whiting, mackerel, saithe and haddock. For these species, diet data exist for each of the main age-groups separately.

Other predators that were sampled in 1991 include elasmobranchs (sharks e.g. tope *Galeorhinus galeus*, lesser spotted dogfish *Scyliorhinus canicula* and rays e.g. starry ray *Raja radiata*), gadoids (pollack *Pollachius virens*, bib *Trisopterus luscus*), gurnards (e.g. grey gurnard *Eutrigla gurnardus*, red gurnard *Aspitrigla cuculus*), sandeels (*Ammodytidae*) and flatfish (e.g. turbot *Scophthalmus maximus* and brill *S. rhombus*). Most of these data exist in national databases and have not been published yet.

In general, a good spatial coverage was achieved in each quarterly period. The diets were quantified as the percentage contribution by weight of each major prey taxon to the stomach contents of each predator.

In case fish were only identified to the family level (e.g. Gadidae, Clupeidae, Pleuronectidae or Soleidae) it was possible to redistribute them within their family as follows:

- Gadidae: cod, haddock, Norway pout, saithe, whiting and non-commercial gadids
- Clupeidae: herring, sprat and non-commercial clupeids
- Pleuronectidae: plaice, dab, lemon sole and non-commercial pleuronectids
- Soleidae: sole and non-commercial soleids.

5. Benthos and habitats

Table 3.16 contains summary of the evaluation of families and benthic habitats that were evaluated for the inclusion in the significant North Sea web.

5.1 Annelida

Aphroditidae

Economic importance: None.

Ecological importance as prey: These polychaetes have been found in the diet of dogfish (Kaiser and Spencer, 1994), cod *Gadus morhua* (Pihl, 1994), wolffish *Anarhichas lupus* (Liao and Lucas, 2000) and plaice *Pleuronectes platessa* (Amara *et al.*, 2001).

Ecological importance as predators: Slow moving carnivores which feed on microscopic animals but sometimes on sessile or slow-moving organisms (Fauchald and Jumars, 1979). We found no information on whether predation by species belonging to Aphroditidae impacts associated fauna.

Functional importance: We found no functional importance for this family.

Societal importance: None.

Arenicolidae

Economic importance: Among Arenicolidae, two species are harvested, *Arenicola marina* and *A. defodiens* which are collected for bait. It is difficult to estimate the scale of the bait digging for the North Sea. Bait is either collected for own use but in some cases, bait diggers are contracted for the bait digging (Olive, 1993). The commercial values for both *Arenicola* species in the UK ranges from £8–12 for 100 worms (Fowler, 1999). Van den Heiligenberg (1987) estimated that about 1% of the total *A. marina* population is removed each year in the western part of the Wadden Sea.

Ecological importance as prey: The lugworm *A. marina* are eaten mainly by bird predators. In the Wadden Sea, lugworms are preyed upon by eiders *Somateria mollissima*, (Leopold, 2002) and bar-tailed godwits *Limosa lapponica* (Scheiffarth, 2001; Tyler-Walters, 2001a). The European sea-bass *Dicentrarchus labrax* eats lugworms but in minor quantities (Kelley, 1987). Smith (1975 cited in Baird *et al.*, 1985) estimated that *A. marina* provided about 94% of the energy content of the diet of *L. lapponica*.

Ecological importance as predators: Not predatory.

Biogeochemical functions: *Arenicola marina* is used routinely as a standard bioassay organism for assessing the toxicity of marine sediments (Bat and Raffaelli, 1998). The species shows a high sensitivity to some synthetic compounds and is used to control infestation by parasites on fish farms (Cole *et al*., 1999). It is moderately sensitive to hydrocarbon contamination (Levell, 1976; Prouse and Gordon, 1976) and fairly resistant to heavy metal contamination (Bryan, 1984). Bioturbation by *A. marina* can promote release of nitrogen from sediments and affect concentration of silicate in the porewater (Huettel, 1990). He concluded that *A. marina* was important for the release of nutrients in Wadden Sea sediments.

Biological activity and habitat functions: The lugworm *A. marina* makes non-permanent L-shaped burrows with the worm deposit-feeding head-down. The burrows of *A. marina* provide an important habitat for micro- and meiofauna and the diversity of meiofauna is enhanced in the funnel area (Reise, 1987). In one study, lugworms accounted for up to 93% of the total meiofaunal density in the entire subsurface sediment (Reise, 1983a). During summer, green algae (*Enteromorpha* spp.) can become attached to the funnels of lugworms and as such may have minor impacts on near-bed flows and facilitate colonisation by meiofauna (Reise, 1983b). The bioturbation of the worm affects densities of some macrofauna species such as *Pygospio elegans*, *Corophium volutator* and *Macoma balthica* (Flach, 1992a; Hiddink *et al*., 2002a). Furthermore, sediment disturbance by lugworms can affect *C. volutator* densities indirectly by forcing them to leave their tubes, which makes them more vulnerable to predation (Flach and De Bruin, 1994). The lugworm is a bioturbator and the rate of sediment reworking varies with substrate type and temperature (Retrauban *et al*., 1996) but can range from 2 ml per worm per day in winter to about 12–13 ml (wet volume) in summer (Sheader, 1995). At frequently occurring densities of some tens of adults per m^2, lugworms can rework the entire upper sediment layer within 1 year (Cadée, 1976).

Societal importance: None.

Chaetopteridae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: *Chaetopterus variopedatus* form parchment like tubes that protrude from the surface. The worm itself is about 25 cm long (Nelson-Smith *et al.*, 1990). Like other large tube-building polychaetes, the physical presence of the tubes may enhance settlement of larvae, alter near-bed flow and increase diversity, but to our knowledge, this has not been investigated.

Societal importance: None.

Magelonidae

Economic importance: None.

Ecological importance as prey: *Magelona* spp. have been recorded in the diet of dab (<40 mm) and sole (Amara *et al*., 2001) and plaice (Rijnsdorp and Vingerhoed, 2001).

Ecological importance as predators: Not predatory.

Functional importance: No important functions were found.

Societal importance: None.

Maldanidae

Economic importance: None.

Ecological importance as prey: Maldanids (mainly *Maldane sarsi*) have been recorded in the diet of long-rough dab *Hippoglossoides platessoides* (Klemetsen, 1993).

Ecological importance as predators: Not predatory.

Biogeochemical functions: Faecal deposition by the maldanid *M. sarsi* when found in high densities can contribute greatly to the organic-carbon supply for detrivorous fauna (Holte, 2001).

Biological activity and habitat functions: Maldanids are tubiculous deep sub-surface head-down feeding (Fauchald and Jumars, 1979). The sediment reworking rate has been estimated for *M. sarsi* in Norway (Holte, 2001).

The faecal wet weight production of a single *M. sarsi* was approx. 1 ml ind.$^{-1}$ day^{-1} and the faecal deposition 4,500 l m^{-2} year^{-2} where their density was highest (20,653 ind. m^{-2}) (Holte, 2001).

Societal importance: None.

Nephtyidae

Economic importance: The largest specimens of *Nephtys hombergii* are used as bait and are particularly sought-after by some anglers, including match fishermen. Some are used as food resource in aquaculture (Fowler, 1999). We have no information on how much bait digging takes place for *Nephtys*.

Ecological importance as prey: The larger sized nephtids are frequently eaten by bird predators. In the Wadden Sea, *N. hombergii* is eaten by eiders (Leopold, 2002) and bar-tailed godwits (Scheiffarth, 2001). It has been recorded in the diet of the long-rough dab (Klemetsen, 1993).

Ecological importance as predators: Nephtids are generally considered carnivores (Fauchald and Jumars, 1979). Numerous field and laboratory experiments have been carried out to investigate the impacts of predation by nephtids on the benthic community structure. In a laboratory experiment, Desroy *et al*. (1998) reported that predation by *N. hombergii* resulted in 8–12 times reduction in the numbers of juvenile *Nereis diversicolor*. Manipulative field experiments have demonstrated predation impacts by *Nephtys* on macrofauna densities (e.g. Schubert and Reise, 1986) while none on meiofauna (Reise, 1979a). Finally, Beukema (1987) analysed long term data from the Wadden Sea and demonstrated a negative relationship in the abundance of *N. hombergii* and two of its prey species, the polychaetes *Scoloplos armiger* and *Heteromastus filiformis*.

Biogeochemical functions: Reported to accumulate polychlorinated biphenyls in Narragansett Bay (RI, USA) (Means and McElroy, 1997).

Biological activity and habitat functions: No information found.

Societal importance: None.

Nereidae

Economic importance: Bait digging for *Nereis* species takes place widely within the North Sea, e.g. on the NE-coast of England (Blake, 1979). It has been estimates that the retail trade for *Nereis virens* which has been collected by bait digging can be worth up to £5 million (Fowler, 1999). Aquaculture for *N. virens* takes now place in NE-England and Netherlands, and these are sold as a bait (Olive, 1999). In the 1990s, the production rose up to 30 tonnes in the late 1990s with a retail value of £750,000. Aquaculture of *N. virens* should decrease the detrimental effects of bait digging for this species.

Ecological importance as prey: Reported predators on nereids are whiting *Merlangius merlangus* (Kaiser and Spencer, 1994), gobies *Pomatoschistus* spp. (Davey and George, 1986), plaice *Pleuronectes platessa* and sole *Microstomus kitt* (Rijnsdorp and Vingerhoed, 2001), waders such as bar-tailed *Limosa lapponica* and black-tailed godwits *Limosa limosa* (Scheiffarth, 2001; Moreira, 1994) and oystercatchers *Haematopus ostralegus* (Boates and Goss-Custard, 1989). In the Ythan estuary, *Nereis diversicolor* is eaten by redshank, curlew, oystercatcher, shelduck *Tadorna tadorna* and flounder *Platichthys flesus* (Raffaelli and Milne, 1987) and by the shore crab *Carcinus maenas* (Davey and George, 1986).

Ecological importance as predators: Nereids are generally considered to be omnivores or carnivores (e.g. Scaps, 2002). Manipulative field experiments have shown that predation by *N. diversicolor* can result in decreased densities of chironomid larvae and *Corophium volutator* (Rönn *et al*., 1988) and of juvenile (<1.5 mm) *Macoma balthica* (Hiddink *et al*., 2002a). In another study, the combined effects disturbance in the top cm of the sediment and predation by *Nereis virens* probably explains reduced numbers of meiofauna (Tita *et al.*, 2000). In contrast, Kennedy (1993) found only minor impact of predation on meiofauna.

Biogeochemical functions: No information found.

Biological activity and habitat functions: The sediment reworking by *Nereis* resembles ‘ploughing’ of surface sediment during food-searching activity. Tita *et al*. (2000) showed that sediment disturbance caused by *N. virens* significantly reduced the diversity of meiofauna in the top cm of the sediment. Other studies have shown reductions in the numbers of the amphipod *Corophium volutator* due to sediment disturbance caused by *Nereis* (Ólafsson and Persson, 1986).

Societal importance: None.

Orbiniidae

Economic importance: None.

Ecological importance: *Scoloplos armiger* was a major prey item for the polychaete *Nephtys hombergii* on tidal flats near the island of Sylt in the North Sea (Schubert and Reise, 1986). Beukema (1987) found a negative relation between biomass and rate of increase in *S. armiger* and abundance of *N. hombergii*. Furthermore, Van der Meer *et al.* (2000) showed that the reproductive rate of *S. armiger* was negatively correlated with density of *N. hombergii*. *Scoloplos armiger* can be important in the diet of shorebirds when found in high densities. Pienkowski (1980 and 1982 cited in Baird *et al.*, 1985) estimated between 4.2 and 8.6% of the annual production of *S. armiger* found on mudflats of Lindisfarne (NE-England) was removed by grey plover *Pluvialis squatarola*, ringed plover *Charadrius hiaticula* and bar-tailed godwits *Limosa lapponica* during winter. *Scoloplos armiger* has been reported to be an important prey item for the bar-tailed godwits *L. lapponica* in the Wadden Sea (Scheiffarth, 2001).

Functional importance: None.

Societal importance: None.

Oweniidae

Economic importance: None.

Ecological importance as prey: Predated upon by long-rough dab *Hippoglossoides platessoides* (Klemetsen, 1993).

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: *Owenia fusiformis* forms tough flexible tubes composed of sand grains or shell fragments glued together in an overlapping fashion. Tubes may be so numerous that they bind the sand together, although many may be empty (Nelson-Smith *et al.*, 1990). Tubes of *O. fusiformis* can stabilise sediments and affect the near bed flow when found in high densities (>2000 cm^2) (Fager, 1964; Eckman *et al.*, 1981). Settlement of larvae of *Lagis koreni* can be enhanced within dense beds of *O. fusiformis*, as dense aggregates of tubes stabilize the sediment and so act as particle traps (Olivier *et al*., 1996).

Societal importance: None.

Pectinariidae

Economic importance: None.

Ecological importance as prey: *Lagis koreni* is important in the diet of dab *Limanda limanda* and plaice *Pleuronectes platessa* (Macer, 1967; Lockwood, 1980; Basimi and Grove 1985; Rijnsdorp and Vingerhoed, 2001).

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: Pectinariids (including *L. koreni*) form tubes of a single layer of sand grains of shell fragments cemented together. Only the tip of the tube projects above the surface of the sand (Nelson-Smith *et al.*, 1990). *Lagis koreni* are found in mobile silts and sands. They browse upside down in sediments, selectively ingesting small and medium sized particles. The sediment surface in areas where high densities of *L. koreni* occur consists of loose fabric of large particles (faecal pellets) with a high water content which is easily eroded (Seiderer and Newell, 1999). These authors estimated the rate of reworking of sediments by this polychaete ranged from 0.56 to 83 mg $ind.^{-1}$ h^{-1}.

Societal importance: None.

Sabellaridae

Economic importance: None.

Ecological importance as prey: Predation on *Sabellaria alveolata* is probably minor, probably due to the tough structures of the tube (Cunningham *et al.*, 1984). These have been recorded in the diet of *Carcinus maenas* and

Blennius pholis (Taylor *et al*., 1962). We lack information on predation on other sabellarid species.

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: Among sabellarids, *S. alveolata* creates tubes of coarse sand grains cemented together (e.g. Wilson, 1971). *Sabellaria alveolata* reefs may take the form of extensive sheets, hummocks or more massive and extensive reefs consisting of hummocks (e.g. Gruet, 1982). They are found on range of substrata from pebble to bedrock (Cunningham *et al.*, 1984). *Sabellaria spinulosa* tubes are harder than that of *S. alveolata* but only rarely forms reefs. The high physical complexity of *Sabellaria* reefs is likely to affect near bed hydrodynamic flow and facilitate passive entrainment of larvae and meiofauna. Associated fauna within reefs of *S. alveolata* have been shown to be more diverse than in adjacent non-reefs areas. Cunningham *et al.* (1984) found 18 associated animal species but 20 plant species within *S. alveolata* reefs, mainly epifauna and crevice species, of which most were largely absent from non-reef habitats. The species composition varied with the age of the *S. alveolata* reef. George and Warwick (1985) reported that the number of species within reefs of *S. spinulosa* was two times greater compared to non-reef areas. The pink shrimp *Pandalus montagui* (Warren and Sheldon, 1967) is often associated with reefs. Some evidence for competition for space exists. *Sabellaria alveolata* has been reported to outcompete other species (Cunningham *et al.*, 1984), whereas this sabellarid can be outcompeted by mussels (Perkins, 1988 cited in Holt *et al.*, 1998).

Societal importance: None.

Sabellidae

Economic importance: None.

Ecological importance as prey: Sabellids are rarely found in diets. They have been recorded in the diet of lemon sole *Microstomus kitt* (Høines and Bergstad, 2002) and long-rough dab (Klemetsen, 1993).

Biogeochemical functions: No information found.

Biological activity and habitat functions: Where dense tubelawns of *Sabella pavonina* occur, fine sediments are accumulated which in turn can facilitate increase in abundance of burrowing invertebrates. A number of species of algae and sessile invertebrate can grow attached to *Sabella* tubes, and many mobile invertebrates and fish can live among the tubes.

Societal importance: None.

Serpulidae

Economic importance: None.

Ecological importance as prey: Serpulids have been reported to be predated upon by the sea urchin species *Echinus esculentus* and *Psammechinus miliaris*, the brittle star *Ophiotrix fragilis* and the starfish *Asterias rubens* (Bosence, 1979a).

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: There is a large number of species found in this polychaete family, but we will limit ourselves to *Serpula vermicularis*. This polychaete forms calcareous tubes and in sheltered areas their tubes can aggregate together to form small reefs (Nelson-Smith *et al.*, 1990). Studies have shown that these reefs provide a habitat for a large number of sessile organisms such as sponges, sea anemones, bivalves, ascidians and other serpulid species (Bosence, 1979a). The diversity and species richness within reefs of *S. vermicularis* can be much greater compared to non-reef areas. Although no information is available, it is likely that tube aggregations and reefs of *S. vermicularis* stabilise sediments and reduce the velocity of near-bed flow.

Societal importance: *Serpula* reefs are included as a Habitat Action Plan under the UK Biodiversity Action Plan.

Spionidae

Economic importance: None.

Ecological importance as prey: Predators on spionids include 0-group dabs (Amara *et al.*, 2001), plaice (Poxton *et al.*, 1983) and long-rough dab *Hippoglossoides platessoides* (Klemetsen, 1993). Poxton *et al*. (1983)

showed that 0-group plaice fed predominately on the palps of the spionids whereas adults on whole individuals.

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: Spionids are small tubiculous polychaetes which can be found in extremely high densities (see e.g. Nelson-Smith *et al.*, 1990; Noji and Noji, 1991; Bolam and Fernandes, 2002). Dense lawns of spionid tubes can increase deposition of fine particular matter greatly (Daro and Polk, 1973). Tubes of the spionid *Pygospio elegans* can stabilise sediments if found in sufficient densities (Brey, 1991; Bolam and Fernandes, 2003). Reise (1983a) showed that the presence of *P. elegans* promoted the abundance of small benthic organisms (Nematoda, Ciliata and Polychaeta) by about 40%. Similarily, Bolam and Fernandes (2003) showed that the community structure within and outside patches with *P. elegans* differed in species composition. In contrast, there is no evidence that tubes of this species provide refuge against predation (Mattilla, 1997). Some evidence exists on biological interactions among spionids although they may not play a big role. Spionids have been thought to inhibit rapid colonization of the polychaete *Capitella* spp. (Whitlatch and Zajac, 1985).

Societal importance: None.

Terebellidae

Economic importance: None.

Ecological importance as prey: The terebellid *Lanice conchilega* is an important food source for many fish predators such as long-rough dab, dab, sole and plaice (Amara *et al.*, 2001; Klemetsen, 1993). *Lanice conchilega* has been reported to occur in more than 50% of plaice stomachs in May, June and July, in more than 50% of dab stomachs in June and in more than 50% of sole stomachs in July (Amara *et al.*, 2001). In the Wadden Sea, oystercatcher *Haematopus ostralegus*, curlew *Numenius arquata* and redshank *Tringa totanus* were found to selectively forage on the associated fauna within tubelawns of *L. conchilega*, whereas the worms themselves were more important in gulls (mainly common gull, *Larus canus*) diets (Petersen and Exo, 1999).

Ecological importance as predators: Not predatory

Biogeochemical functions: *Lanice conchilega* has been shown to accumulate organochlorine residues (Goerke and Weber, 1998).

Biological activity and habitat functions: Among terebellids, the biology and ecology of *L. conchilega* is best known. Dense tube fields of this species have been shown to facilitate colonisation by other animals. Zühlke (2001) showed that the diversity and species richness were enhanced within dense tubefields of *L. conchilega*. Similarily, empty *Lanice* tubes can themselves provide a habitat for the polychaetes *Harmothoe lunulata* and *Eumida sanguinea* (Hartman-Schröder, 1971; Eagle, 1975; Carey, 1982). Tubes of *Lanice* affect the near-bed flow and therefore may facilitate settlement of larvae and meiofauna. In addition, mussels can attach themselves directly to the tubes with byssus threads (Callaway, 2003). Zühlke *et al.* (1998) showed that the tubes of *Lanice* and tube mimics facilitated settlement of spionids, *Capitella capitata* and juveniles of *Mya arenaria*. Similarily, numbers of the predatory polychaetes *Eteone longa* and *Nereis diversicolor* were also enhanced, presumably as a result of higher prey abundance. The stabilisation of sediments by the terebellid *L. conchilega* is very pronounced, sometimes resulting in formation of mounds or a 'plateau' which has been shown to elevate the bed by 20–30cm (Féral, 1989). Mound formation is often mediated by algae caught by the tube-caps (Carey, 1987).

Societal importance: None.

5.2 Arthropoda

Ampeliscidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: Amphipods belonging to Ampeliscidae are tube-builders. The tubes of this amphipod may stabilise sediments. Biological interactions among *Ampelisca*, snails and spionids have been reported from the USA (Conlan, 1994) but we have no information on such interactions for the North Sea.

Societal importance: None.

Axiidae

Economic importance: None.

Ecologically importance as prey: Has been recorded in the diet of cod, haddock, the Norway lobster *Nephrops norvegicus* and the four-bearded rockling *Onos cimbrus* (Buchanan, 1963)

Ecologically importance as predator: Not predatory.

Biogeochemical functions: As for other crustacean megafaunal crustacean burrowers, the deep burrowing activity of *Calocaris macandreae* can contribute to the mineralization of carbon and oxygenation of the sediment (Rosenberg *et al.*, 2000). Rosenberg *et al.* (2000) showed that in areas where *C. macandreae* and *Maera loveni* were abundant; the redox potential discontinuity (RPD) of sediments was a most at 11 cm depth.

Biological activity and habitat functions: Axiids construct deep (up to 22 cm) generally U-shaped tunnels, with a cluster of circular burrow openings of 1–2 cm wide; sometimes up to 2–17 surface openings per individual burrow system (Nash *et al.*, 1984; Rosenberg *et al.*, 2000). Bioturbation rates for this species have not been investigated (Hughes and Atkinson, 1997). Widdicombe *et al.* (2000) investigated the effects of bioturbation of *C. macandreae* on other macrofaunal organisms. Biotubation by this crustacean had no impact on species richness or community structure but caused some decrease in abundances of the polychaetes *Heteromastus filiformis* and *Pholoe minuta* while increase in *Chaetozone setosa*.

Societal importance: None.

Callianassidae

Economic importance: None.

Ecological importance as prey: Callianassids have been found in stomachs of plaice (Rijnsdorp and Vingerhoed 2001).

Ecological importance as predators: Not predatory.

Biogeochemical functions: Due to the deep burrows this species makes, the area of the water/sediment interface is increased which allows oxygen to penetrate deeper into sediments (Ott *et al*., 1976; Astall *et al*., 1997). The efflux of phosphate from *Callianassa subterranea* burrows was significantly greater compared to sediments not containing this crustacean (Hughes *et al*., 2000). The intensive bioturbation by *C. subterranea* is likely to have a large impact on physical and chemical processes (e.g. Branch and Pringle, 1987).

Biological activity and habitat functions: *Callianassa subterranea* is primarily a sub-surface deposit feeder but can also supplement its diet by suspension feeding. The burrow consists of a lattice of tunnels and chambers connected to the surface by an inhalant and exhalant shaft and can reach depths of greater than 86 cm (e.g. Nickell *et al*., 1995). Nickell *et al*. (1995) estimated that, at a minimum, 8 g dry weight m^{-2} d^{-1} were ejected to the surface during bioturbation and about 34 g m^{-2} d^{-1} transported subsurface. Rowden *et al*. (1998) estimate the annual sediment turnover as a result of bioturbation by *C. subterranea* in the North Sea to be around 11 kg dry weight m^{-2} y^{-1}. The bioturbation by *C. subterranea* alters the structural and geotechnical characteristics of the substratum (Rowden *et al*., 1998). Several studies carried out outside the North Sea have reported large impact of bioturbation by *Callianassa* species on associated fauna (e.g., Posey, 1986; Tamaki, 1988). Impacts of sediment reworking by *C. subterranea* on associated fauna have not been studied in the North Sea. However, there is some evidence that the burrows of *C. subterranea* in the North Sea provide a temporary refuge for fish such as gobies and errant polychaetes (Nickell and Atkinson, 1995).

Societal importance: None.

Cancridae

Economic importance: *Cancer pagurus* is harvested in the South Western Irish Sea for their claws in the spring and whole meat in the autumn and is important as a bait for the whelk fishery. At the peak of the fishery, 470 tonnes of brown crab were going into the whelk fishery each year (Fahy, 1999). This species is harvested within the North Sea (QSR, 2000) but we found no further information on this fishery. However in the UK, the total number of crabs landed increased from 22,500 tonnes in 1997 to 25,700 in 2001 (DEFRA, 2001).

Ecological importance as prey: *Cancer pagurus* has been recorded in the diet of elasmobranchs such as angel shark *Squatina squatina*, starry smoothhound *Mustelus asterias*, thornback ray *Raja clavata*, lesser spotted dogfish *Scyliorhinus canicula*, and spurdog *Squalus acanthias* (Ellis *et al.*, 1996).

Ecological importance as predators: *Cancer pagurus* is an active predator which preys manly on bivalves but to lesser extent on crustaceans and polychaetes (Shelton *et al.*, 1979). The foraging behaviour and prey size selectivity has been investigated for this species (Lawton and Hughes, 1985; Lake *et al.*, 1987; Mascaro and Seed, 2001).

Biogeochemical functions: No information found.

Biological activity and habitat functions: Sediment disturbance by the crab *C. pagurus* may have some impact on fauna. During feeding, *C. pagurus* creates pits of approximately 30 cm in diameter and 10 cm deep (Thrush, 1986a). Hall *et al*. (1991) showed that both diversity and abundance of fauna was reduced within the perimeter of the feeding pit. However, in a subsequent study where *C. pagurus* was excluded from areas of 2 × 2 m for 12 months, no differences in benthic community within and outside the excluded area could be detected. They concluded that pit digging by *C. pagurus* had no long term, large scale (landscape) effects on benthic community structure.

Societal importance: None.

Corophiidae

Economic importance: None.

Ecological importance as prey: Predator-prey relationships for *Corophium volutator* have been studied extensively. This amphipod constitutes a very important prey item for a large number of fish, bird and invertebrate predators. In the Ythan estuary, it is extensively preyed upon by waders such as redshank *Tringa totanus* (Goss-Custard, 1977), oystercatcher *Haematopus ostralegus* and shelduck *Tadorna tadorna* (Raffaelli and Milne, 1987), flounder *Platichthys flesus* (Summers, 1980) and the brown shrimp *Crangon crangon* (Raffaelli *et al*., 1989). It is probably preyed upon by all wader species which forage on intertidal mudflats, such as the grey plover *Pluvialis squatarola* (Durell and Kelly, 1990). Several studies have investigated the impacts of invertebrate predation on *C. volutator* populations. Field experiments have shown reduced numbers of *Corophium* in plots containing the polychaetes *Nereis virens* (Commito, 1982) *and Nereis diversicolor* (Rönn *et al*., 1988). These authors concluded that the decrease of *C. volutator* was a result of combination of predation and that sediment disturbance from worms' feeding activity. In contrast, other studies found limited evidence for predation impacts by *Carcinus maenas, C. crangon* (Raffaelli *et al*., 1989) or the sand goby *Pomatoschistus minutus* (Jaquet and Raffaelli, 1989) on *C. volutator* densities.

Ecological importance as predators: Not predatory.

Biogeochemical functions: Corophiid amphipods have been shown to accumulate copper, zinc and cadmium (Bat *et al*., 1998). Their influence on nutrient dynamics is not clear. Mortimer *et al*. (1999) showed that the mudflat macrofauna (dominated by *Nereis diversicolor*, *Macoma balthica* and *C. volutator*) of the Humber Estuary, modified the nutrient fluxes during periods of high mudflat sediment stability, whereas the impact of *Corophium per se* on nutrient fluxes were not possible to discern (Mortimer *et al*., 1999).

Biological activity and habitat functions: Amphipods belonging to Corophiidae are tube-builders. The tubes are small and only protrude slightly the sediment surface. They are sensitive towards bioturbation and often found in reduced abundances in areas where sediment reworking by the lugworm *Arenicola marina* and common cockles *Cerastoderma edule* takes place (Flach, 1992b). Furthermore, these bioturbators can force *Corophium* to leave their burrow, increasing the risk that they will be predated (Flach and De Bruin, 1994). Sediment disturbance and predation by *Nereis* species have been shown to reduce the density of *Corophium* (Ólafsson and

Persson, 1986). Finally, weed mats overlying sediments can result in serious declines in *Corophium* densities (Hull, 1987). The biological activity of this amphipod can both stabilise and destabilise (by inhibiting formation of diatom films) sediments, but *C. volutator* populations have the potential to reduce significantly the densities of benthic diatoms during feeding (Grant and Daborn, 1994; Gerdol and Hughes, 1994)

Societal importance: None.

Corystidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: *Corystes cassivelaunus* buries itself during the day but emerges during the night for foraging. The prey consists almost entirely of burrowing invertebrates, predominantly lamellibranchs, polychaetes and amphipods (Hartnoll, 1972).

Functional importance: No information found.

Societal importance: None.

Crangonidae

Economic importance: The average landings of the brown shrimp *Crangon crangon* from the North Sea was roughly 25,000 t per year over the period 1995–1999 (QSR, 2000). The shrimp is mainly caught in the coastal zones in the Wadden Sea along the coasts from Denmark to Belgium. Most of the fishery takes place in the Wadden Sea with landings of *C. crangon* between 1983 and 1993 on average 22,000 t year^{-1} (Del Norte-Campos and Temming, 1998).

Ecological importance as prey: *Crangon crangon* is an important prey for dab (Høines and Bergstad, 2002), long-rough dab (Ntiba and Harding, 1993), starry ray (Skjæraasen and Bergstad, 2000) and cod and whiting (Greenstreet, 1996; Pihl, 1994). Finally, the brown shrimp may be an important food resource for whiting during winter (Henderson and Holmes, 1989).

Ecological importance as predators: *Crangon crangon* is strictly predatory and preys on juvenile fish and invertebrates. The diet differs greatly between sediment types. Predator-prey relationships of *C. crangon* have been extensively investigated. Predation by this species have been shown to reduce densities of 0-group flounders and plaice and interfere with settling behaviour of juvenile plaice (Van der Veer and Bergman, 1987; Van der Veer *et al*., 1991). In contrast, Burrows *et al*. (2001) found no impact of predation by this species on 0-group larvae. Effects of predation by *C. crangon* in Ythan were limited although some effects on size distribution of *Corophium volutator* were found (Raffaelli *et al*., 1989). However, Bonsdorff and Pearson (1997) concluded that *C. crangon* may affect densities of *Capitella* spp. indirectly by cropping their tails and destroying their tubes during feeding. Predation pressure on 0-group bivalves such as *Macoma balthica* can be high in the low intertidal but not in the high intertidal as the vertical distribution of the shrimp is limited up the shore (Hiddink *et al*., 2002b). Dolmer *et al*. (2001) showed that *Crangon crangon* scavenges on damaged fauna in recently dredged areas.

Biogeochemical functions: *Crangon crangon* is known to accumulate PCB's, organochlorines and cadmium (e.g. Roose *et al*., 1998).

Biological activity and habitat functions: *Crangon crangon* has high ecological importance as a predator. However, we found little evidence that it was of functional importance.

Societal importance: None.

Galatheidae

Economic importance: Among Galatheidae, there is a very small fishery of *Munida rugosa*, with annual landings of about 10 tonnes. Most of the fishing takes place in the Clyde area (Hughes, 1998a), predominately using pots (Fowler, 1999). We found no information whether these crabs are harvested in the North Sea.

Ecological importance as prey: Reported to be predated upon by starry ray *Raja radiata* (Skjæraasen and Bergstad, 2000).

Ecological importance as predators: No information found.

Functional importance: No information found.

Societal importance: None.

Laomediidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information found.

Biological activity and habitat functions: *Jaxea nocturna* inhabits very deep (up to 90 cm) burrows of obliquely-descending tunnels, sometimes with one or more vertical shafts (Nash *et al*., 1984; Pervesler and Dworschak, 1985; Nickell *et al*., 1995; Nickell and Atkinson, 1995). The animal deposit-feeds from the walls of its burrow and may also scavenge organic material from the sediment surface. It is a bioturbator on muddy bottoms but little is known about the rate of sediment reworking. One study estimated the rate of sediment ejected to the sediment surface to be around 4 g dry matter ind.$^{-1}$ d^{-1} (Hughes and Atkinson, 1997; Nickell *et al*., 1995).

Societal importance: None.

Majidae

Economic importance: Species belonging to Majidae are rarely fished for human consumption in the UK (Fowler, 1999). There is a small fishery for *Maja squinado* in the North Sea (QSR, 2000).

Ecological importance as prey: In the US, *Hyas* species are important in the diet of the eider *Somateria mollisima* (Guillemette *et al*., 1992). We found no information on predation on *Hyas* species within the North Sea.

Ecological importance as predators: Two species belonging to Majidae occur within the North Sea, *Hyas coarctatus* and *H. araneus*. Arsenault and Himmelman (1996) concluded that in a study carried out in Canada that predation pressure by *H. araneus* on scallop populations was considerable. We found no information on predation impacts by Majidae in the North Sea.

Functional importance: No information found.

Societal importance: None.

Nephropidae

Economic importance: The Norway lobster *Nephrops norvegicus* is of high commercial importance. Prior to the 1950s, *N. norvegicus* was not heavily exploited but since then has grown rapidly in importance to the UK fishing fleet. In 1995, the most important grounds in the North Sea were the Fladen Ground (7,087 tonnes), the North and South Minches (3,656 and 4,678 tonnes respectively) and the Firth of Forth (Hughes, 1998a). Over the period 1996–2000, landings in UK by all vessels ranged between 28 and 31 thousand tonnes. Out of roughly 29,000 tonnes of *Nephrops* landed by UK fleet in 2000, 42% (12,000 tonnes were caught in the North Sea (Area IV) (DEFRA, 2001). The landings for UK were much higher than by North Sea countries (Table 3.15). There is some fishery for the common lobster *Homarus gammarus* on the east coast of Scotland. There have been several stock studies in order to enhance stocks of *H. gammarus* at various localities in the UK, Norway and France. This involve release of hatchery-reared juveniles to the wild and which are harvested after 4–5 years by which these have attained minimum legal size (e.g. Burton, 2001).

Table 3.15 Average landings of *Nephrops* (t) in 1998–2000 in the North Sea (area IV) and in among the countries in area VII which are part of the North Sea (VII) in (ICES, 2002b)

Country	Area IV	Area VII
Belgium	423	2
Denmark	1,714	
France		2,945
Netherlands	642	
UK	11,954	6,434
Norway	127	
Total	**14,860**	**9,381**

Ecological importance as prey: The Norway lobster *N. norvegicus* is very an important prey item for wolffish, long rough dab, haddock, skate, dogfish and cod (Hughes, 1998a).

Ecological importance as predators: *Nephrops norvegicus* is a predator (Hughes and Atkinson, 1997) and has been reported to prey on the burrowing shrimp *Calocaris macandreae* (Smith, 1988). We found no more information on predation by this species.

Biogeochemical functions: Burrows allow oxygen to penetrate deeper into the sediment (Ott *et al*., 1976; Astall *et al*., 1997).

Biological activity and habitat functions: Burrows of *Nephrops norvegicus* may be very large, with tunnels over a metre in length and with oblique openings >10 cm in diameter. Burrows range from straight or T-shaped tunnels to highly complex systems formed by groups of individuals, penetrating the sediment to a depth of 20–30 cm. Large piles of excavated sediment are often seen around the burrow entrances (Rice and Chapman, 1971; Tuck *et al*., 1994; Hughes and Atkinson, 1997). Burrows of *N. norvegicus* can be utilised by other burrowing megafauna and vice versa. Tuck *et al*. (1994) reported that about 34% of *N. norvegicus* burrows showed evidence of interactions with other species, predominately with the Echiuran worm *Maxmuelleria lankesteri* (70%) but to lesser extent the goby *Lesueurigobius friesii* and the thalassinidean *Jaxea nocturna*. *Nephrops norvegicus* is a bioturbator which reworks the sediment in similar manner as other large burrowing megafauna such as *Callianassa* and *Upogebia*. No published data on sediment reworking rates for *N. norvegicus* exist (Hughes and Atkinson, 1997).

Societal importance: None.

Paguridae

Economic importance: Species belonging to Paguridae (hermit crabs) are sometimes used as fish bait together with other crabs (Fowler, 1999).

Ecological importance as prey: Known predators are wolffish *Anarhichas lupus* (Liao and Lucas, 2000) long-rough dab *Hippoglossoides platessoides* (Ntiba and Harding, 1993) and starry ray *Raja radiata* (Skjæraasen and Bergstad, 2000).

Ecological importance as predators: Little is known about predation effects of hermit crabs. Reise (1979a) concluded that predation by *Pagurus bernhardus* had minor impact on meiofauna. *Pagurus bernhardus* have been shown to migrate into recently trawled areas where they scavenge on fauna which has been damaged or exposed as a result of trawling (Ramsay *et al*., 1996). Lack of scavenging response by *Pagurus prideaux* may be due to the fact that *P. bernhardus* can outcompete its conspecific in areas where discarding takes place (Kaiser *et al*., 1998a).

Biogeochemical functions: The content of five cyclic organochlorine compounds has been determined in eggs and adults of *P. bernhardus* in the North Sea (Knickmeyer and Steinhart, 1990).

Biological activity and habitat functions: We found no information on functional importance, apart from competitive interactions between *P. bernhardus* and *P. prideaux* (Kaiser *et al*., 1998a).

Societal importance: None.

Pandalidae

Economic importance: *Pandalus borealis* is commercially exploited by demersal shrimp trawlers in the North Sea, mainly in Skagerrak and Norwegian Deeps. Landings from ICES sub-area IV (which covers most of the North Sea) ranged between 3,807 and 9,284 tonnes over the period 1991–2001. Over the period 1997–2001, the proportion of landings of shrimps by country was as follows: Denmark (27.6%), Norway (34.8%), Sweden (2.3%), England (0.7%) and Scotland (6.8%) (ICES, 2003d). The stock seems to be within safe biological limits and has increased from 1990 and onwards. Fishing effort has declined since 1993 and is currently estimated to be at the lowest observed level (ICES, 2003d). Over the period 1990–1999, the average commercial value of landing was £10.9 million (Anon., 2000a).

Ecological importance as prey: The shrimp *Pandalus borealis* are preyed upon by gadoids, redfishes, halibut, long rough dab, skates, rayfish and dogfish (Muus and Dahlstrøm, 1985, ICES, 2003d), 0-group whiting (Bromley *et al.*, 1997) and long rough dab (Ntiba and Harding, 1993). It has been reported in the diets of the roundnose grenadier *Coryphaenoides rupestris* and great silver smelt *Argentina silus*, in the Skagerrak (Bergstad *et al.*, 2001). The predator-prey relationships between *P. borealis* and the cod have been much studied outside the North Sea such as in NW Atlantic and Barents Sea. Several studies have concluded that cod predation can regulate shrimp densities (e.g. Berenboim *et al.*, 2000). To our knowledge, predator-prey relationships between cod and shrimp have not been investigated to any extent in the North Sea.

Ecological importance as predators: None.

Functional importance: None.

Societal importance: None.

Portunidae

Economic importance: In the UK, three species belonging to Portunidae are harvested. There is a small fishery with pots for *Necora puber*. *Liocarcinus depurator* is sometimes collected for bait and *Carcinus maenas* is in some places collected for human consumption (Fowler, 1999).

Ecological importance as prey: Portunids were reported in the diet of wolffish *Anarhichas lupus* (Liao and Lucas, 2000).

Ecological importance as predators: Among Portunidae, predator-prey relationships have been well studied for *Carcinus maenas*. Buschbaum (2002) showed that exclusion of *C. maenas* from areas of a rocky shore resulted in greater numbers of *Balanus crenatus* and concluded that recruitment of this barnacle was strongly affected by crab predation. In another study, predation by *C. maenas* caused reductions in densities of the bivalves *Macoma balthica* and *Cerastoderma edule*, but the magnitude of effects were location and substrate type specific (Richards *et al*., 1999). Raffaelli *et al*., (1989) demonstrated minor predation impacts by this crab on densities of estuarine inafaunal macrofauna. Jensen and Jensen (1985) postulated that juvenile *C. maenas* can prey so heavily on spat of common cockle *C. edule* that further development of beds can be prevented. The combined effects of predation effects and sediment disturbance during feeding activity of *C. maenas* can result in decreased meiofaunal densities (Schratzberger and Warwick, 1999). Less is known on predation impacts among other portunid species. Hall *et al*. (1990a) found little evidence that *L. depurator* had impact on abundance of macrofaunal densities, while Thrush (1986b) demonstrated significantly reduced numbers of the spionid *Pseudopolydora pulchra*.

Biogeochemical functions: The shorecrab *Carcinus maenas* is known to accumulate PCB and heavy metals of various kinds such as mercury and cadmium (e.g. Bondgaard *et al*., 2000).

Biological activity and habitat functions: Portunids are of high ecological importance as scavengers and predators. We found no information which suggested that they were of high functional importance.

Societal importance: None.

Upogebiidae

Economic importance: None.

Ecological importance as prey: Known predators are thornback ray *Raja clavata* haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* (Hall-Spencer and Atkinson, 1999).

Ecological importance as predators: None.

Biogeochemical functions: The very deep burrows of upogebiids increase the area of the water/sediment interface and introduce oxygenated conditions at depth in the sediment (Ott *et al*., 1976; Astall *et al*., 1997).

Biological activity and habitat functions: Burrows are relatively simple, consisting of one or two connected U- or Y-shaped components penetrating the sediment to depths of up to 25 cm (Dworschak, 1983; Nickell and Atkinson, 1995; Astall *et al*., 1997). Shafts descending from the main U-component may penetrate much more deeply into the sediment. Surface openings are usually inconspicuous holes without associated mounds. *Upogebia* species are primarily suspension-feeders, actively pumping water through their burrows and filtering out particulate matter (Dworschak, 1983). Burrows of *Upogebia* (and other burrowing megafauna) increase the subsurface complexity of the habitat. The mud-lined burrows provide a habitat for organisms such as the bivalve *Mysella bidentata*, which is known to be associated with the burrows of other species (Dworschak, 1983; Hall-Spencer and Atkinson, 1999).

Societal importance: None.

5.3 Bryozoa

Alcyonidiidae and Flustridae

Economic importance: None

Ecological importance as prey: Sea urchins (such as *Strongylocentrotus droebachiensis*, *Echinus esculentus* and *Psammechinus electra*) have been shown to prefer algae containing bryozoans (Ryland, 1962). Moore (1973a) discusses the role of predation on bryozoans found on kelp holdfasts.

Ecological importance as predators: Not predatory.

Functional importance: The bryozoan families belonging to Flustridae and Alcyonidiidae have been shown to prefer to settle on algae found on lower shore such as *Fucus serratus*, *Chondrus crispus* and *Gigartina stellata* rather than on those found in the higher shore (Ryland, 1962). They are found commonly on kelp holdfasts. Bryozoans may be important to provide a substrate for settlement e.g. for larvae of *Mytilus edulis* (Moore, 1973a).

Societal importance: None.

5.4 Cnidaria

Caryophylliidae

Economic importance: *Lophelia pertusa* reefs are economically important indirectly as they provide important habitats for several commercial fish species. In Norway, fishing with long lines takes place close adjacent to or within coral areas (Husebø *et al*., 2002).

Ecological importance as prey: The higher biomass and abundances of fauna within the coral reefs of *Lophelia pertusa* makes them very important feeding grounds for fish (such as tusk *Brosme brosme*; Husebø *et al*., 2002) and, without doubt, invertebrate predators. Predator-prey relationships within *L. pertusa* reefs are poorly known.

Ecological importance as predators: None.

Biogeochemical functions: The skeleton of *L. pertusa* consists of calcareous (aragonite) exoskeleton (Cornelius *et al.*, 1990). Presumably, *L. pertusa* absorbs some amounts of calcium, which is released when corals disintegrate.

Biological activity and habitat functions: The size and shape of reefs of *L. pertusa* are very diverse, ranging from colonies not larger than 5–10 m in diameter, up to mounds of 50–500 m in diameter and banks up to 5 km in length (e.g. De Mol *et al*., 2002). The living part of the coral forms a network of branches that grow into thickets. The complexity of the *Lophelia* reef habitat is very high (e.g. Wilson, 1979a, b). In total of 800 species have been recorded within *Lophelia* reefs in the NE-Atlantic. The species richness within reefs can be three times greater compared to non-reef areas. The species composition and diversity vary with geographical location and the size and shape of the reef. Jensen and Frederiksen (1992) showed that the associated fauna within the coral consisted mainly of suspension feeders. Furthermore, their findings indicate that species diversity increases with the size of the coral reef. Coral reef habitats play probably a very important role as nursery, spawning and feeding grounds and to provide refuge from predation (e.g. Fosså *et al*., 2000). Husebø *et al*. (2002) showed that redfish *Sebastes marinus*, ling *Molva molva,* and tusk *Brosme brosme* were more numerous and larger bodied within reef habitats. The complex structure of the *Lophelia* coral reefs may affect the near bed hydrodynamics and may therefore facilitate deposition of fine particulate matter and larvae but this, however, has not been investigated.

Societal importance: *Lophelia pertusa* reefs are only found in a few locations within the North Sea. Outside the North Sea, one area has been closed for fishing, which is Sula Ridge in Norway. Within the North Sea, the Worldwide Fund for Nature (WWF) has suggested that the Hvaler reef, which is located in the northern part of the Skagerrak, on the border between Norway and Sweden, should be designated as a protected area. In the Swedish part of the area, some 426 km^2 has already been declared a Special Area of Conservation under the EU Habitats Directive (ICES, 2003e). *Lophelia pertusa* is listed under the UK Biodiversity Action Plan, CITES and EC Habitats Directive.

Hydrozoa

Economic importance: None.

Ecological importance as prey: Little is known about the predation on hydrozoans. They have been found in the diet of small dab (<40 mm) (Breyst *et al*., 1999). In a study carried out in Maine, USA, the nudibranch *Cuthona nana* was a specialised predator on hydroids (Folino, 1993). We have no information on predation by invertebrates on hydroids in the North Sea.

Ecological importance as predators: No important predators.

Biogeochemical functions: No information found.

Biological activity and habitat functions: Hydroids can be found on various hard substrata including other organisms such as mussels, whelks and hermit crabs. Competition for space has been reported among hydrozoan species (McFadden, 1986) and between hydroids and sessile polychaetes and bryozoans (Karlson and Shenk, 1983).

Societal importance: None.

Pennatulacea

Economic importance: The ‘sea-pen and burrowing megafauna habitat’ is of considerable economic importance because of the fishery for *Nephrops norvegicus* which takes place within these habitats (Hughes, 1998a).

Ecological importance as prey: Little is known about predation on pennatulaceans but *Virgularia mirabilis* and *Pennatula phosphorea* have been recorded in the diet of haddock *Melanogrammus aeglefinus* (Hoare and Wilson, 1977) and Dover sole *Solea solea* (Mackie, 1987) respectively. The tissue of *P. phosphorea* contains chemical substances of narcotic and anorectic properties which act as feeding deterrants for fish predators such as the Dover sole (Mackie, 1987). On the whole, it is likely that the predation pressure on pennatulaceans is low. There are strong suggestions that the nudibranch *Armina loveni* predates on *V. mirabilis* (Picton and Morrow, 1994), but a highly related species *Armina californica* is a specialised predator on seapens in the USA (Birkeland, 1974).

Ecological importance as predators: Not important predators. *Virgularia mirabilis* are suspension feeders (small particulate matter) and passive carnivores (zooplankton).

Biogeochemical functions: The tissue of *P. phosphorea* contains chemical substances of narcotic and anorectic properties which act as feeding deterrants for fish predators such as the Dover sole *Solea solea* (Mackie, 1987).

Biological activity and habitat functions: Pennatulaceans are found on muddy bottoms dominated by large burrowing megafaunal species such as *Nephrops norvegicus*, *Callianassa subterranea* and *Maxmuelleria lankesteri*. Bioturbation by these megafaunal burrowers may impact densities of pennatulaceans, but this remains to be investigated (Hughes, 1998a).

Societal importance: Considered a threatened and declining habitat by OSPAR. The 'sea-pen and burrowing megafauna habitat' has been designated as Special Areas of Conservation in the UK (Hughes, 1998a).

5.5 Echinodermata

Amphiuridae

Economic importance: None.

Ecological importance as prey: Amphiurids are preyed upon by dab *Limanda limanda* (Duineveld and Noort, 1986; Pihl, 1994), plaice (Pihl, 1994) and Norwegian lobster *Nephrops norvegicus* (Baden *et al*., 1990). These predators do not generally consume the entire animal but crop only the arms, which are later regenerated. An energy budget estimated for the *Amphiura filiformis* population of Galway Bay suggested that arm regeneration contributed significantly to the total annual production of this species (O'Connor *et al*., 1983). Duineveld and Noort (1986) estimated that the annual consumption of *Amphiura* arms by dab in the North Sea to be 0.84 g wet weight m^{-2}, which is equivalent to 420 arms or 6% of the total arm population.

Ecological importance as predators: Not predatory.

Biogeochemical functions: As for other echinoderms, amphiurids are known to be efficient concentrators of heavy metals, including those that are biologically active and toxic (Hutchins *et al*., 1996). *Amphiura filiformis* and *A. chiajei* have been found to accumulate polychlorinated biphenyl (PCB), and the accumulation was greater in the coastal populations compared to those found offshore (Gunnarsson and Sköld, 1999).

Biological activity and habitat functions: Bioturbation by *Brissopsis lyrifera* can negatively affect the growth of body and gonads of *A. chiajei* (Hollertz *et al*., 1998).

Societal importance: None.

Antedonidae

Economic importance: None.

Ecological importance as prey: Predation on these crinoids seems to be minor. The corkwing wrasse *Crenilabrus melops* have been found to predate on *Antedon bifida*, but they only consume pinnules and arm tips of the crinoid (Nichols, 1996)

Ecological importance as predators: Not predatory.

Biogeochemical functions: No information

Biological activity and habitat functions: Antedonidae have been found to be associated with maerl (Keegan, 1974). No other information on functional importance of this family was found.

Societal importance: None.

Asteriidae

Economic importance: *Asterias rubens* predates on cultured mussels *Mytilus edulis* and is therefore indirectly of commercial importance (Hancock, 1958).

Ecological importance as prey: *Asterias rubens* has been recorded in the diet of dab and plaice (Braber and De Groot, 1973).

Ecological importance as predators: Among Asteriidae, predator-prey interactions have been mainly investigated for *Asterias rubens*. This species is a predator and scavenger which typically feeds on bivalves, polychaetes, small crustaceans and other echinoderms. Predation by this starfish on mussels can determine their lower distribution limits within the intertidal zone (e.g. Barker and Nichols, 1983). Seed (1969) reported that *A. rubens* and *Nucella lapillus* eliminated mussels from the lower intertidal along a shore line on the east coast of England. Finally, *A. rubens* can aggregate into large groups and virtually 'clean' areas of their prey. Dare (1973) described such invasion where this starfish was found in very high density (450 ind. m^{-2}) consumed about 4,000 tonnes of mussels in an area of 2 hectares. *Asterias rubens* predates as well on infaunal bivalves such as *Abra alba* and *Spisula subtruncata* (Allen, 1983).

Biogeochemical functions: The starfish *A. rubens* has been used as a reference species to monitor changes of marine heavy metal pollution (Temara *et al*., 1997). Temara *et al*. (1998) examined the contamination of *A. rubens* along spatial gradients of Pb, Cd and Zn identified in the Sørfjord, southwest Norway. They concluded that *A. rubens* appeared to be a valuable bioindicator of spatial and temporal trends of Pb and Cd contamination.

Biological activity and habitat functions: Predation by *A. rubens* may affect benthic community structure indirectly. As an example, intensive predation of mussels can create bare areas within mussel beds which in turn can impact associated fauna and allow invasion by other primary space occupiers.

Societal importance: None.

Astropectinidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Christensen (1970) investigated the feeding biology of *Astropecten irregularis* in Jutland, Denmark. She showed that their diet was dominated by bivalves, especially of *Spisula subtruncata*. She estimated the consumption of a single *A. irregularis* to be about 200 newly settled *S. subtruncata* a day. Numbers of *A. irregularis* varied greatly with season, ranging from 6 ind. ha^{-1} in December to 130 ind. ha^{-1} in July. In another study (Freeman *et al*., 2001) showed that numbers of *A. irregularis* rose during summer and autumn, coinciding with settlement periods of their bivalve prey.

Biogeochemical functions: No information found.

Biological activity and habitat functions: No information found.

Societal importance: None.

Echinidae

Economic importance: The roe (the male and female gonads) of *Echinus esculentus* was eaten in some parts of England. The tests are sometimes sold as ornaments (Sloan, 1985). There was a limited fishery for *E. esculentus* in Cornwall and Scilly isles in the eighties (Nichols, 1981). There is some interest among Scottish fishermen to start a fishery for sea urchins (Kelly *et al*., 2001). There is limited aquaculture for *Psammechinus miliaris* but the gonads from these are considered as a delicacy in continental Europe (Kelly *et al*., 1998). A small-scale fishery for sea urchins (mainly *Strongylocentrotus intermedius*) takes place in Norway (FAO, 1995 in Keesing and Hall, 1998). In 1999, 1.2 tonnes of roe were exported from Norway to Japan with a value of £27,000. There is a small fishery for sea urchins in Brittany (France), which is predominately targeting *Paracentrotus lividus* but catches have decreased (Andrew *et al*., 2002).

Ecological importance as prey: Reported predators on echinids are wolffish (Liao and Lucas, 2000), long-rough dab (Ntiba and Harding, 1993; Klemetsen, 1993) and the asteroid *Luidia ciliaris* (Brun, 1972).

Ecological importance as predators: The effects of grazing by *Strongylocentrotus droebachiensis* on kelps has been thoroughly investigated in the North Atlantic (e.g. Hagen, 1995) while this is not the case for the North Sea. Jones and Kain (1967) concluded that the lower limit of the kelp species *Laminaria hyperborea* was partly determined by the grazing pressure by *E. esculentus*. In that study, 3,000 sea urchins were removed over a 3 year period from a 10 m wide strip. Such removal resulted in increase in abundance of *L. hyperborea* sporelings (22.7 ind. m^{-2} within the strip compared to 5.1 ind. m^{-2} outside of it). Vost (1983) showed that species richness and biomass of understorey epiliths were greater in the urchin free areas

Biogeochemical functions: We found no information on the importance of echinids in nutrient dynamics. Breakdown of plant material during grazing by the sea urchins should result in elevated nutrient levels but, to our knowledge, this has not been investigated. *Echinus esculentus* have been reported to accumulate large amounts of aliphatic hydrocarbons, naphthalenes, pesticides and heavy metals (Zn, Hg, Cd, Pb, and Cu) (Gomez and Miguez-Rodriguez, 1999).

Biological activity and habitat functions: The sea urchin species, *Psammechinus miliaris* and *E. esculentus* are known to provide shelter for the commensal bristle worm species *Flabelligera affinis* (Mortensen, 1927). Comely and Ansell (1988) recorded 21 invertebrate species associated with *E. esculentus*, four were ecto-parasitic or commensals while the remainder were casuals. About <0.8% of the sea urchins had the endoparasitic nematode *Echinomermella grayi*. The amphipod *Euonyx chelatus* occurred in 0.4–3% of *E. esculentus* from shallow or deep water respectively (Comely and Ansell, 1988).

Societal importance: *Echinus esculentus* is on IUCN Red List (category LR/nt: Taxa which do not qualify for Conservation Dependent, but which are close to qualifying for 'vulnerable').

Ophiotrichidae

Economic importance: None.

Ecological importance as prey: *Ophiotrix fragilis* is preyed upon by plaice (Rijnsdorp and Vingerhoed, 2001), wolffish (Liao and Lucas, 2000) and sometimes by the hermit crab *Pagurus bernhardus*, flounder *Platichthys flesus* and the dragonet *Callionymus lyra* (Warner, 1971).

Ecological importance as predators: Not predatory.

Biogeochemical functions: The brittlestar *O. fragilis* can be found in extremely high densities, from 2,000 ind. m^{-2} (Davoult, 1989) up to >10,000 ind. m^{-2} (Keegan and Könnecker, 1979). In high-density areas, large amounts of suspended particulate matter can be removed from the water column (Davoult and Gounin, 1995). These brittlestars play an important role in nutrient exchanges in estuarine and coastal environments (Lefebvre and Davoult, 1997). Precipitation of calcium carbonate in skeletal ossicles by this species is a source of carbon dioxide in seawater (Ware *et al*., 1992). Migné and Davoult (1997) estimated that the amount of carbon respired annually in relation to phytoplankton production in the Eastern English Channel could provide 35% of the phytoplankton carbon requirements. In another study, Migné *et al*. (1998) estimated the production of calcium carbonate by dense beds of *Ophiothrix fragilis* to be 682 g $CaCO_3/m^2$/yr, sufficient to result in the release of 4.8 mol CO_2/m^2/yr. Gounin *et al*. (1995) investigated the uptake of heavy metals by the brittlestar *O. fragilis* and suggested that this brittle star species can be used as a biological indicator of the elemental composition of the water mass entering the North Sea.

Biological activity and habitat functions: These brittlestars are found on hard bottoms where the habitat complexity is high. They can conceal themselves in crevices so the tentacles are only visible, presumably to avoid predation (D'yakanov, 1967). *Ophiothrix fragilis* has been considered as a keystone species in the coastal marine ecosystem of the eastern Channel and a dominant species of gravel communities (Lefebvre and Davoult, 1997). In areas where *O. fragilis* dominates, it can account for up to 62% of the biomass in coarse sediment communities (Migné and Davoult, 1997). Despite the apparent dominance of *O. fragilis,* up to 78 species have been recorded from a brittle star bed, the most common of which was the bivalve *Abra alba* (Warner, 1971).

Societal importance: None.

Ophiuridae

Economic importance: None.

Ecological importance as prey: *Ophiura albida*, *O. affinis* and *O. sarsi* are preyed upon by long-rough dab (Klemetsen, 1993; Ntiba and Harding, 1993), plaice, dab and lemon sole (Høines and Bergstad, 2002, Greenstreet, 1996).

Ecological importance as predators: Large *O. ophiura* can eat a wide variety of small bivalves, polychaetes and crustaceans (Feder, 1981). *Ophiura*

ophiura have been shown to forage on damaged bivalves, echinoderms, crustaceans, whelks and polychaetes in areas where beam trawling takes place (Ramsay *et al*., 1998).

Biogeochemical functions: No information found**.**

Biological activity and habitat functions: Mesocosm studies have shown that disturbance caused by sediment reworking by the two ophiolepids *O. affinis* and *O. albida* had minor impact on the epifauna but causing reduction in numbers of surface dwelling species. Diversity decreased after 12 weeks within plots containing high densities of brittlestars (Ambrose, 1993)

Societal importance: None.

Solasteridae

Economic importance: No commercial importance.

Ecological importance as prey: No information found.

Ecological importance as predators: The solasterid *Crossaster papposus* has often been observed feeding on echinoderms (e.g. sea urchins), bivalves, cnidarians, and tunicates (Coleman, 1991). Cannibalism in *C. papposus* is rare and has only been observed after long starvation in captivity (Sloan, 1984). Studies in Canada have shown that *C. papposus* preys intensively on scallops and declines in population size of *C. papposus* following a crash in scallop stocks has been reported (Nadeau and Cliché, 1998).

Biogeochemical functions: No information was found but solasterids probably accumulate heavy metals and synthetic chemicals as other starfish species.

Biological activity and habitat functions: No information found.

Societal importance: None.

Spatangidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Not predatory.

Biogeochemical functions: Among the Spatangidae, the ecology and biology of *Brissopsis lyrifera* and *Echinocardium cordatum* is best known. Bioturbation by *B. lyrifera* can play an important role in controlling chemical, physical and biological processes in marine sediments, especially when the influences of physical disturbances such as wave action or strong currents are minimal (Widdicombe and Austen, 1999). During sediment reworking, shallow respiratory funnels are formed which increase the depth of the oxygenated sediment (Widdicombe and Austen, 1999), decreases the rates of denitrification and increases the precipitation of phosphate (Widdicombe and Austen, 1998). Bird *et al*. (1999) showed that the flux of dissolved substances across the sediment-water interface was 2.3–3.9 times higher in the presence of the burrowing species *Neocallichirus limosus, Biffarius arenosus* and *Echinocardium cordatum*.

Biological activity and habitat functions: Sediment reworking activity by *B. lyrifera* has a major impact on sediment structure and stability (De Ridder and Lawrence, 1982). The bioturbatory activity *B. lyrifera* can increase both the microbial and meiofaunal productivity (Widdicombe and Austen, 1998). Where *B. lyrifera* is found in high densities, the functional composition of the nematode community can been altered (Austen and Widdicombe, 1998). In one study, bioturbation by *B. lyrifera* resulted in increased species richness, and also in an increased number of individuals within low density plots, whereas a decrease in high density plots (28 versus 71 *Brissopsis*) was observed, suggesting increased diversity at intermediate disturbance levels (Widdicombe *et al.*, 2000). The biological activity of *B. lyrifera* can affect the growth of gonads and body of the brittlestar *Amphiura chiajei* (Hollertz *et al*., 1998). The rate of sediment reworking by *B. lyrifera* is greatly influenced by temperature. The amount of sediment reworked was 22 ml sediment/hr at 13°C whereas only 14 ml sediment/hr at 7°C. Similarly, the amount of sediment ingested rose with temperature and was 0.08 and 0.02 g dry sediment/hr at 13°C and 7°C, respectively. This implies that the sediment reworked during biological activity of this sea urchin species is about 60–150 times higher than the volume ingested (Hollertz and Duchene, 2001).

Societal importance: None.

5.6 Echiura

Echiuridae

Economic importance: None.

Ecological importance as prey: Echiuroids have been reported in the diet of several demersal fish species, and abundant populations may significantly contribute to the nutritional requirements of the eel (Rachor and Bartel, 1981).

Ecological importance as predators: Not predatory.

Biogeochemical functions: The efflux of nitrate within chambers enclosing burrows of the echiurid *Maxmuelleria lankesteri* was considerably higher compared to controls. Similarly, the nitrate efflux was considerably greater over *M. lankesteria* ejecta mounds and the authors suggested that these features may be localised sites of enhanced nitrification (Hughes *et al*., 2000). The burrows of *M. lankesteria* may act as a sink for surface-derived radionuclides. Because the bioturbation by this echiurid involves mainly redistributing sediments on the sediment surface, there is probably minor return of the deeply burrowed material (including radionucleides) to the sediment surface (Hughes *et al*., 1996a).

Biological activity and habitat functions: Sediment reworking and ventilating activities of echiurids creates a favourable habitat for other organisms such as foraminiferans. This may be partly due to the higher concentration of food within the burrows (Rachor and Bartel, 1981). The worm lives in U-shaped burrows and performs a key role for the development of a rich associated fauna because of its ventilating and sediment reworking activities (Rachor and Bartel, 1981). Sediment reworking by *Echiurus echiurus* can increase the numbers of bacteria and foraminiferans (Thomsen and Altenbach, 1993). The rates of bioturbation by *M. lankesteri* was generally about 13 g dry weight day^{-1} and the sediment ingestion rate was estimated to be 1.7 g day^{-1} (Hughes *et al*., 1996a). The rate of ejection can be extremely variable and the highest recorded has been about 97 g dry weight/burrow/day although on average the rate of ejection was 7.53 g dry weight/burrow/day. The rate of sediment ejection was found to be correlated with the percentage of labile material in the sediment organic matter (Hughes *et al*., 1999). Finally, Hughes and Atkinson (1997) estimated that the rate of sediment ejection was about 39 g m^{-2} d^{-1} at a density of three *M. lankesteria* per m^2. Burrows of *M lankesteria* can be occupied opportunistically by other burrowing species such as *Jaxea nocturna* and the black goby *Gobius niger* (Hughes *et al*., 1996b). The fauna surrounding the burrow of *M. lankesteria* is likely to be affected as the sediment surface over a horizontal distance of 1–2 m is affected by sediment reworking (Hughes *et al*., 1996a).

Societal importance: None.

5.7 Mollusca

Arcticidae

Economic importance: None.

Ecological importance as prey: Cod has been reported to scavenge on quahogs *Arctica islandica* which have been damaged as a result of fishing activities (Arntz and Weber, 1970).

Biogeochemical functions: This species is a filter feeder and is known to accumulate heavy metals (Swaileh, 1996). It can be found in high densities and may therefore filter out large quantities of plankton.

Biological activity and habitat functions: It may compete for space with other infaunal bivalves. We found no information on the functional importance on this species, although as large burrowing bivalves, they may affect sediment turnover and nutrient recycling.

Societal importance: *Arctica islandica* has been included on the OSPAR list of threatened and declining species (BDC 03/2/-E, Annex I cited in ICES, 2003f).

Buccinidae

Economic importance: The total landing of whelks in England and Wales in 1995 was 4,276 tonnes (IMPACT 98/41-E) but we do not know the proportion of the catch originating from the North Sea. The total landings of *Buccinum undatum* at English, Welsh and Scottish ports between 1977 and 1994 ranged from 391 t (in 1990) to 2,966 t (in 1978) (Nicholson and Evans, 1997). Whelks are caught in pots baited with a combination of dogfish *Scyliorhinus* spp. and brown crab *Cancer pagurus* (Fahy, 2001).

Ecological importance as prey: Buccinids have been found in the diet of wolffish (Liao and Lucas, 2000). It is likely that large size and thick shell protects them against predation. However, Ramsay and Kaiser (1998) have shown that *B. undatum* damaged as a result of scallop dredging can be heavily preyed upon by the starfish *Asterias rubens*.

Ecological importance as predators: Among buccinids, the information on the feeding ecology of *B. undatum* is best known. This species is probably primarily a scavenger which can locate carrion with chemoreception (Nickell and Moore, 1992a) such as exposed and damaged animals in recently fished areas (Bergmann *et al*., 2002). *Buccinum undatum* predates on bivalves such as *Mytilus edulis* by using the lip of the shell as a wedge and inserting its proboscis in the gap and using the radula to tear out the flesh (Thompson, 2002). *Neptunea antiqua* is predatory, feeding on bivalves and polychaetes, but is a scavenger as well (Shimek, 1984 in Britton and Morton, 1994).

Biogeochemical functions: *Buccinum undatum* is known to accumulate organotin compounds, such as TBT (Mensink *et al.*, 1997) and TOT (Ide *et al*., 1997). Long term exposure to these compounds can result in imposex. Nicholson and Evans (1997) showed that TBT had little if any impact on the breeding performance of *B. undatum* because imposex was mostly mild.

Biological activity and habitat functions: The shell of *B. undatum* provides a habitat for sessile organisms such as hydroids. Otherwise, we found little evidence that buccinids have an impact on benthic community and interactions seem to be few.

Societal importance: None.

Cardiidae

Economic importance: Common cockles *Cerastoderma edule* are collected by hand or mechanically using tractor dredges or suction dredges for the commercial market (Fowler, 1999; Kaiser *et al.*, 2001). Landings of cockles in the UK ranged from 12.1 to 24.2 thousand t (DEFRA, 2001), but 21.3 thousand t were landed in 1995 (IMPACT 98/4/1-E). In the Netherlands, cockles are fished commercially with suction dredging but some fishermen collect them with hand raking. The total value of the cockle catch in 1998 was £16.5 million. Cockle landings in the Netherlands are variable from year to year but peaked in 1989 with about 12 tonnes of meat, but was lowest in 1996 with less than 1 tonne of meat (Kamermans and Smaal, 2002).

Ecological importance as prey: The common cockle is a very important prey for the eider *Somateria mollisima* in the Wadden Sea (Leopold, 2002). It has been postulated that reduced spatfall, heavy fishing pressure for cockles and low stocks in mussel cultures may partly explain the increase in mortality of eiders during the winter 1999 to 2000 (Camphuysen *et al.*, 2002). Similarly, cockles are heavily predated upon by waders such as oystercatchers *Haematopus ostralegus*, knots *Calidris canutus*, dunlins *Calidris alpina* and grey plovers *Pluvialis squatarola* (Goss-Custard *et al.*, 1977). Various invertebrate predators such as the crab *Carcinus maenas* feed on cockles. Jensen and Jensen (1985) concluded that predation by juvenile *C. maenas* can have large impacts on cockle spat biomass.

Biogeochemical functions: Swanberg (1991) reported higher chlorophyll *a* concentrations and sediment primary productivity, 27.9 mg C m^{-2} h^{-1} *vs.* 14.7 mg C m^{-2} h^{-1} in plots with and without cockles, respectively. Similarly, filter feeding by *C. edule* can increase significantly the release of nitrates (NH_4^+) and phosphates (PO_4^{3-}) to the overlying water. *Cerastoderma edule* has been shown to accumulate heavy metals and hydrocarbons (e.g. Porte *et al*., 2000). Dense beds of cockles can filter out large quantities of particulate matter and phytoplankton. However, we found no evidence from the literature that such filtration was sufficient to improve water quality or that it results in large reduction of phytoplankton biomass.

Biological activity and habitat functions: Bioturbation by *C. edule* can impact associated fauna because of their ‘bulldozing’ behaviour which can destabilise the sediment, modify sediment grain size and affect bacterial biomass (Goni *et al*., 1999). Sediment reworking activity by *C. edule* have been shown to suppress numbers of *Corophium volutator* densities, probably by inducing the amphipod to leave their burrow and so making them more vulnerable to predation (Flach, 1992b; Flach and De Bruin, 1994). We found no evidence that *C. edule* has impact on the overall benthic community structure or on meiofaunal populations (Kennedy, 1993).

Societal importance: None.

Myacidae

Economic importance: Among Myacidae, *Mya arenaria* is occasionally collected for bait or food in UK. We lack information on the harvest of these bivalves in other parts of the North Sea.

Ecological importance as prey: *Mya arenaria* has been reported to be preyed upon by eider ducks *Somateria mollisima* in the Wadden Sea (Leopold, 2002) and epibenthic predators. Strasser and Günther (2001) concluded that predation by juvenile *Carcinus maenas* can have a large impact on recruitment success of *M. arenaria*.

Biogeochemical functions: No information found.

Biological activity and habitat functions: No information found.

Societal importance: None.

Mytilidae: *Mytilus edulis*

Economic importance: The blue mussel *Mytilus edulis* is harvested by hand picking from mussel beds or using dredgers which operate on the high tide. Large quantities of mussels are collected from mussel beds in some location in the UK. The minimum (non-statutory) size required for sale is 55 mm (Fowler, 1999). In total, 9,190 tonnes were fished in England and Wales in 1995 (IMPACT 98/4/1-E). In Denmark, mussels have been harvested and some relaid/restocked for many years. The activity could be characterised as being in-between fisheries and a kind of sea ranching. The annual landings are around 100,000 t annually (Dolmer *et al*., 1997). Landings of commercially exploited mussels in the Danish Wadden Sea peaked in 1985 at 27,099 t, but remained high in 1986 and 1987 with

17,564 and 17,384 t, respectively. The average landings for the period 1989–1998 were 3,611 t (Munch-Petersen and Kristensen, 2001). The average production of blue mussels on leased mussel beds in the Wadden Sea along the Schleswig-Holstein coasts was on average 17,085 t over the period 1997–1999 (Rosenthal and Hilge, 2000). The average landings of cultured mussels over the period 1995–2000 in the Netherlands (Dutch Wadden Sea and the Oosterschelde estuary) were 80,000 t (Smaal and Lucas, 2000). In the UK, culture of mussels (raft-and-line) is limited to Scotland, with production which is generally less than 1,000 tonnes per year (McKay and Fowler, 1997). There is a seed fishery for mussels in the UK with a value of the harvest of £3.6 million in 1998 (Burton *et al.*, 2001). In the Netherlands, there is intensive seed fishery where mussel spat (10–30 mm in length) is transferred to deeper waters and fished when these have attained market sizes (>45 mm). The Netherlands is the fourth largest producer of the blue mussel in the world. In 1999, the total landing value of mussels was £34 million. The mussel landings in the Netherlands from 1969 onwards exceeded 1,000 tonnes (fresh weight) (Kamermans and Smaal, 2002).

Ecological importance as prey: Oystercatchers and eider ducks are the major predators on blue mussels. It is not uncommon that more than 60% of the eiders diet consists of mussels (Seed and Suchanek, 1992). Raffaelli *et al*. (1990) estimated that a flock of 500 eider ducks removed about 36% of mussels in the 6–30 mm size range. Hilgerloh *et al*. (1997) estimated that herring gulls *Larus argentatus* in the Wadden Sea consumed 13 mussels/m^2 (0.3 g AFDW/m^2) during one day and oystercatchers 1.7 mussels/m^2 (0.1 g AFDW/m^2). In another study, the estimated annual consumption of mussels by birds on the intertidal flats in the Wadden Sea was 165 t AFDW. The dominant consumers were oystercatchers (54%), eiders (39%) and herring gulls (7%) (Hilgerloh, 1997). In the east Scheldt estuary, the Netherlands, 40% of the annual mussel production was consumed by oystercatchers (Meire and Ervynck, 1986). In Conway, North Wales, oystercatchers were found to consume up to 574 mussels (average length 25.7 mm) at each low tide (Drinnan, 1958). Similarly, mussels are an important prey item for predatory invertebrates such as *Asterias rubens* and *Nucella lapillus* in the UK (Seed, 1969).

Biogeochemical functions: Mussels biodeposit large amounts of faeces and pseudofaeces (Dahlbäck and Gunnarson, 1981; Kaspar *et al*., 1985; Kautsky and Evans, 1987; Hatcher *et al*., 1994). The complex habitat formed by the mussel also enhances deposition of fine particulate matter from the water column as a result of reduced flow of water through the mussel matrix (e.g. Kautsky and Evans, 1987). However, Widdows *et al*. (1998) showed that the biodeposition rates by the mussel *M. edulis* could be up to 40 times greater than the natural sedimentation rates. Mussel biodeposition results in elevated amounts of a variety of nutrients such as phosphorus and nitrogen (e.g. Kaspar *et al*., 1985; Kautsky and Evans, 1987). Biodeposition of faeces and pseudofaeces can attain 70 g C m^{-2} d^{-1} (Muschenheim and Newell, 1992).

Biological activity and habitat functions: The high structural complexity of the mussel bed matrix creates microhabitats which provide various organisms with shelter and/or a refuge from predation (e.g. Seed 1976; Suchanek 1985, 1992). Similarly, the rate of flow though the mussel matrix is greatly reduced (e.g. Commito and Rusignuolo, 2000), facilitating passive entrainment of particulate matter and larvae of macrofauna and meiofauna. The abundance, composition and the diversity of the fauna within mussel beds tend to be greater compared to non-mussel areas (Radziejewska, 1986; Commito, 1987; Dittman, 1990). On rocky shores, the mussel is able to outcompete other large sized sessile fauna (e.g. Dayton, 1971). However, physical disturbances such as wave action, ice-scour and wave-driven logs (e.g. McCook and Chapman, 1991) can create open areas within mussel beds which are available for colonization by opportunist competitors (Hewatt, 1935). On soft bottoms, biodeposition has been shown to have significant impact (such as smothering and anoxia) on faunal composition and abundance (Mattsson and Lindén, 1983; Tsuchiya and Nishihira, 1986; Radziejewska, 1986; Suchanek, 1992). The abundance of species which are sensitive to smothering, such as spionids, can decrease within dense beds of mussels, whereas other species may benefit from the input of organic matter to sediments such as deposit feeders like *Capitella* spp. (Mattsson and Lindén, 1983). Dense beds of mussels can filter out large quantities of fine particulate matter. They have been thought to be important to maintain water quality; they may even serve as natural control on eutrophication (e.g. Officer *et al*., 1982; Doering and Oviatt, 1986). They filter out larvae which may affect recruitment by other benthic organisms (Cowden *et al*., 1984). Biodeposition by mussels on a sandy substratum can result in mound formation (Thiesen, 1968). Removal of beds due to physical disturbances (e.g. storms, ice scour) will result in destabilisation of underlying sediments and loss of the fine particulate matter which has accumulated within beds (e.g. Ragnarsson and Raffaelli, 1999). In mussel beds where the density of mussels is very high (>1400 mussels m^{-2}), erosion is reduced by 10-fold (Widdows *et al*., 1998).

Societal importance: In England and Wales, local Sea Fisheries Committee bylaws (or Several and Regulating Orders in Scotland) prohibit disturbance of mussel beds without defining the species (UKBAP). In some cases fisheries legislation may require mussel fisheries to be developed without defining the species.

Mytilidae: *Modiolus modiolus*

Economic importance: *Modiolus modiolus* (horse mussel) is fished locally in Scotland, probably mainly for bait (Comely, 1978; Fowler, 1999). There is no large-scale fishery for *M. modiolus* in the UK (Holt *et al*., 1998). There is a fishery for *M. modiolus* in Norway but we lack further information on it.

Ecological importance as prey: Crabs and starfish are commonly found within *M. modiolus* beds and may prey on small horse mussels. However, large *M. modiolus* are probably relatively predator free as only the largest crabs and starfish can open horse mussels larger than 50 mm (Anwar *et al*., 1990).

Biogeochemical functions: Like the blue mussel, the horse mussel produces large amounts of biodeposits which play important role in recycling of nutrients (Navarro and Thompson, 1997). Peterson and Heck (1999) showed that biodeposition by *M. modiolus* increases the levels of nitrogen and phosphate in the water column, which in turn can lead to enhanced seagrass productivity. Finally, *M. modiolus* can filter out large quantities of plankton.

Biological activity and habitat functions: Like the mussel, the high complexity of the *Modiolus* beds provides a habitat and refuge from predation for a large variety of animals (Witman, 1985) thereby enhancing species richness and diversity (Holt *et al*., 1998). The complex structure of the *Modiolus* beds is likely to alter near-bed flow.

Societal importance: Beds of *M. modiolus* may be protected under the Habitats Directive within the Annex I habitats 'Reefs' and 'Large shallow inlets and bays' and potentially within the habitat 'Estuaries' (Jones *et al*., 2000). *Modiolus* beds are included as a Habitat Action Plan under the UK Biodiversity Action Plan (Anon., 1999a) and some areas have been considered for Special Areas of Conservation (SAC) sites. In England and Wales, local Sea Fisheries Committee bylaws (or Several and Regulating Orders in Scotland) prohibit disturbance of mussel beds without defining the species (UKBAP). In some cases fisheries legislation may require mussel fisheries to be developed without defining the species.

Ostreidae

Economic importance: Oysters were formerly an important food source, but due to intensive harvesting they are now rare in the intertidal and shallow sublittoral in the UK. Landings of oysters in England and Wales in 1995 were 814 tonnes (where of cultivated 288 tonnes) (IMPACT 98/4/1-E). The production of oysters in mariculture was on average 482 t in 1996–1997 but 762 t in 1998. The annual value of the landings is about £1.1 million (Burton *et al*., 2001). There is considerable mariculture for oysters in Denmark. In Limfjorden, the yearly production has varied between 100,000 and 4 million individuals (Hoffman, 1981). *Crassostrea gigas* was introduced for cultivation in the south-west and south-east UK (Fowler, 1999) and to Denmark in 1978 (Hoffman, 1981). On average, 80,000 t of cultured oysters were landed annually over the period 1995–2000 in the Netherlands (Smaal and Lucas, 2000).

Ecological importance as prey: The crab *Carcinus maenas* has been reported to predate on *C. gigas* (Richardson, 1993). The snail species *Buccinum undatum* and the starfish *Asterias rubens* have been reported to predate on oysters (Jackson, 2003a).

Biogeochemical functions: Oysters have been reported to accumulate diarrhetic shellfish toxins (DST) (Svensson *et al*., 2000), TBT (tri-butyl tin) and heavy metals (Carrascal *et al*., 1996).

Biological activity and habitat functions: Dense beds of the oyster *O. edulis* can occur on muddy sand and fine sand, where a substantial proportion of the substratum consists of dead oyster shells. Clumps of dead shells and oysters can support large polychaetes such as *Chaetopterus variopedatus* and terebellids. In the Wadden Sea, the natural oysterbeds have disappeared from many areas and these have been replaced by the blue mussel *Mytilus edulis* (Riesen and Reise, 1982).

Societal importance: *Ostrea edulis* is included in 'UK Biodiversity Action Plan' and is considered a threatened and declining habitat by OSPAR.

Pectinidae

Economic importance: Within the North Sea, fishing for scallops (predominately *Pecten maximus*) takes place mostly around Shetland, Orkney and in the Moray Firth. Landings peaked in 1996 with 4,257 t. In Scotland, landings reached 1,900 t in 1995 but fell to 678 t in 1996. In Norway, landings of scallops were highest in the period 1994–1995 and amounted to 7,700 t. There is mariculture for *P. maximus* which relies on active spat collection and in 1998, the production was 41 tonnes with an landing value of approx. £1 million (Burton *et al*., 2001).

Ecological importance as prey: Among pectinids, predation on *P. maximus* has been investigated in most detail as this species is becoming more important in aquaculture. Lake *et al.* (1987) showed that predation by *Carcinus maenas* and *C. pagurus* was minimal on those *P. maximus* with shell height greater than 7 cm. Reported fish predators of pectinids are dabs (Høines and Bergstad, 2002) and wolffish (Liao and Lucas, 2000). Studies carried out in US and Canada, have shown that predation pressure by starfish on pectinid populations can be considerable (Nadeau and

Cliché, 1998; Naidu *et al*., 1999). To our knowledge, the impact on starfish predation on scallops has not been investigated in the North Sea.

Biogeochemical functions: Pectinids have been found to store toxins from microalgal blooms in muscle, gonads, digestive gland and kidneys (Lassus *et al*., 1996; Cembella and Shumway, 1989) and faecal pellets of some pectinid species contain living poisonous dinoflagellates (Bauder and Cembella, 2000).

Biological activity and habitat functions: Dead shells provide refuge to juvenile scallops and break down into shell sand. A number of epizoans such as sponges grow often on scallops (pers. obs.). Juvenile scallops often attach themselves to dead shells (Arsenault and Himmelman, 1996). Biotic interactions between *P. maximus* and the gastropod *Crepidula fornicata* have been reported (Thouzeau *et al*., 2000).

Societal importance: None.

Mactridae

Economic importance: A fishery for *Spisula* spp. takes place along the coastline of Netherlands and Denmark (QSR, 2000) and Germany (Meixner, 1994; Ruth, 1995). The extremely cold winter in 1995/1996 resulted in decreased biomass of *Spisula* spp. in the Wadden Sea (e.g. QSR, 2000; Camphuysen *et al*., 2002) and some areas have been closed for fishing.

Ecological importance as prey: We found limited information about predation on *Spisula* species. Eider ducks are known to forage on *Spisula* spp. (Camphuysen *et al*., 2002). *Spisula* spp. have been recorded in the diet of plaice (Braber and De Groot, 1973). The starfish species *Asterias rubens* (Allen, 1983) and *Astropecten irregularis* (Christensen, 1970) are known to predate intensively on *Spisula subtruncata*.

Biogeochemical functions: No information found.

Biological activity and habitat functions: No information found.

Societal importance: None.

Scrobiculariidae

Economic importance: None.

Ecological importance as prey: The scrobicularid *Abra alba* can be important in the diet of plaice (Basimi and Grove, 1985). Similarly, *A. nitida* has been shown to be important prey for plaice in Skagerrak (Pihl, 1994). Scrobicularids may be an important food source for juvenile fish in the Kiel Bay (Rainer, 1985). *Asterias rubens* is known to predate on *A. alba* (Allen, 1983).

Ecological importance as predators: Not predatory.

Biogeochemical functions: Densities of the bivalve *A. alba* has been reported to increase where dumping of sewage takes place possibly in response to the increased supply of nutrients (Caspers, 1981).

Biological activity and habitat functions: *Abra alba* is a subsurface deposit/suspension feeder that reworks the top 0.5 cm surface of the sediment. It has been estimated in an aquarium study that, one *A. alba* was able to rework an area of 7 cm in diameter (Eagle, 1975). Bioturbation by *A. alba*, when found in very high densities (>3000 m^{-2}), can result in the decreased abundance and decreased diversity of associated fauna (Widdicombe and Austen 1999; Widdicombe *et al*., 2000).

Societal importance: None.

Solenidae

Economic importance: Hydraulic dredging for *Ensis* spp. occurs in Orkney and the Shetlands and have been shown to cause selective but short term impact to benthic communities (e.g. Eleftheriou and Robertson, 1992). Fishing for these bivalves also takes place along the west coast of Scotland (e.g. Fowler, 1999).

Ecological importance as prey: Among Solenidae, *Ensis* spp. have been recorded in the diet of long-rough dab (NE-England) between May and July (Ntiba and Harding 1993), dab (Braber and De Groot, 1973) and plaice (Rijnsdorp and Vingerhoed, 2001). In the Wadden Sea, *Ensis americanus* is predated upon by eider ducks *Somateria mollissima* and oystercatchers *Haematopus ostralegus* when stocks of mussels and cockles are low (Smit *et al*., 1998).

Biogeochemical functions: No information found.

Biological activity and habitat functions: *Ensis* spp. are found in hydrodynamically rigorous sandy beaches where densities of macrofauna is generally low. We found very little functional importance for this family and they are likely to have limited influence upon its environment (Armonies and Reise, 1999), although as they live in deep burrows, transport of substances between the surface and sub-surface layers could be affected.

Societal importance: None.

Tellinidae

Economic importance: No commercial importance.

Ecological importance as prey: *Macoma balthica* is an extremely important prey for bird and invertebrate predators and probably for fish predators as well. Tellinids probably constitute an important prey item for most waders feeding on mudflats, such as for the knot *Calidris canutus* in the Wadden Sea (Zwarts *et al*., 1992; Piersma *et al*., 1993) and the dunlin *C. alpina* (Worrall, 1984). In the Wadden Sea, 20% of the diet of male bar-tailed godwits *L. lapponica* in spring consisted of *M. balthica* (Scheiffarth, 2001). *M. balthica* can become an alternative prey when biomass of other bivalve species is severely reduced. As an example, *M. balthica* were heavily predated upon by oystercatchers in Morecambe Bay following a collapse in cockle stocks during the severe 1962/63 winter (Dare, 1973). Various invertebrate predators predate on 0-group *M. balthica* such as *Crangon crangon* and 0-group *Carcinus maenas*. Hiddink *et al*. (2002b) concluded that 0-group *M. balthica* was under high predation pressure by epibenthos in the low intertidal but not in the high intertidal as the densities of predators were reduced towards the upper shore limits. Furthermore, Richards *et al*. (1999) concluded that predation by this crab was responsible for reduction in densities on *M. balthica* and *Cerastoderma edule*. Invertebrate predators such as *C. maenas* may forage on siphons of adult *M. balthica*, which can result in sublethal effects (Bonsdorff *et al*., 1995). Tellinids have been found in the diet of dab (Hall *et al*., 1990b), long rough dab (Ntiba and Harding, 1993) and plaice (Braber and De Groot, 1973; Poxton *et al*., 1983).

Biogeochemical functions: *Macoma balthica* have been reported to enhance ammonia and nitrite release (Mortimer *et al*., 1999).

Biological activity and habitat functions: *Macoma balthica* has been classified as biodestabiliser. Widdows *et al*. (2000) found a significant relationship between sediment erodability (mass of sediment eroded and erosion rate) and the density of *M. balthica*.

Societal importance: None.

5.8 Tunicata

Ascidiidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Not predatory.

Biogeochemical functions: Ascidians filter out large amount of seawater during feeding. It has been reported that *Ciona intestinalis* can have large grazing impact on the phytoplankton biomass in shallow water areas (Riisgård *et al*., 1998). We would therefore expect *Ascidiella scabra* to have similar grazing impact on phytoplankton biomass, and therefore on nutrient dynamics and water quality.

Biological activity and habitat functions: *Ascidiella scabra* is a fast colonizing species and may be a fouling organism (Schmidt, 1983).

Societal importance: None.

5.9 Porifera

Superitidae

Economic importance: None.

Ecological importance as prey: No information found.

Ecological importance as predators: Not predatory.

Functional importance: Although sponges belonging to Superitidae are very common in the North Sea their biology and ecology is poorly known. For that reason, we cannot determine whether they play important role in the ecosystem although as they filter large quantities of water they may remove particulate matter.

Societal importance: None.

5.10 Vegetative habitats

Laminariaceae

Economic importance: Within the North Sea, *Laminaria hyperborea* is harvested commercially in Brittany (France), Scotland and Norway, sometimes with dredging (Birkett *et al*., 1998). About 75–80,000 t of kelp are harvested commercially annually in Brittany but we lack information for other areas (Dauvin *et al*., 1997 cited in Birkett *et al*., 1998). Drift kelp is used as an agricultural fertiliser and soil conditioner. Recently, kelps have been harvested for the alginate industry which produces valuable emulsifiers and gelling agents for cosmetic, pharmaceutical and food industry (for reviews see Birkett *et al*., 1998; Wilkinson, 1995; Guiry and Blunden, 1991).

Ecological importance as prey: Sea urchins and the snail *Helcion pellucidum* are known to graze on kelp. Lobsters, crabs and fish species are known to predate on molluscan and echinoderm herbivores within kelp beds (Birkett *et al*., 1998).

Biogeochemical functions: *Laminaria* species are efficient in absorbing nitrate and phosphate from seawater. The amounts of nutrients can determine the growth rates of kelp. Kelp species respond towards increased nutrient levels by an increase in the rate of uptake of these nutrients. Similarly, some kelp species have been reported to increase productivity in response to addition of fertilisers (Lüning, 1990). Birkett *et al*. (1998) summarises the primary impacts by kelp beds on its environment, which includes reducing the light available to the deeper parts of the kelp bed, reducing ambient levels of macronutrients and increasing the levels of DOM and POM.

Biological activity and habitat functions: Kelp beds act as energy dampers, reducing the surge effects of waves and the velocity of the flow within dense kelp forests (Birkett *et al*., 1998). Kelps provide a highly complex habitat for many types of organisms. The species composition of benthic organisms can differ between the different parts of the algae, i.e. the blade, the stipe and the holdfast itself. The blades of *L. hyperborea*, support various species of snails, bryozoans and hydrozoans and algae. The stipes can contain a very diverse assemblage of algae. The diversity of fauna within the kelp holdfast can be extremely high. Kelp holdfasts provide an extremely complex habitat for a large number of organisms, generally dominated by mobile fauna and crevice dwelling organisms (Birkett *et al*., 1998). Moore (1973b) recorded 389 species from holdfasts collected from the north east coast of Britain. In Helgoland, the species richness associated with *L. hyperborea* was greater than that for *L. digitatum* (Schultze *et al*., 1990). The associated fauna can be sensitive to pollution but Jones (1973) showed that 45% of those species found in unpolluted waters were not found in kelp holdfasts from polluted habitats. Kelp habitats play an important role in providing refuge from predators for various fish species, many of which are of commercial importance. Habitat preferences for the cod (*Gadus morhua*) have been investigated with a field experiment (Gotceitas *et al*., 1995). They concluded that the cod utilises the kelp habitat as a refuge when exposed to a predator, but was not preferred if predators were absent.

Societal importance: None.

Rhodophyceae

Economic importance: Maerl is harvested in northern France (Brittany), with grabs or pump dredgers. The landings of maerl peaked in 1977 with 650,000 t but decreased down to 520,000 t in 1984. Maerl is used mainly as a calcium/magnesium soil additive in animal fodder (Blunden *et al*., 1975; Guiry and Blunden, 1981) and can be a better soil conditioner than magnesium and calcium carbonate mixtures (Brain *et al*., 1981). In the

UK, up to 30,000 tonnes of maerl were harvested between 1975 to 1991 (Birkett *et al*., 1998). We have little information on the harvest of maerl for other North Sea countries.

Ecological importance as prey: Various herbivores graze algae off the maerl thalli, such as *Tectura virginea* (Birkett *et al*., 1998). Maerl can also provide habitat for species which themselves become a prey for other organisms. This includes when, seaweed that attach themselves to the maerl attract other animals e.g. *Aplysia punctata* and rissoids which feed on the weed (Birkett *et al*., 1998).

Biogeochemical functions: Maerl beds are an important source of calcium carbonate particles for other coastal habitats, such as beaches and dunes. Bosence (1980) showed that *Lithothamnion corallioides* and *Phymatolithon calcareum* were able to accumulate over 400 g CaCO3 m^{-2} y^{-1} in Ireland. Similarly, maerl can adsorb large amounts of phosphorus (Gray *et al*., 2000).

Biological activity and habitat functions: The three-dimensional structure of maerl thalli forms an interlocking lattice that provides a wide range of niches for infaunal and epifaunal invertebrates. Due to the high structural complexity, the diversity of fauna and flora can be high. Within UK maerl beds, 150 species of macroalgae and 500 species of benthic species have been recorded (Birkett *et al*., 1998). Benthic communities within maerl beds can have higher diversity compared to gravel and shell bottoms of equivalent granulometry (Cabioch, 1969). Some groups may become more abundant within maerl beds such as epifauna and boring infauna (Bosence, 1979b), although species richness and diversity can be influenced by sediment type (De Grave, 1999). The high complexity of the maerl beds may be important in providing refuge from predation (Grall and Glemarec, 1997) and stabilise sediments. The structural integrity and sediment stability is further increased by animals such as byssus forming bivalves and tube-building polychaetes (Birkett *et al*., 1998).

Societal importance: *L. corallioides* and *P. calcareum* maerl biotopes are included within Annex 1 Habitat ‘Sandbanks slightly covered by seawater all of the time’ of the European Habitats and Species Directive 1992. *Phymatolithon calcareum* is listed on Annex Vb. *L. corallioides* and *P.*

calcareum are covered by a UK Biodiversity Action Plan and *P. calcareum* is listed on the UK BAP 'long list' (Anon., 1995). Two maerl species are protected under Annex V of the EU Habitats Directive 1992 (*L. corallioides* and *P. calcareum*). Special Areas of Conservation (SACs) have been developed for maerl beds in the UK which have been interpreted from 'sandbanks covered by sea water at all times' from the EU Habitats Directive 1992. Maerl is a component in the UK Joint Nature Conservancy Council guidelines for the selection of intertidal SSSIs of the tidal rapids part of saline lagoons. The guidelines also list 'tide-swept algae' as a community of at least national importance, which could include maerl on the lower shore.

Salt marshes

Economic importance: Salt marsh habitats are important for agricultural use and important as a habitat for grazing livestock (Breckling, 1994; Kellermann, 1995). A number of salt marsh plants have traditionally been used for medical, nutritional or even industrial purposes (Liebezeit *et al.*, 1999). The salt marsh fringe reduces erosion of sediments (review in Boorman *et al.*, 2002).

Ecological importance: Salt marshes are grazed by livestock (Esselink *et al.*, 2000) and by brent geese in the Dutch Wadden Sea (Van der Wal *et al.*, 2000). They provide important feeding grounds for mobile fish and invertebrate predators, such as the shore crab *Carcinus maenas* (Elkaim and Rybarczyk, 2000). Moderate grazing by livestock was found to increase the diversity of halophytic plants (Esselink *et al.*, 2000).

Functional importance: Salt marsh habitats are dominated by species which are capable of tolerating a wide range in environmental conditions such as wave action, tidal change, salinity, temperature, oxygen content, sediment loads, and tidal currents (Lockwood *et al.*, 1996). They provide a valuable habitat for a large number of organisms, including invertebrates and breeding birds and nursery grounds for shrimps and fish (Lockwood *et al.*, 1996). Saltmarshes can be important as a breeding ground for the redshank *Tringa totanus* (Esselink *et al.*, 2000). Forelands and salt marshes on the German North Sea coast contribute significantly to the protection and safety of the artificial coastline (Lieberman *et al.*, 1997). Marshes are of importance in flood control and rainfall drainage. During the last decades, large amounts of the nutrients nitrogen and phosphorus from anthropogenic origin have entered the Wadden Sea. The salt marshes in the Wadden Sea probably have been loaded with phosphorus and nitrogen since both nutrients reach the marshes with flooding water, and nitrogen is also brought in by atmospheric deposition. Nitrogen can cause an increase in biomass of some salt-marsh plant species but reduction in plant diversity (Leendertse *et al.*, 1992). Salt marshes at various locations in the Wadden Sea were found to accumulate large amounts of cadmium. Sandy sediments had comparatively higher contaminant loads compared to muddy sediments (Runte, 1997). The diversity of fauna in salt marsh habitats can vary along the intertidal gradient. The species richness in tidal pools within salt marshes at the upper intertidal can be low. However, salt marsh ditches at the upper intertidal are less accessible to epibenthic predators and hence of some importance as refuge or nursery for the macrofauna (Haase, 1993). In saltmarshes in the Bay of Somme (eastern English Channel), a total of 96 species were recorded. Many of the species belonging to Amphipoda, Talitridae, Coleoptera, Carabidae and Trechidae, Araneida and Lycosidae were found to be highly associated to salt marsh habitats (Elkaim and Rybarczyk, 2000). Mathieson *et al.* (2002) showed that salt marsh habitats are important habitats for juvenile fish and of providing refugia for life stages vulnerable to predation.

Societal importance: Salt marsh habitats are generally regarded as important and unique habitats (Boorman *et al.*, 2002). Salt marsh habitats are listed on Annex I (European Commission Habitat Directive 92/43/EEC).

Zosteraceae

Economic importance: Sea grasses have been put to a number of uses in the past for example, sound-proofing, insulation, roofing thatch, binding soil, packaging, basket weaving and in the manufacture of ‘coir’ matting (see Van Keulen, 1999 for review). In some areas, bait digging for cockles takes place within *Zostera* biotopes (Davison and Hughes, 1998). These habitats are of economic importance as large number of commercially important fish species are found within these areas.

Ecological importance as prey: Seagrasses such as *Zostera marina* (eelgrass) is an important component in the diet of brent geese *Branta bernicla*, wigeon *Anas penelope*, swans, *Cygnus olor* and *C. cygnus* (Davison and Hughes, 1998). The brent geese forage heavily on *Z. marina* during stopovers on spring and/or autumn migration, in the Wadden Sea and in British estuaries. During the 1930s, a viral disease affected *Z. marina* populations resulting in loss of this seagrass from many areas which subsequently resulted in a major decline in the North Sea brent geese population (Ganter, 2000). *Zostera marina* beds provide important feeding grounds for fish and invertebrate predators, including those of commercial importance such as the bass *Dicentrarchus labrax* (Davison and Hughes, 1998).

Biogeochemical functions: *Zostera marina* is important in nutrient dynamics and is an important source of organic matter (through grazing and as detritus). The *Zostera* biotopes are highly productive, sedimentary environments. Seagrass detritus is rich in microorganisms and is very important in nutrient cycling (Davison and Hughes, 1998). It has been demonstrated that the food chain of seagrass biotopes is driven by microbial decomposition of seagrass detritus but not of phytoplankton or terrestial organic matter as previously thought (Thresher *et al*., 1992).

Biological activity and habitat functions: *Zostera* biotopes provide an important habitat for invertebrates and fish, which utilise them as spawning grounds or refuge from predation. Species which are found amongst *Zostera* beds include the pipefish species *Syngnathus typhle* and *Entelurus aequoraeus*, the sea anemones *Cereus pedunculatus* and *Cerianthus lloydii* and the neogastropod *Hinia reticulatus.* Similarly, a large number of species such as the small prosobranch molluscs (e.g. *Rissoa* spp., *Lacuna vincta*, *Hydrobia* spp. and *Littorina littorea*) graze on the leaves (Davison and Hughes, 1998). *Zostera* beds are thought to play an important role in providing a refuge from predation for many kinds of organisms (Orth *et al*., 1984). Such protection may only be important for the smaller size classes of fish (Jackson *et al*., 2001) such as juvenile cod (Gotceitas *et al*., 1997). Seagrass beds have been shown to provide important habitat for deep-burrowing bivalves (Beal, 1997) and nursery ground for fish, many of which are of commercial value (Davison and Hughes, 1998; Jackson *et al*., 2000). The high complexity of seagrass habitats has been shown to enhance fish abundance, biomass, species richness, dominance and diversity. Removal of seagrass can result in a serious decline in abundance and biomass of associated fauna (Hughes *et al*., 2002). Eelgrass plays an important role in maintaining the stability of the shoreline. The dense network of rhizomes binds the sediment and reduces erosion in shallow waters while the roots allow the oxygen to penetrate deeper into sediments (Davison and Hughes, 1998). *Zostera* beds slow currents and facilitate deposition of fine particulate matter (e.g. Jackson *et al*., 2001). Likewise, it is thought that beds facilitate passive settlement of meiofauna and larvae of macrofauna, hence explaining why recruitment of e.g. bivalves can be enhanced in such areas (Eckman, 1987).

Societal importance: Three species belonging to *Zostera* are found in the UK *(Z. marina*, *Z. noltii* and *Z. angustifolia*). These are found in 11 out of 12 UK Marine SAC Project demsonstration sites and are key elements of 5 out of 7 Annex I habitats (Davison and Hughes, 1998). *Zostera noltii* and *Z. marina* are both included in UK Biodiversity Action Plan (http://www.ukbap.org.uk/default.htm). Some coastal seagrass habitats have been designated Ramsar sites (http://www.ramsar.org), SPAs (under the EC Birds Directive) and voluntary marine protected areas. *Zostera marina* is strictly protected under the Berne Convention (http://www.nature.coe.int/english/cadres/bern.htm).

Table 3.16 Overview over economic, societal, functional and ecological importance of benthos and habitats within the North Sea (see also appendix 6). The importance is (wherever possible) ranked in order of importance, where ‘0’ = no importance or not relevant; ‘1’ = low importance; ‘2’ = high importance; ‘?’ = no information was available; ‘0–2?’ = ranking based on best guess. For the economic importance, the ranking ranged from 0 to 3. For ecological importance, the importance of invertebrate prey in the diet of birds (b), fish (f) and invertebrates (i) is ranked. For the ‘affects diversity’ column, the effect of a species or habitat is evaluated as to whether it increases (‘I’) or decreases (‘D’) diversity (can be abundance or species richness) of the associated fauna. In some cases, a species may promote an increase in density of one (or more) species, whereas it may decrease densities in others (‘I/D’). Functional groups: Lifestyle: E= epifaunal, I= infauna, i= sediment water interface, t= tube-builder, b= burrower, cr=crevice. Feeding mode: su= suspension feeder, ps= passive suspension feeder, as= active suspension feeder, h= herbivore, c= carnivore, sd= surface deposit feeder, b= burrowing, df= subsurface deposit feeder, sc= scavenger, gr= grazer, om= omnivore. Mobility: m= mobile sm= semi-mobile, s= sessile. Feeding apparatus: j= jawed, nj= non-jawed, t= tentaculate, md= mucous devices, p= pumping. Depth distribution: i=intertidal, (i)=sometimes recorded intertidally, s=sublittoral

Family	Key species	Evaluation of importance				Functional importance: Biogeochemical			Functional importance: Biological activity and habitat functions							Ecological importance		Functional groups						
		Economic	Societal	Functional	Ecological	Nutrient recycling	Bioaccumulates	Water quality	Habitat complexity	Alters flow	Refugia	Affects diversity	Interactions	Biostabilisation	Bio-destabilisation	Prey	Predator	Bioturbators	Habitat forming	Lifestyle	Feeding mode	Mobility	Feeding apparatus	Depth distribution
Annelida																								
Aphroditidae	*Aphrodita aculeata*	0	0	0	1	0	?	0	0	0	0	?	?	0	0	1(f)	1	0	0	E	c	m	j	s
Arenicolidae	*Arenicola marina*	2	0	2	1	2	1	0	0	1?	1	I/D	2	0	2	2(b), 1(f)	0	2	0	I	df	sm	nj	i/s
Chaetopteridae	*Chaetopterus variopedatus*	0	0	2	1	?	?	0	2	2?	2	I?	?	?	0	1	0	0	2	t	su/(sd)	s	p	(i)/s
Magelonidae	*Magelona* spp.	0	0	0	1	?	?	0	0	0	0	0	0	0	0	1(f)	0	0	0	I/b	sd	sm	t	(i)/s
Maldanidae	*Maldane sarsi*	0	0	1	1	1	?	0	0	0	0	0?	?	0	1	1(f)	0	1	0	I/b	df	s/sm	nj	s
Nephtyidae	*Nephtys* spp.	1	0	1	2	0?	1	0	0	0	0	D	1	0	0	1(f), 2(b)	2	0	0	i/b	c/sc	m	j	i/s
Nereidae	*Nereis diversicolor, N. virens*	2	0	2	2	0?	1	0	0	0	0	D	2	0	0	2(b), 2(f), 2(i)	1	1	0	i/b	h/c/su/sd	m	j/p	i/s
Orbiniidae	*Scoloplos armiger*	0	0	0	2	1?	0	0	0	0	0	0	0	0	0	2(i), 2(b)	0	0	0	I/b/i	df	m	nj	i/s
Oweniidae	*Owenia fusiformis*	0	0	1	1	0?	?	0?	1	1	1	?	?	1	0	1(f)	0	0	0	t	su/sd	sm	t	i/s
Pectinariidae	*Lagis koreni*	0	0	1	2	0?	?	0	1	?	0	0	?	0	1	2(f)	0	1	0	t	b/df	sm	nj	(i)/s
Sabellariidae	*Sabellaria* spp.	0	2	2	1	0?	?	0?	2	1	2	I	2	2	0	1(i)	0	0	2	E/t	ps	s	t	(i)/s
Sabellidae	*Sabella pavonina*	0	0	1?	1?	0	0	0	1	1?	1	?	1?	1?	0	1(f)	0	0	1	E/t	su/sd	s	t	i/s
Serpulidae	*Serpula vermicularis*	0	2	2	1	0?	?	1?	2	1?	1?	I	1?	2	0	1(i)	0	0	2	E/t	su	s	t	i/s
Spionidae		0	0	1	1	0?	?	0?	1	1	0	I	1	1	0	1(f)	0	0	1	t	su/sd	sm	t	i/s
Terebellidae	*Lanice conchilega*	0	0	2	2	0?	1	0?	2	2	2	I	1	2	0	2 (b), 2 (f)	0	0	2	t	as/sd	s	t	i/s

Table 3.16 Continued.

Family	Key species	Evaluation of importance				Functional importance: Biogeochemical			Functional importance: Biological activity and habitat functions							Ecological importance		Functional groups						
		Economic	Societal	Functional	Ecological	Nutrient recycling	Bioaccumulates	Water quality	Habitat complexity	Alters flow	Refugia	Affects diversity	Interactions	Biostabilisation	Bio-destabilisation	Prey	Predator	Bioturbators	Habitat forming	Lifestyle	Feeding mode	Mobility	Feeding apparatus	Depth distribution
Arthropoda																								s
Ampeliscidae	*Ampelisca* spp.	0	0	?	1?	0?	?	?	1	0?	0	?	1?	1?	?	1?	0	0	0	t	su/sd	m	p	s
Axiidae	*Calocaris macandreae*	0	0	1	1	2?	?	?	1	?	?	0	1	?	1	1(f), 1(I)	0	2	1	I/b	df	sn		s
Callianassidae	*Callianassa subterranea*	0	0	2	1	2	?	?	1	?	1	D?	1?	0	2	?	0	2	1	I/b	df/su	sm		s
Cancridae	*Cancer pagurus*	1?	0	1	1	?	?	0	0	0	0	0	1	0	1	1(f)	1	X	0	E	c/sc	m		(i)/s
Corophiidae	*Corophium* spp.	0	0	0	2	1	1	?	0	0	0	0	1	1	1	2(f), 2(b), 2(i)	0	X	0	t	sd/su	sm/m		i/s
Corystidae	*Corystes cassivelaunus*	1?	0	?	?	1?	?	?	?	?	?	?	?	?	?	?	1	0	0	E/I/b	c	m		(i)/s
Crangonidae	*Crangon crangon*	3	0	0	2	?	1	0	0	0	0	D	1	0	0	2(f), 2 b)	2	0	0	E	c/s	m		(i)/s
Galatheidae	*Munida rugosa*	1?	0	0	?	?	?	?	?	?	?	?	?	?	0	1	?	0	0	E	s/c	m		s
Laomediidae	*Jaxea nocturna*	?	0	2	?	2	?	?	?	?	?	?	?	0	2	?	0	1	1	I/b	df/sc/su	sm		s
Majidae	*Hyas* spp.	1	0	?	1	?	?	?	?	?	?	?	?	?	0	1(f)	1	0	0	E	s/c	m		(i)/s
Nephropidae	*N. norvegicus, H. gammarus*	3	0	2	1	2?	1	?	1	0	0	?	1	?	2	2(f)	1	2	2	I/b	c/sc	lm/m		s
Paguridae	*Pagurus bernhardus*	1	0	?	?	1?	1	0	0	0	0	?	1	?	0	1(f)	1	0	0	E	s	m		s
Pandalidae	*Pandalus borealis*	2	0	0	2	0	1	0	0	0	0	0	0	0	0	2(f)	0	0	0	E	sc/om	m		s
Portunidae	*Carcinus maenas*, *Liocarcinus* spp.	1	0	?	2	1?	1	0	0	0	0	?	1	?	1	1(f)	2	0	0	E	s/c	m		i/s
Upogebiidae	*Upogebia deltaura*	0	0	2	1	2?	0	0	1	0	0	?	?	0	2	1(f)	0	2	1	I/b	su	sm	p	s
Bryozoa																								
Alcyonidiidae	*Alcyonidium diaphanum*	0	0	0	1?	1	1?	1?	1	1?	0?	0?	0?	0?	0?	1	0	0	1	E	su	s		s
Flustridae	*Flustra foliacea*	0	0	0	1?	1	1?	1?	1	1?	0?	0?	0?	0?	0?	1	0	0	1	E	su	s		s
Cnidaria																								
Caryophyllidae	*Lophelia pertusa*	1	2	2	1	1?	?	?	2	2	2	I	?	1?	0	0	0	0	2	E	su	s		s
Hydrozoa		0	0	1	1	?	?	?	1	0	0	?	1	0	0	1	1	0	1	E	c	s		s
Pennatulacea	*Pennatula phosphorea*	1	2	1	1?	?	?	?	1	?	1?	I?	1?	?	?	1(f)	0	0	1	E	c/su	s		s
Echinodermata																								
Amphiuridae	*Amphiura filiformis*	0	0	1	2	?	1	1?	0	0	0	0?	0	0	0	2(f)	0	?	0	I/i	ps/sd	m	j	s
Antedonidae	*Antedon bifida*	0	0	0	1	0	0	0	1	?	?	?	?	0	0	1(f)	0	0	1	E	ps	S		s
Asteriidae	*Asterias rubens*	1	0	0	2	?	1	0	0	0	0	D	1?	0	0	1(f)	2	0	0	E	sc/c	m	j	i/s
Astropectenidae	*Astropecten irregularis*	0	0	0	1	?	?	?	0	0	0	D?	1?	0	0	?	2	0	0	E	sc/c	m	j	s

Table 3.16 Continued.

		Evaluation of importance				Functional importance										Ecological importance		Functional groups						
						Biogeochemical			Biological activity and habitat functions															
Family	**Key species**	Economic	Societal	Functional	Ecological	Nutrient recycling	Bioaccumulates	Water quality	Habitat complexity	Alters flow	Refugia	Affects diversity	Interactions	Biostabilisation	Bio-destabilisation	Prey	Predator	Bioturbators	Habitat forming	Lifestyle	Feeding mode	Mobility	Feeding apparatus	Depth distribution
Echinidae	*Echinus esculentus*	1	1	0	1	?	1	0	0	0	1	D	1	0	0	1	0	0	0	E	gr/om	m	j	(i)/s
Ophiotrichidae	*Ophiotrix fragilis*	0	0	2	1	2	1	1	0	0	1	D?	?	0	0	1	0	0	0	E/cr	ps	sm		s
Ophiuridae	*Ophiura* spp.	0	0	?	2	?	?	0	0	0	0	D	1	0	1	2	1	1	0	E	c/om	m		s
Solasteridae	*Crossaster papposus*	?	0	0	1	?	1	0	0	0	0	?	?	0	0	0?	1	0	0	E	c	m	j	(i)/s
Spatangidae	*B. lyrifera*, *E. cordatum*	0	0	2	1	2	1	0	0	1	0	I/D	1	0	2	0?	0	X	0	I/b	df/sd	sm		i/s
Echiura																								
Echiuridae	*Maxmuelleria lankesteri*	0	0	2	1	2	?	0	0	0	0	I/D?	?	0	2	1	0	2	0	I	df	sm		s
Mollusca																								
Arcticidae	*Arctica islandica*	0	1	0	1	1?	1	1?	0	0	0	?	?	0	0	1(f)	0	0	0	I	as	s	p	s
Buccinidae	*Buccinum undatum*	1?	0	?	1	0	1	0	0	0	0	?	?	0	0	1	2	0	1	E	s/c	m		s
Cardiidae	*Cerastoderma edule*	3	0	2	2	2	1	2?	0	0	0	D?	2	0	1	2(b),1(i)	0	1	0	I	as	s/sm	p	i/s
Myacidae	*Mya arenaria*	0	0	?	1	1?	1	?	0	0	0	?	?	0	1	1	0	1	0	I	as	sm	p	i/s
Mytilidae	*Mytilus edulis*	3	1	2	2	2	1	2	2	2	2	I	2	1	0	2(b), 2(i), 1(f)	0	2	2	E	as	s/sm	p	i/s
Mytilidae	*Modiolus modiolus*	1?	2	2	1	2	1?	2?	2	2?	2	I	2?	1	0	1	0	2	2	E	as	s/sm	p	s
Ostreidae	*Ostrea edulis*	3	2	1	1	1?	1	2?	1	1?	0	?	?	0	0	?	0	0	1	E	as	s	p	i/s
Pectinidae	*Pecten maximus*	3	0	?	1	?	1	2?	0	0	0	?	?	0	0	2?(i)	0	0	1	E	su	sm	p	s
Mactridae	*Spisula solida*	1	0	0	1	?	1?	1?	0	0	0	0?	?	0	1	1(i),1(f)	0	0	0	I	f/su	s	p	(i)/s
Scrobiculariidae	*Abra alba*	0	0	1	1	1	1	1?	0	0	0	D	0	0	1	1(f), 1(i)	0	1	0	I	su/sd	s	p	(i)/s
Solenidae	*Ensis* spp.	1?	0	0	1	1	1	1?	0	0	0	0	0	0	1	1(b)	0	0	0	I	as	s	p	(i)/s
Tellinidae	*Macoma balthica*	0	0	2	2	1	1	1?	0	0	0	D?	1?	0	1	2(b), 2(i), 1(f)	0	1	0	I	f/su	s	p	(i)/s
Tunicata																								
Ascidiidae	*Ascidiella scabra*	0	0	1	1?	1?	?	2?	1	1	1?	0?	?	0	0	1?	0	0	0	E	f/su	s	p	s
Porifera																								
Superitidae	*Superites* spp.	0	0	0?	1?	1?	?	?	1	1?	1?	1?	1?	0	0	1?	0	0	0	E	f/su	s	p	s
Vegetative habitats																								
Laminariaceae	*Laminaria* spp.	1	0	2	0	2	?	?	2	2	2	I	2	0	0	1	0	0	2					(i)/s
Rhodophyceae	*Lithothamnium*	2	2	2	0	2	?	?	2	2	2	I	1	1	0	0	0		2					s
Salicornidae	*Salicornia* spp.	0	2	2	0	2	1	?	2	2	2	I	?	2	0	2	0		2					i/s
Zosteraceae	*Zostera* spp.	2	2	2	1	2	0	0	2	2	2	I	0	2	0	1	0		2					i/s

CHAPTER FOUR

Discussion

1. Seabirds

Deciding which species of seabirds should be included in the ‘significant web’ is driven to some extent by their charismatic status since many seabirds are protected by many conservation directives and legislation. However, while rare species and breeding seabird species are protected under annexes of the Bird Directive, other species also have charismatic status based on stakeholders’ opinions of their value, i.e. ornithologists desire to watch these species e.g. the puffin colonies at the Farne Islands in the North Sea. This in turn carries a financial value (Blondel, 2002), as ‘birders’ pay tourist operators and other traders for the pleasure of observing bird species. Similarly, many birds, while not necessarily being charismatic species, may have ecological and functional importance as top predators in the North Sea ecosystem. The inclusion of some of the scavenging seabirds, e.g. the kittiwake and fulmar, is primarily driven by their high abundances in the North Sea, which links to their ecological and economic importance in the marine ecosystem. Not all species should be included in the ‘significant web’; for example, based on the assessment of its ecological, economic, societal and functional roles the puffin (*Fratercula arctica*) is not included. Many of the Annex I seabird species, e.g. the roseate tern are only present in the North Sea in small populations and are of little ecological, economic and functional importance. This does not mean that they should not be included in the ‘significant web’. Based on their societal status, they are important, but these Annex I species should not be considered further in modelling scenarios other than generically.

It is probable that the management objectives cited in the EFEP will relate to the reduction of fishing effort with concomitant reduction of discards and offal. Furthermore, the control of discards and offal may be advocated. Many abundant scavenging seabird species are thought to have benefited from discards and offal as energy subsidies and their populations have increased. Lindeboom and De Groot (1998) state that discards and offal provide a source of food for a number of scavenging seabird species which can make up to one third of their food requirements. Scavenging species of seabirds such as the fulmars (*Fulmarus glacialis)*, gannets (*Morus bassanus)*, common gull (*Larus canus canus*), herring gull (*L. argentatus*), lesser black-backed gull (*L. fuscus*), great black-backed gull (*L. marinus*) and kittiwakes (*Rissa tridactyla*) have been identified as utilising discards and offal in the North Sea (Gislason, 1994; Camphuysen *et al*., 1993; Camphuysen *et al*., 1995). The expansion in breeding numbers and range of the fulmar (*F. glacialis*) over the last two centuries is generally attributed to an increased availability of fish offal and discarded fishes from commercial fisheries (Phillips *et al*., 1999a) and the reduction in hunting and persecution in the past century. Oro (1996) found that discard availability was an important factor in supporting the egg production in the lesser black-backed gull. Discard management measures will reduce a potentially valuable resource for seabirds, the effects on these populations need to be assessed and understood.

Additionally, there is a competitive hierarchy among the seabirds attending fishing vessels. The gannet (*Morus bassanus)*, the great black-backed gull (*Larus marinus*) and the great skua (*Catharacta skua*) are consistently the species that rank highest in the dominance hierarchy, whereas fulmar and kittiwakes (*Rissa tridactyla)* are most vulnerable to kleptoparasitism. Small species such as kittiwakes and common gulls (*Larus canus*) usually avoid fights for discards in situations which they are constantly outcompeted by leaving the area (Camphuysen *et al*., 1995; Garthe and Hüppop, 1998). These hierarchies can be used to predict the effect of changes in the amount of discards produced at sea (Furness, 1992). For instance, if competition behind fishing vessels increases, the smaller and less competitive species will suffer first and with the greatest effects. Sudden changes in the food supply, caused by a reduction in fishing effort, may result in seabirds modifying their diet ‘prey switching’ and preying directly on other seabirds. Large gull species and great skuas (*C. skua*) exhibit this behaviour. Fishery stock collapses have led to a reduced availability of small pelagic fishes and discards to the gulls and great skuas and these birds were observed to switch to prey on smaller seabirds e.g. the kittiwake (Regehr and Montevecchi, 1997; Tasker *et al*., 2000).

Pelagic species such as sprats, sandeels and herrings are important prey to seabirds. Therefore with regard to mitigation measures that allow the stocks of large, piscivorous fish stocks to recover it should be realised that this may result in a reduced availability of small forage fishes to seabirds. This may affect those species that feed predominantly on forage fishes, e.g. guillemots, terns and, especially, the kittiwakes which show a reduced ability to switch to other prey (Lewis *et al*., 2001).

Food consumption by seabirds is not uniform across the North Sea, i.e. on a large spatial scale. Seabirds are unlikely to compete with fisheries on a large spatial scale; for example, the main sandeel industrial fisheries are conducted offshore in the northern North Sea and the central North Sea, apart from the relatively small sandeel fishery near Shetland. The areas fished offshore are outside those generally used by breeding seabirds (ICES, 2003a). But this does not imply that seabirds are unaffected by commercial fishing; it is important to consider the effect of fishing on birds at a local scale (Lewis *et al.*, 2001; Tasker *et al.*, 2000). There are areas, mainly in the western, north-western North Sea (IVa West), where large quantities of prey are taken by seabirds. But analyses are often not sufficiently spatially disaggregated to identify 'hot spots' (Hunt and Furness, 1996; Votier *et al*., 2003). However, seabirds tend to remain close to their colonies (Furness and Tasker, 1997; Wanless *et al*., 1985) as foraging over further distances for resources imparts a cost on seabirds (Krebs and Davies, 1993) to the possible detriment of the chick and adult survival. In this respect, it is more important to focus on local changes in prey abundance than on overall stock changes at a North Sea scale (5NSC, 1997). This necessitates the need to ensure that local stocks with retrospect to known aggregations of birds, e.g. identified in SPAs, are protected.

Limitations on data

Seabird censuses used to map abundances concentrate on breeding populations and non-breeders may fill in breeding vacancies as they arise. Furthermore, due to the delayed maturity of seabirds, the number of breeding adults can be significantly lower than the total number of seabirds, so responses at the population level will lag behind the changes in environmental conditions (Perrins and Birkhead, 1983; Gill, 1995)

Considerations to improve modelling of seabirds

There is a need to investigate food intake of adults, non-breeders and chicks plus changes in diet over seasons. This is technically difficult, and most sampling of seabird diet has been based on work during the breeding season.

Many studies provide data on percentage occurrences of prey items which give an indication of prey importance, but a more biologically useful measure would be biomass composition.

2. Marine mammals

Marine mammals is a term used to encompass both cetaceans (whales and dolphins) and pinnipeds (seals). Deciding on which species of the marine mammals to be included in the significant web is predominantly driven by their charismatic status since marine mammals are protected by many conservation directives and legislations. Secondly, total abundance or presence of resident populations drives their inclusion in the significant web, e.g. the harbour porpoise and the bottlenose dolphin. Some species of cetacean are not common in the North Sea, i.e. the long-finned pilot whale (*Globicephala melaena*), false killer whale (*Pseudorca crassidens*), fin whale (*Balaenoptera physalus*), common dolphin (*Delphinus delphis*), Risso’s dolphin (*Grampus griseus*) and sperm whale *(Physeter catodon*), nor are there any resident populations necessitating SAC protection under the EU Habitat and Species Directive 92/43/EEC. While this does not preclude their inclusion in the significant web, based on their societal status, it is the goal to create a tractable ‘significant web’ and as their functional and economic status is for all intents and purposes minor in the ecosystem, they should not be considered further in modelling scenarios other than generically. The pinnipeds, the ringed seal (*Phoca hispida*), harp seal (*P. groenlandica)*, hooded seal (*Cystophora crista*) and the bearded seal *(Erignathus barbatus*) are infrequent, rarely encountered vagrant visitors in the North Sea, and as no resident populations are found, these do not require SAC protection. Similarily, due to their low abundance, ecological, economic and functional importance in the ecosystem is negligible. These species were therefore not included in the ‘significant web’. Bax (1991) reviewed the fish biomass flow to fish fisheries to marine mammals in various systems including the North Sea, and calculated generically that fisheries (of all types) consumed 1.4–6.1 t km^{-2}, whereas marine mammals consumed in the region of 0–5.4 t km^{-2}. The annual consumption by the most abundant cetacean in the North Sea, the harbour porpoise, has been calculated at hundreds of thousands of tones per annum. Thus marine mammals can be considered as significant consumers of fish production. In the North Sea, the harbour porpoise by far consumes the most biomass on an annual basis, closely followed by the grey seal and the common (harbour) seals. It is difficult to assess the impact of other cetaceans as consumers of prey due to a lack of data. In the North Sea, the diet of cetaceans is dominated by fish species, mainly small shoaling species in pelagic (e.g. herring and sprat) and demersal (e.g. whiting) habitats (Santos *et al*., 1994; Santos *et al*., 1995). The diet of seals is composed predominantly of fish species including sandeels, whitefish (cod, haddock, whiting, ling), and flatfish (plaice, sole, flounder, dab) (Brown *et al*. 2001; Hall *et al.*, 1998; Hammill and Stenson, 2000; Prime and Hammond, 1990).

As noted marine mammals prey on many fish species and their diet will obviously be influenced by the prey species in the immediate system. An observation which is illustrated by the prey composition of the harbour porpoise of the Scottish coast compared with the diet of juvenile and adult harbour porpoises in the Kattegat and Skagerrak. Along the Scottish coast, sandeels and Gadidae were the main food items in stomachs of harbour porpoises (Santos *et al*., 1994; Santos *et al*., 1995) and along the Kattegat and Skagerrak herring (*Clupea harengus*) and the Atlantic hagfish were important dietary items (Börjesson *et al*. (2003). Minke whale diet also shows spatial differences. It is dominated by sandeels along the Scottish coast and spring spawning herring in the Norwegian Sea (Olsen and Grahl-Nielsen, 2003; Olsen and Holst, 2001). A degree of spatial resolution in the EFEP models may be necessary to accurately assess the scenarios (Appendix 2) relating to marine mammals and commercial species to be addressed further in the EFEP project.

Limitations on data

In assessments of cetaceans accurate abundance data is limited and is based on summer surveys (Hammond *et al*., 2002). The data on pinnipeds is more robust, given their haul out behaviour on shore (JNCC, 2003).

Stomach analysis and faecal analysis

Diet composition data is reported as observed prey items, items in stomach dissections, biomarkers, and faecal analyses. Analyses will only indicate consumption over a limited period of time. Food resides in seal stomachs only for a relatively short period after ingestion. Murie and Lavigne (1985 – reported in Pierce and Boyle, 1991) recorded stomach clearance rates of grey seals to be 190–280 g per hour after consumption of 6 kg of herring. Stomach contents were essentially undigested after three hours, after 6 hours; flesh and bones were fragmented and no hard-skeletal parts remained after 18 hours. Håkanson (1984) proposed that biomarkers in triacylglycerols were an indicator of recent feeding in copepods, whereas biomarkers wax esters were an indicator of feeding over a longer period exceeding a week. Experiments on the digestion rates in marine mammals indicate that sagittal otoliths pass through the digestive track within 3–30 hours (Da Silva and Neilson, 1985; Murie and Lavigne, 1986).

MacMahon and Tash (1979) found that otoliths of green sunfish (*Lepomis cyanellus*) were still identifiable after 12 hours, in 0.01 N hydrochloric acid solution (a simulated gastric acid condition), but were completely dissolved after 24 hours. In a predator's stomach, the dissolution may take longer due to two processes: the buffering of gastric juices by ingested food and the acid solution needs to penetrate the fish head to reach the sagittal otoliths. The size of the otoliths also affects the rate of disintegration; smaller otoliths erode rather quickly (Jobling and Breiby, 1986).

Due to differences in erosion rates, the contribution of species with large otoliths (e.g. silvery pout, blue whiting and hake) can be overestimated compared to species with more fragile otoliths (e.g. mackerel, sandeel and herring). The smaller and more delicate the otoliths, the more likely that they are damaged by digestion, subsequently impeding identification (Pierce and Boyle, 1991). However, it can be noted that retrieval of the tiny otoliths (e.g. of mackerel) would indicate that the contribution of larger, more robust fish would not be underestimated.

Consideration of these issues is required, with respect to quantifying the amounts consumed. Analyses presented in this document are formed from the best data available.

3. Zooplankton

Zooplankton have been identified for inclusion in the significant web primarily on their abundance and biomass and as dietary items important to commercial species, where known. All of the species/genera chosen display profound spatial, seasonal and yearly variation in abundance and biomass which relate to extrinsic drivers such as climate, and intrinsic drivers such as density-dependant mortality. The time series databases collected show these changes over time. *Calanus finmarchicus*, one of our significant species, has over several decades shown a decrease in abundance in the North Sea (Beaugrand *et al.*, 2002; Johns and Reid, 2001) and presumably will continue to change in the future. Many of the data collated refer to years prior to 2001, forecasting abundance and biomasses of select zooplankton species to future decades will add a degree of uncertainty to any modelling work.

It may be practical for modelling purposes to create an aggregate group(s) similar to the 1981 food web model of the North Sea (Christensen, 1995), to supplement data from the large zooplankton species identified as important in the significant web. Suitable data taken from literature has been supplied – see the zooplankton spreadsheet ('zooplankton.xls').

Limitations on data

It needs to be considered that the sampling methods employed at the Dove Marine Laboratory and for the CPR differ: WP3/WP2 hauls at a fixed station (Dove Marine Laboratory) compared with monthly samples of zooplankton taken with a specially designed net which is towed behind cargo vessels and ferries on regular routes in the North Sea and North Atlantic (CPR). According to Clark *et al.* (2001) both techniques pick up similar patterns of year-to-year fluctuations in abundance and that the taxa that show significant correlations with one another constitute over one-third of the total abundance in each time series. Further, seasonal cycles also display a good comparison. However, absolute abundance values differ (as much as fifteen times) and this is thought to be due to passive avoidance as a result of hydrodynamic factors, resulting in a lower catch in the CPR tow. Despite the differences between local data and CPR data comparisons can be made (Clark *et al.*, 2001; Greve *et al.*, 1996).

4. Fish

Selection of significant components

Economic importance

The target fish species in the North Sea can be grouped into demersal or pelagic, for human consumption or for industrial purposes. The demersal fisheries for human consumption usually target roundfish species (cod, haddock and whiting) and flatfish (plaice and sole). The demersal fishery in particular has a considerable by-catch of various non-target roundfish, flatfish and elasmobranch species (sharks, rays). The four gadoid species, cod, haddock, whiting and saithe make up between 73 and 80% of the total biomass of the demersal piscivore predator guild (Greenstreet, 1996). The pelagic fisheries target fish species such as herring, mackerel, and horse mackerel, with most of the landings landed for human consumption. The industrial fisheries are targeted at sandeels, Norway pout and sprat, but other species, such as haddock, herring and whiting may be caught accidentally in these fisheries (ICES, 2002c). Among the non-target fish species, a number of species were found to be of some economic and/or ecological importance (e.g. dab, lemon sole, sharks, skates and rays, gurnards).

Societal importance

Society has committed itself to the protection of biodiversity and the marine environment through international agreements and legislation. Some of those species in need of protection are described in the OSPAR list of threatened and/or declining species and habitats (ref. nr. 2003-14). The fish species on that list relevant for the North Sea are *Acipenser sturio* (sturgeon), *Alosa alosa* (allis shad), *Ceteorhinus maximus* (basking shark), *Dipturus batis* (common skate), *Raja montagui* (spotted ray), *Gadus morhua* (cod), *Petromyzon marinus* (sea lamprey) and *Salmo salar* (salmon). Of particular note is the large number of elasmobranchs (sharks, rays, skates) on this list. Elasmobranchs mature late and have few offspring, which makes them vulnerable to the effects of additional mortality caused by fishing. A general problem with the species on this list is that because of their low abundance they are difficult to monitor and very little is known on the (by-)catch of these species or the relative importance of potential predator-prey relationships with other components of the North Sea ecosystem.

Inclusion of components that are considered important by society was often hampered by the availability of data. Therefore it was decided to group all elasmobranchs together into one component of the significant web representative of the fish species that are of societal importance because of their K-selectedness (slowly maturing, few offspring). As this is not a very abundant group, with very limited information on the smaller sizes, no size-based strata should be distinguished. The elasmobranchs may have value as an indicator group for the effects of fishing on species with similar life history characteristics but which are not part of the significant web. Cod is already included in the list of significant ecosystem components because of its commercial value; other species were not included.

Ecological importance

Most commercial species are members of the predatory guild due to their large size. The species that are caught in industrial fisheries make up most of the staple food for the large gadoid species, seabirds and seals. As fish go through major changes in terms of diet or habitat preference during ontogeny, it is necessary to distinguish various ontogenetic stages. This can be achieved by distinguishing age-groups or size-classes. Although it is common to distinguish age-groups for the commercial species, these data are often lacking for the non-target species, so size-classes can be used instead.

Considering that most of the ecological changes occur during the first few years of life, it is sufficient to distinguish ages 1, 2, 3 and a 4+ group in which all fish of 4 years and older are combined. These age groups dominate in terms of numbers and often biomass too. For the non-target species no information is available (i.e. age-length keys) to determine the age, and no age-based models have been developed to determine the abundance per age-group. In order to take the ontogenetic differences into account, it should suffice to group the non-target species into 10 cm size-classes and pool all fish larger than 30 cm in one group. So for the non-target species we have classes: 0–10, 10–20, 20–30 and 30+.

Functional importance

Because the fish species make up a considerable part of the biomass of (higher trophic level) marine biota, they are not only of ecological but also of high functional importance. Other than that, many of the demersal species, and notably the flatfish, will contribute to bioturbation by disturbing the upper layer of the sediment.

Significant components

When deciding which fish components should be selected for the 'significant web', the most obvious distinction is between commercial and non-target fish as commercial species have economic value; because of their large variety in diet and relatively large biomasses they also have high ecological and functional value. This also applies for the remaining non-target fish as a whole and therefore it should be included as a significant component. Because different fisheries operate on this group of species, a distinction should be made between the demersal non-target and pelagic non-target component. Finally, the elasmobranchs should be incorporated as a significant component because of their societal importance. Note that both in the demersal non-target component and elasmobranch component there are various species that have economic value (e.g. dab, lemon sole, sharks, skates and rays, gurnards) but for which there is no targeted fishery.

The changes in behaviour (feeding and otherwise) during ontogeny can be incorporated by distinguishing ontogenetic stages within each of the components. For the commercial species it was chosen to use age-classes since this fits in well with the existing advice framework (CFP), for the non-target species 10 cm size-classes are used. Thus, the significant food web should consist of the fish components shown in Table 4.1.

Table 4.1 Grouping of the main fish components including size- and age-based subgroups

Common name	Scientific name	Sub-groups
Cod	*Gadus morhua*	ages 1–4+
Haddock	*Melanogrammus aeglefinus*	ages 1–4+
Whiting	*Merlangius merlangus*	ages 1–4+
Saithe	*Pollachius virens*	ages 1–4+
Norway pout	*Trisopterus esmarki*	ages 1–4+
Sandeel	*Ammodytes* spp.	ages 1–4+
Plaice	*Pleuronectes platessa*	ages 1–4+
Sole	*Solea vulgaris*	ages 1–4+
Herring	*Clupea Harengus*	ages 1–4+
Sprat	*Sprattus sprattus*	ages 1–4+
Mackerel	*Scomber scombrus*	ages 1–4+
Non-target demersal		0–10, 10–20, 20–30 and 30+
Non-target pelagic		0–10, 10–20, 20–30 and 30+
Elasmobranchs		none

5. Benthos and habitats

Appendix 6 contains various supplementary information such as distribution, abundance, biology and mortalities of benthic families which were evaluated for the inclusion in the ‘significant web’ (see also Table 3.16). The species of high societal importance were the polychaetes *Sabellaria* spp. and *Serpula vermicularis*, the coral *Lophelia pertusa* and the bivalves *Modiolus modiolus* and *Ostrea edulis*, pennatulids and three vegetative habitats, maerl, saltmarshes and seagrasses. It should be noted that *L. pertusa* is only found in few locations within the North Sea, and may therefore have only very localised importance.

We found information on in total of 30 species of invertebrates and algae which are harvested within the North Sea (see Appendix 7). Of these, only 11 species were found to be of high and medium commercial importance. For species of less commercial importance, we had, in general, very limited information.

The identification of functionally and ecologically important benthic families and habitats was more difficult. Of the families selected for evaluation, the amount of knowledge amongst them was highly varied. Families and habitats of commercial and/or societal importance, and those found intertidally, have been better studied compared to those found in the subtidal or those which are of no commercial or societal importance.

The dominant North Sea infaunal species, in terms of both abundance and frequency of occurrence, are generally small sized polychaetes, bivalves and crustaceans (Appendix 8). Of the 15 families of infauna which dominate in abundance, seven were evaluated while only two (both echinoderms) were selected as part of the significant web. The ones we rejected seem neither to be important in fish diets nor provide any important function. However, this may be due partly to the lack of research on these groups. Similarly, many of the dominant polychaete families within the North Sea seem not to be important in fish diets. However, this may be due to the fact that many of these consist largely of soft parts and for that reason can be rapidly digested in fish stomachs. To avoid the lengthy process of identifying the harder parts of polychaetes, such as chaete and jaws, these are often lumped together on a coarser taxonomic resolution than family.

The most frequently recorded epifaunal species in the North Sea are shown in Appendix 9. While the majority of families on that list were evaluated, only a few were selected to be included as part of the significant North Sea web. Groups not selected include Bryozoa, Hydrozoa and Porifera. Although these are frequently recorded within the North Sea, we found limited support for their importance to ecosystem functioning.

Economic importance

Species of **high economic importance** were *Nephrops norvegicus*, *Crangon crangon*, *Cerastoderma edule*, *Mytilus edulis* and *Pecten maximus* (Appendix 7). In the UK, the valuable species were the Norwegian lobster *N. norvegicus* and the scallop *P. maximus*. The fishery for *C. crangon* is important along the coast of Wadden Sea and Denmark. In Denmark, the UK, and especially in the Netherlands, there is considerable seed fishery for mussels. The fishery for cockles is important in the Netherlands.

Species of **medium economic importance** were *Arenicola marina*, *Nereis* spp., pennatulids, *Homarus gammarus* and *Pandalus borealis*. *Arenicola marina* and *Nereis* spp. (mainly *Nereis virens*) are important as bait for anglers and are of minor importance in aquaculture. There is a fishery and sea-ranching of the common lobster *Homarus gammarus.* A fishery for the northern shrimp (*Pandalus borealis*) takes mainly place in the Skagerrak/Norwegian Deeps, the

Fladen ground and the Farn Deep with annual landings about 20,000 t (QSR, 2000).

The majority of benthic species which are harvested within the North Sea are of *low* economic importance. We found limited information on the crab fishery within the North Sea. In the UK, the commercial value of crab fishery was on average £13 million over the period 1996–2000, but it seems that this fishery is more important on the West Coast of Scotland and Ireland.

<u>Mariculture</u>

The mariculture of shellfish is a growing industry within the North Sea (see Appendix 7). In the Netherlands, there is an intensive culture of mussels and oysters with average landing values from cultured mussels and oysters of approx. £35 million annually (Smaal and Lucas, 2000). In Norway, there is only a limited culture of shellfish (blue mussel, scallops and oysters) with landings only of about 600 tonnes in 1999 (Maroni, 2000). In Scotland, there is an aquaculture for scallops, oysters and mussels but we lack information how much of it takes place within the North Sea (Henderson and Davies, 2000). In France, the aquaculture is dominated by the cupped oyster (*Crassostrea gigas*) with around 150,000 tonnes produced each year, with an annual turnover of about £150 million. Some of the culturing takes place within the North Sea in Brittany and Normandy (Dosdat and De la Pomelie, 2000).

Ecological importance

<u>Prey</u>

Benthic organisms constitute a large proportion of the diet of fish, bird and invertebrate predators in the North Sea. However, to evaluate the importance of each family as a prey proved to be difficult. Firstly, our understanding of predator-prey relationships differs greatly between families. Secondly, species that consist largely of soft parts can be rapidly digested and for that reason, their importance in the diets may be underestimated. Finally, there is considerable spatial variation in the diet of fish predators. As an example, the dominant prey items in the diet of plaice differed between the southern North Sea, Kattegat and

Norway. We selected those prey groups as being important that were widely recorded in the diets (Table 4.2, Appendix 5).

Table 4.2 Families which were selected to be important as a prey. 2= high importance in diet, 1=low importance in diet, for bird (b), fish (f) and invertebrate (i) predators.

Family	Key species	Ecological importance as prey
Nereidae	*Nereis* spp.	2(b), 2(f), 2(i)
Arenicolidae	*Arenicola marina*	2(b), 1(f)
Nepthtyidae	*Nepthys* spp.	1(f), 2(b)
Pectinariidae	*Lagis koreni*	2(f)
Terebellidae	*Lanice conchilega*	2 (b), 2 (f)
Orbiniidae	*Scoloplos armiger*	2(i), 2(b)
Corophiidae	*Corophium volutator,*	2(f), 2(b), 2(i)
Nephropidae	*Nephrops norvegicus*	2
Crangonidae	*Crangon crangon*	2
Amphiuridae	*Amphiura filiformis*	2
Ophiolepidae	*Ophiura* spp.	2
Cardiidae	*Cerastoderma edule*	2(b),1(i)
Mactridae	*Spisula* spp.	2(i),1(f)
Mytilidae	*Mytilus edulis*	2(b), 2(i), 1(f)
Tellinidae	*Macoma balthica*	2(b), 2(i), 1(f)

Polychaetes are very important as prey, sometimes dominant in the diets of flatfish e.g. *Lagis koreni* (Pectinariidae). Rijnsdorp and Vingerhoed (2001) showed that polychaetes are more important in diets now than early last century. They concluded that these result are consistent with findings of loss of slow growing organisms and the increase in populations of opportunistic polychaetes as a result of increased beam trawl effort (e.g. Reise, 1982). Most polychaetes found intertidally, including *Nepthys* spp. and *Lanice conchilega*, are important prey in the diet of waders and gulls while *Nereis* is important prey for all predator types.

Among the crustaceans, the amphipod *Corophium volutator* is extremely important prey for fish, invertebrate and bird predators as it is generally extremely abundant on intertidal mudflats. *Crangon crangon* is heavily predated upon by fish, such as by cod and whiting (Pihl, 1994).

Brittlestars are heavily predated upon by flatfish species such as plaice, dab and long rough dab. Amongst bivalves, the mussel is especially important for many kinds of predators. The consumption of mussels varies greatly between predators. While the starfish *Asterias rubens* (12 cm arm length) can consume one mussel in three days (Saier, 2001), eider, oystercatcher and herring gull can consume 150 mussels (on the average size of 40 mm) in one day (Nehls, 1995) 2 hours and 30 minutes respectively (Hilgerloh, 1997). Many other infaunal bivalves are important prey too.

Predators

Out of the 12 families which were found to be predatory (as well as scavenging in some cases), we found evidence of strong predation impacts by the following five species: *Nepthys* spp., *Carcinus maenas, Crangon* spp., *Asterias rubens* and *Astropecten irregularis*. Other predators (e.g. *Nereis* spp. and *Cancer pagurus*) may affect associated fauna as a result of sediment disturbance (e.g. pit digging by crabs and sediment 'ploughing' by *Nereis*) rather than predation.

Functional importance

The majority of benthic families and habitats which were evaluated as being of high functional importance were either habitat formers and/or bioturbators and were generally of large body size. We identified seven families of bioturbators which we considered to have a large impact on the physical and the biological environment: Arenicolidae (*Arenicola marina*), Laomediidae (*Jaxea nocturna*), Callianassidae (*Callianassa subterranea*), Upogebiidae (*Upogebia deltaura*), Nephropidae (*Nephrops norvegicus)*, Spatangidae (*Brissopsis lyrifera*) and Echiuridae (*Maxmuelleria lankesteri*) (Table 4.3). Whilst the bioturbation impacts of *A. marina* and *B. lyrifera* are well understood, this is not the case for the remaining families which are hereafter termed as megafaunal burrowers. The rate of sediment reworking by these megafaunal burrowers can be high. As an example, the amount of sediment reworked annually by *C. subterranea* populations in the North Sea has been estimated to be 11 kg dry wt m^{-2} y^{-1} (Rowden *et al.*, 1998) and 15.5 kg dry wt m^{-2} y^{-1} (Stamhuis *et al.*, 1997). Bioturbation by these animals is likely to structure some benthic communities but this remains to be investigated.

It should be noted that bioturbation impacts are not only correlated with the amount of sediment reworked, but also with the degree of mobility and burrowing activity of the organisms (Swift, 1993, Appendix 10). Although mussels are not generally considered bioturbators, the intense biodeposition which occurs within dense beds can affect sediment properties, nutrient dynamics and associated fauna (e.g. Ragnarsson and Raffaelli, 1999). Small sized bioturbators such as *Lagis koreni* and *Maldane sarsi*, may exert considerable impacts when found in high densities, although this has been little studied (e.g. Holte, 2001).

Table 4.3 Published information on sediment reworking rates. Figures were calculated as material (in ml or g dry weight) ejected to the sediment surface per individual per day.

Species	Reworking rate $ind.^{-1}\ d^{-1}$	Source
Arenicola marina	2–12 ml	Sheader, 1995
Maldane sarsi	1 ml	Holte, 2001
Lagis koreni	0.00056–0.083 g	Seiderer and Newell, 1999
Jaxea nocturna	4 g	Hughes and Atkinson, 1997; Nickell *et al*. 1995
Callianassa subterranea	0.6–3 g	Hughes and Atkinson, 1997
Maxmuelleria lankesteri	8–13 g	Hughes and Atkinson, 1997, Hughes *et al.*, 1999
*Mytilus edulis**	0.5–4.8 g	Kautsky and Evans 1987

*Amount of sediment deposited as faeces and pseudofaeces.

We found some evidence from the literature that bioturbation and filter feeding by *Arenicola marina*, *Callianassa subterranea*, *Maxmuelleria lankesteri*, *Cerastoderma edule* and *Mytilus edulis* can influence nutrient dynamics. Such effects include enhanced fluxes of nutrients at the sediment-water interface and release to the overlaying seawater, which in turn can stimulate primary productivity such as of microphytobenthos in sediments (Swanberg, 1991). However, we found limited evidence that enhanced nutrient levels caused by bioturbation influence processes at higher trophic levels. For example, Worm and Reusch (2000) showed that due to biodeposition by mussels within seagrass beds, the levels of ammonium (NH_4^+) and phosphate (PO_4^{3-}) in the water column and the pore water were greatly enhanced, ranging between 27% and 84%. Nevertheless, they found no evidence for enhanced seagrass growth in response to the increased nutrition load. Dense beds of mytilids can remove a considerable proportion of the large phytoplankton biomass (e.g. Haamer and Rodhe, 2000).

Important habitat forming species

Families which were considered important as habitat formers in the North Sea were the tube-builders Terebellidae (*Lanice conchilega*), Sabellariidae (*Sabellaria* spp.) and Serpulidae (*Serpula vermicularis*), the coral *Lophelia pertusa*, mytilids (*Mytilus edulis* and *Modiolus modiolus*), sea grass (*Zostera* spp.), saltmarshes (*Salicornia* spp.) and maerl (Rhodophyceae). All these habitat forming species were shown to perform important functions such as providing feeding and nursery grounds for fish and birds and providing refuge from predation. These habitats tend to support a more diverse fauna and than found in adjacent areas.

Many of the tube-building species belonging to Crustacea and Polychaeta are abundant within the North Sea. In contrast to the larger sized habitat forming species selected for the 'significant web', these are mostly of small size. Whilst these may provide some important functions such as enhancing settlement of larvae and meiofauna via alteration in flow, their effects are less obvious in comparison to those of larger species. However, many of the small bodied tube-builders have been found to be opportunistic, rapidly colonising recently disturbed areas (e.g. Pearson and Rosenberg, 1978). Overall, it is clear that the importance of the dominant infauna in the North Sea ecosystem is poorly understood. Finally, marine scavengers are opportunistic omnivores capable of obtaining nutrition from various sources. Their populations may be enhanced as a result of fishing practices where they accumulate in high numbers where trawling with bottom gears takes place to feed on exposed or damaged animals, which otherwise would not be available to them as prey. There is, however, little understanding on the effects of an increased scavenger population on the ecosystem functioning.

CHAPTER FIVE

Review of conservation measures and actions within the North Sea

1. Preamble

There are many international treaties, agreements and legislation instruments which provide legal protection for the conservation and protection for marine wildlife on both regional and global scales.

2. European level conventions, agreements and legislations

EU Habitats and Species Directive (1992). The EU Habitats Directive (the European Community Council Directive on the Conservation of Natural Habitats and Wild Fauna and Flora (92/43/EEC)) aims to ensure that biodiversity is maintained through the conservation of important, rare or threatened habitats and species. EU member countries are selecting terrestrial and marine sites which include the best examples of a variety of habitats and species.

The Birds Directive (1979; implemented 1981). The Birds Directive (European Community Council Directive on the Conservation of Wild Birds (79/409/EEC)) aims to establish protected areas for birds in Europe. The aim of the Birds Directive is to protect endangered and sensitive birds and their habitats. Article 4 of the Birds Directive, requires Member States to classify the most suitable territories (in number and size) for the protection and conservation of species of rare, wild birds that are listed in Annex I of the Directive, and of regularly occurring migratory species not listed in Annex I.

Bern Convention (1979; implemented 1982). Convention on the conservation of European Wildlife and Natural Habitats. The convention is concerned with the protection of habitats, especially those considered endangered.

Bonn Convention (1979; implemented 1983). Convention of the Conservation of Migratory Species, which provides strict protection for endangered species, guidelines for the conservation and management for other migratory species.

Regulation 2371/2002 of the Common Fisheries Policy. The regulation requires that fishing should not have a negative impact on marine ecosystems.

OSPAR (Oslo and Paris Convention 1992; implemented 1998). The convention for the Protection of the Marine Environment of the Northeast Atlantic provides, in Annex V, for the 'protection and conservation of the ecosystem and biological diversity of the maritime area', and Appendix 2 gives criteria for 'identifying human activities for the purpose of Annex V'.

ASCOBANS (1992; implemented 1994). The Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. This was established under the Bonn Convention and applies to odontocete cetaceans (except the sperm whale) within the area of the Agreement. Under the Agreement, provision is made for the protection of specific areas, monitoring, research, information exchange, pollution control and heightening public awareness of marine mammals. Measures cover the monitoring of fisheries interactions and disturbance, resolutions for the reduction of by-catches in fishing operations, and recommendations for the establishment of specific protected areas for cetaceans.

3. Global conventions and agreements.

CITES (1973; implemented 1975) (Convention on International Trade in Endangered Species of Wild Fauna and Flora). Prohibits the trade of many marine species.

International Convention for the Regulation of Whaling (1946; implemented 1948, with a subsequent protocol amendment to the Convention in 1956). The convention aims to 'provide for proper conservation of whale stocks and thus make possible the orderly development of the whaling industry'.

4. Site assessments leading to habitat area ramifications for seabirds in WP3

4.1 Special Protection Areas for seabirds

Special Protection Areas (SPAs) are a significant method of seabird protection and are created to protect and conserve seabird diversity within them. SPAs are identified under the Wild Birds Directive.

SPAs should:

1. Afford protection to seabird populations from damaging human activities.
2. Ensure the effective conservation of habitats and associated biological processes that are important to seabird populations.

A consideration of spatial scale is important in designating these areas. Due the mobility and patchy distribution of seabirds, there is some debate whether SPAs are truly useful mechanisms to protect these animals. SPAs at an ocean level scale are not feasible and networks of SPAs may prove more effective. Since seabirds tend to form colonies, some areas are likely to be more valuable to their populations than others, e.g. nesting grounds (Gill, 1995), and these areas are the obvious sites which could be selected as SPAs. There is also a need to consider temporal and spatial variations in scale, e.g. for the protection of areas during the breeding season.

EC Birds Directive

According to the Birds Directive, the selection of SPAs should take into account the protection requirements of Annex I and Annex II birds in the geographical sea and land area of the European territory of the Member States. In the process of considering measures for the protection and conservation of species, including the establishment of SPAs, Member States are to take account of:

- species in danger of extinction;
- species vulnerable to specific changes in their habitat;

- species considered rare because of small populations or restricted local distribution and
- other species requiring particular attention for reasons for the specific nature of their habitat.

The classification of SPAs by member states is determined by the Directive:

- that they comprise the most suitable territories in number and size taking into account protection requirements of the species;
- for Annex 1 species that account be taken of such species as listed above;
- for migratory species, that account be taken of their breeding, moulting and wintering areas and staging-posts and
- for migratory species, that particular attention be paid to wetlands, particularly those of international importance.

SPAs have been classified in the terrestrial environment, but no marine SPAs for the specific protection and conservation of seabirds outside territorial waters have yet been classified.

OSPAR

OSPAR aims to establish SPAs to:

- protect, conserve and restore species, habitats and ecological processes that are adversely affected as a result of human activities;
- prevent degradation of and damage to species, habitats and ecological processes, following the precautionary approach and
- protect and conserve areas that best represent the range of species, habitats and ecological processes in the OSPAR area.

The criteria for selection as an OSPAR SPA include consideration (based on the best available scientific knowledge) of whether the area:

- is important for species, habitats/biotopes and ecological processes that appear to be under immediate threat or subject to rapid decline;
- is important for other species and habitats/biotopes;
- has a high proportion of a habitat/biotope type or a biogeographic population of a species at any stage in its life cycle;
- has important feeding, breeding, moulting, wintering or resting areas;

- has important nursery, juvenile or spawning areas;
- has high natural biological productivity of the species or features being represented;
- has a naturally high variety of species or includes a wide variety of habitats/biotopes;
- contains a number of habitat/biotope types, habitat/biotope complexes, species, ecological processes or other natural characteristics that are representative for the OSPAR Area as a whole or for its different biogeographic regions;
- contains a high proportion of very sensitive or sensitive habitats/biotopes or species and
- has a high degree of naturalness, with species and habitats/biotope types still in a very natural state as a result of the lack of human-induced disturbance or degradation.

4.2 Designated areas

U.K. protected areas

Eighty seven coastal or island SPAs have been identified for breeding seabirds in the UK (http://www.jncc.gov.uk/UKSPA/sites/UKIndex.htm) (Figures 5.1–5.9). Only a proportion are in the North Sea region others are west coast of the U.K. and Ireland. The figures below indicate the location of all SPAs along the eastern coast of the UK. Further details are available on the JNNC website.

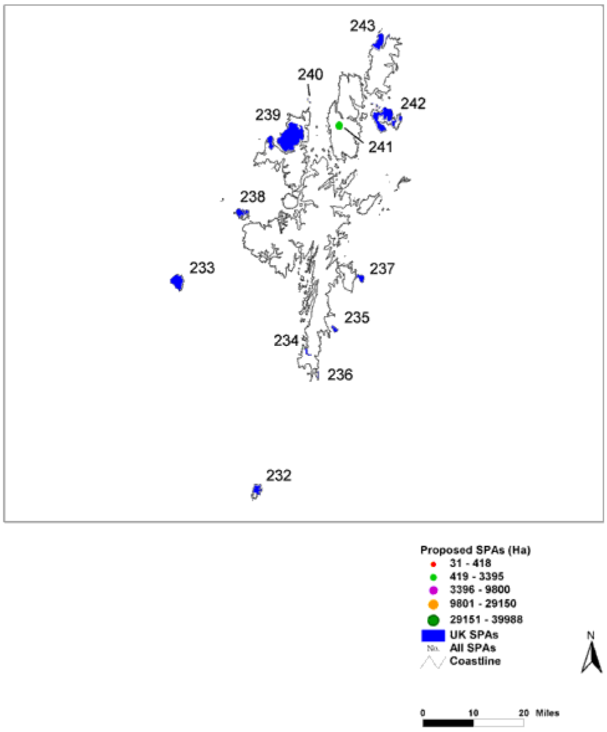


Figure 5.1 Shetland SPAs.

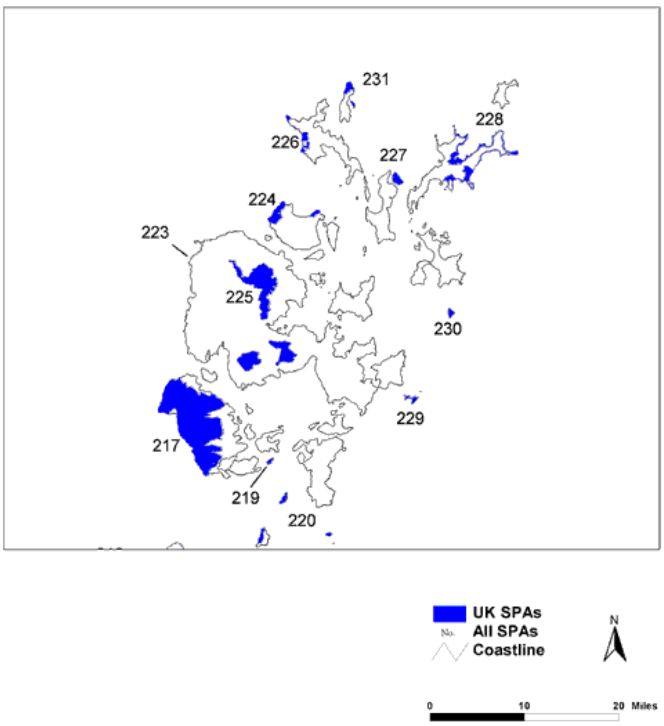


Figure 5.2 Orkney SPAs.

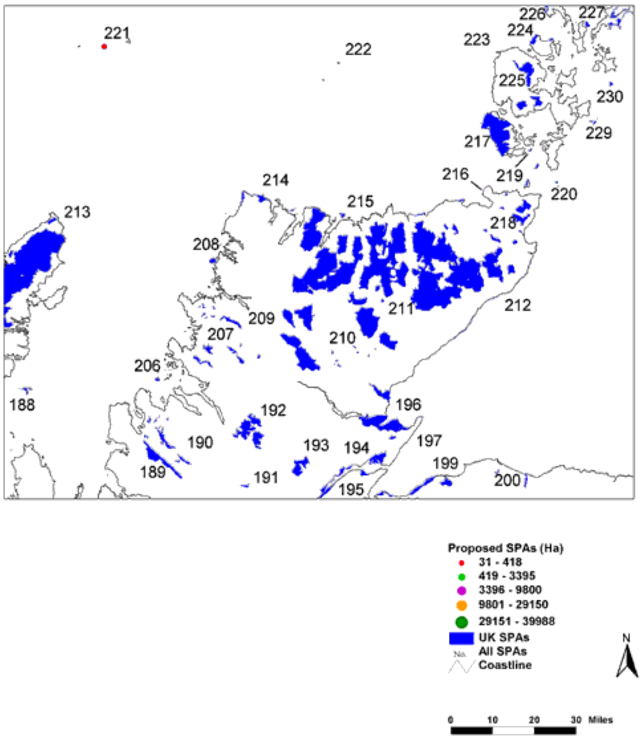


Figure 5.3 Northern Scotland SPAs.

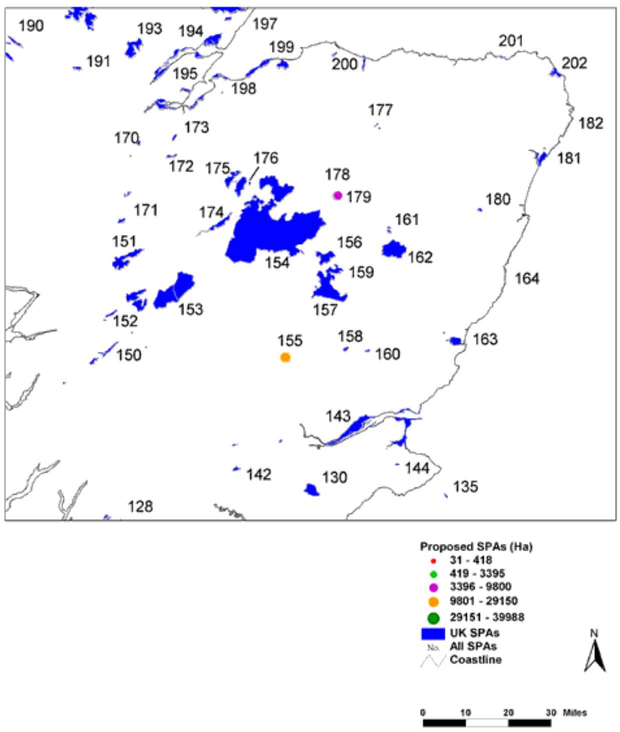


Figure 5.4 Eastern Scotland SPAs.

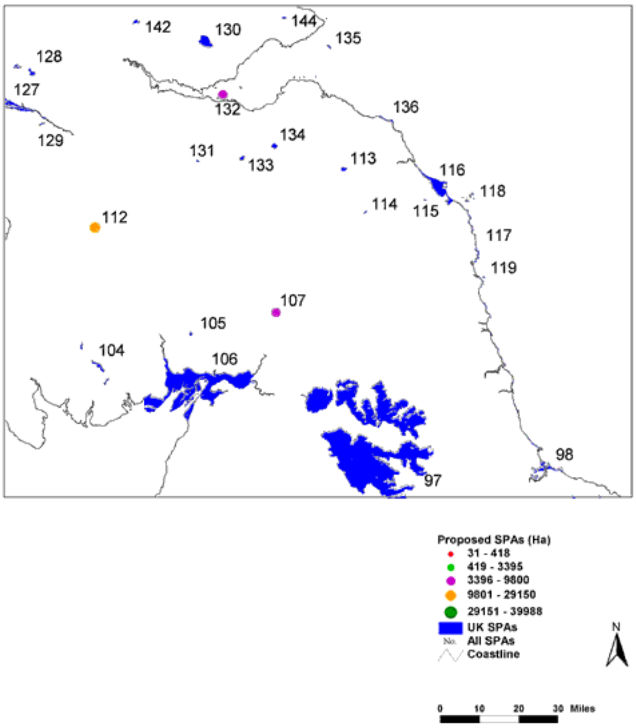


Figure 5.5 Southern Scotland and Northern England SPAs.

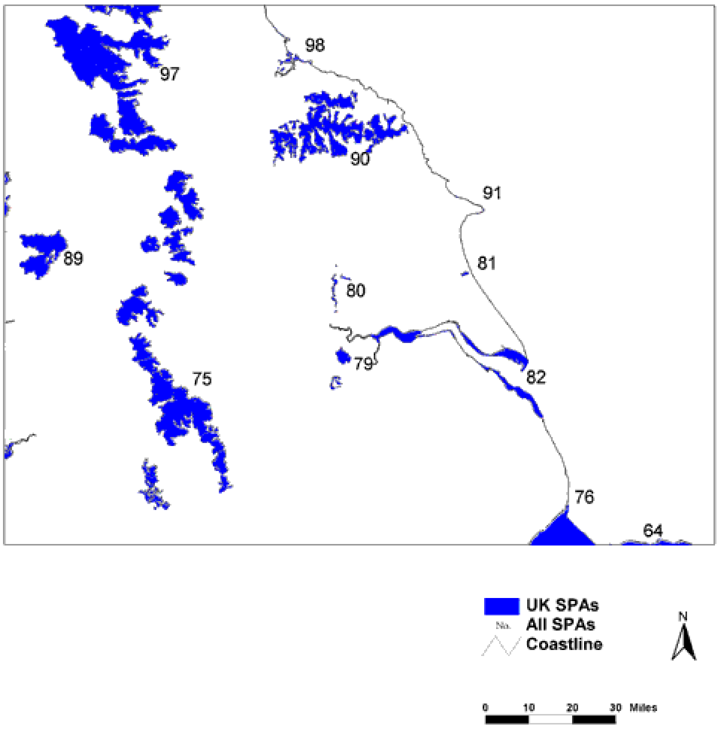


Figure 5.6 North-east England SPAs.

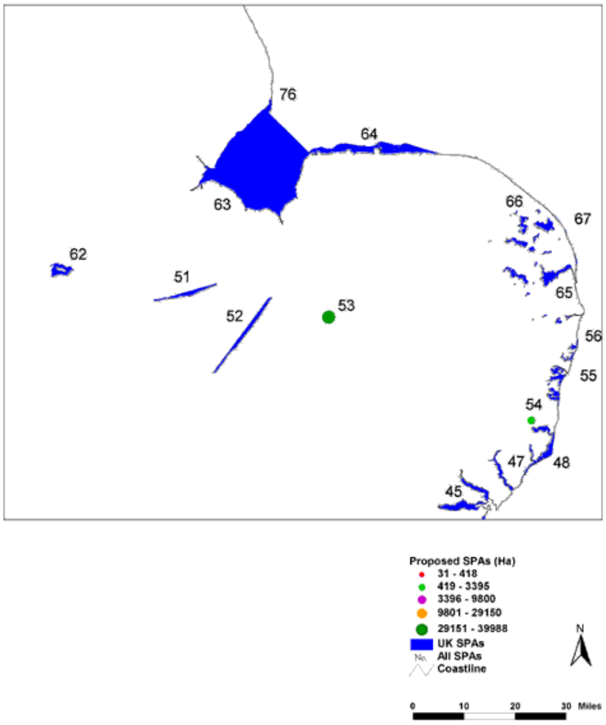


Figure 5.7 East England SPAs.

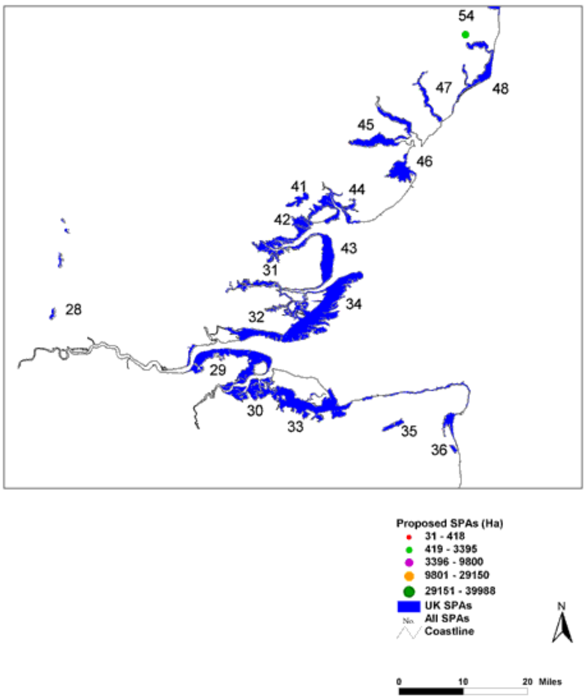


Figure 5.8 Thames Region SPAs.

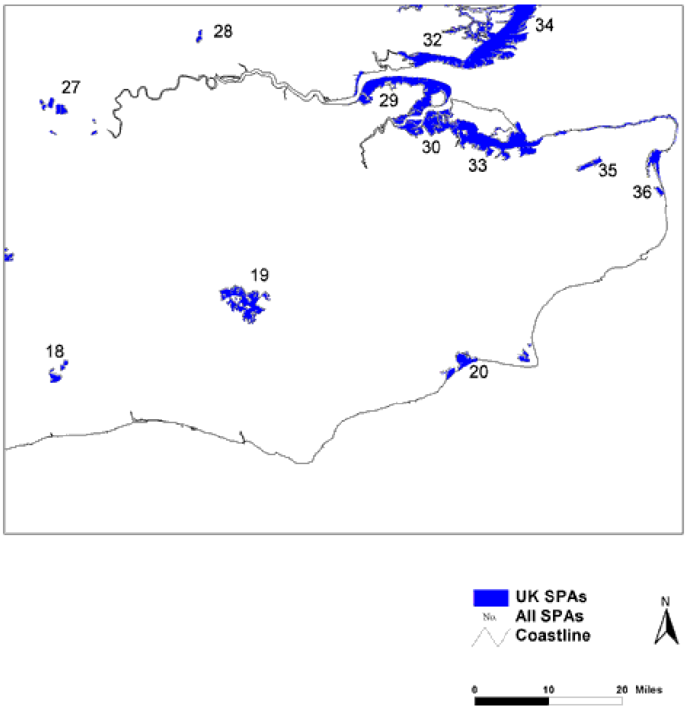


Figure 5.9 Southern England SPAs.

Belgium protected areas

Belgium presently has six Ramsar sites with a surface area of 7,935 hectares (http://www.ramsar.org/profiles_belgium.htm). All of which are important to birds but four of the sites are inland, the remaining two:

- Vlaamse Banken. Vlaamse Gewest; 1,900 ha; 51º10'N 002º44'E,
- Zwin. Vlaamse Gewest; 530 ha; 51º21'N 003º22'E

border the southern North Sea/English Channel region.

Netherlands protected areas

The Netherlands presently has 49 Ramsar sites, with a surface area of 818,908 hectares (http://www.ramsar.org/profiles_netherlands.htm) but all are irrelevant to the EFEP as many of these are found inland. However, the Voordelta SPA (51°43'N 003°35'E) is an extensive region of coastal waters and covers an area of 90,000 ha. The region is also proposed as a SAC under the Habitat Directive 92/43/EEC. The site meets at least three Ramsar criteria:

- it preserves particularly good examples of wetlands like intertidal mudflats, extensive marine waters, sandbanks permanently slightly covered by sea water;
- it harbours large congregations of waterbirds – 39,000+ (data of 1992–97) and
- it is a refuge for more than 1% of the biogeographical populations of four waterbird species (spoonbill, scaup, grey plover, and redshank).

Denmark protected areas

In Denmark, a total of 540,000 ha of marine areas (i.e. below mlw) have been designated as SPAs. Thirty seven SPAs were designated solely because of their importance for Annex I species listed in the Birds Directive. Fifteen SPAs were designated solely because of high numbers of other staging migrant birds. Fifty nine areas fulfilled both criteria (http://www.sns.dk/natur/netpub/birds/kap01.htm). The SPAs applicable to the EFEP are in the Wadden Sea region (see section on the Wadden Sea).

Germany protected areas

There is some confusion regarding the designation of SPAs in the German EEZ due to interpretation in the extant international rules, laws and conventions. This is further complicated due to the governmental system: territory stops at the 12-nautical-mile-zone, the German part of the North Sea is now divided into responsibility of the Federal State of Lower Saxony (within the 12-mile-zone, southern part), the Federal State of Schleswig-Holstein (within the 12-mile-zone, northern part) and the Central Government (for the EEZ). (See section on the Wadden Sea)

4.3 North Sea summary (habitat areas)

There are many internationally important sites along the North Sea coast of the UK (Table 5.1 and Figure 5.10). For further information on the spatial distribution of seabirds see Appendix 1.

Table 5.1 Internationally important seabird breeding colonies (SEA 3, 2002).

Species	Colony	Count in 1987–1993		Seabird 2000	
		Year	Count	Year	Count
Cormorant	Farne Islands	1993	268	2001	196
	Marsden Bay	1993	225	1999	248
Shag	Farne Islands	1993	1 948	2001	1 373
Kittiwake	Farne Islands	1993	5 889	2001	5 781
	Marsden Bay	1986	7 700	1999	2 031
	Filey North Cliffs	1990	5 666	2002	5 120
	Bempton Cliffs	1987	75 000	2000	24 870
	North Cliff, Flamborough	1987	8 368	2000	17 707
Sandwich tern	Farne Islands	1989	3 445	2001	2 364
	Coquet Island	1992	2 131	2001	1 190
	Blakeney Point	1992	4 000	2000	100
Arctic tern	Farne Islands	1989	3 710	2000	1 526
Common tern	Coquet Island	1992	842	2000	1 033
Roseate tern	Coquet Island	1992	29	2001	42
Little tern	Blakeney Point	1993	160	2000	100
	Great Yarmouth	1991	277	2000	220
Guillemot	Farne Islands	1993	25 309	2001	35 436
	Bempton Cliffs	1987	29 300	2000	32 860
Puffin	Farne Islands	1993	34 710		No count
	Coquet Island	1993	13 273	2001	17 208
Razorbill	Bempton Cliffs	1987	7 350	2000	5 710

Note:
1. The numbers on brackets relate to the year of colony survey
2. There are various definitions of population numbers of importance at the Britain & Ireland, European and biogeographical scales. This, coupled with changes in the population sizes at individual colonies over time, results in changes in the relative importance of certain colonies (SEA 3, 2002).

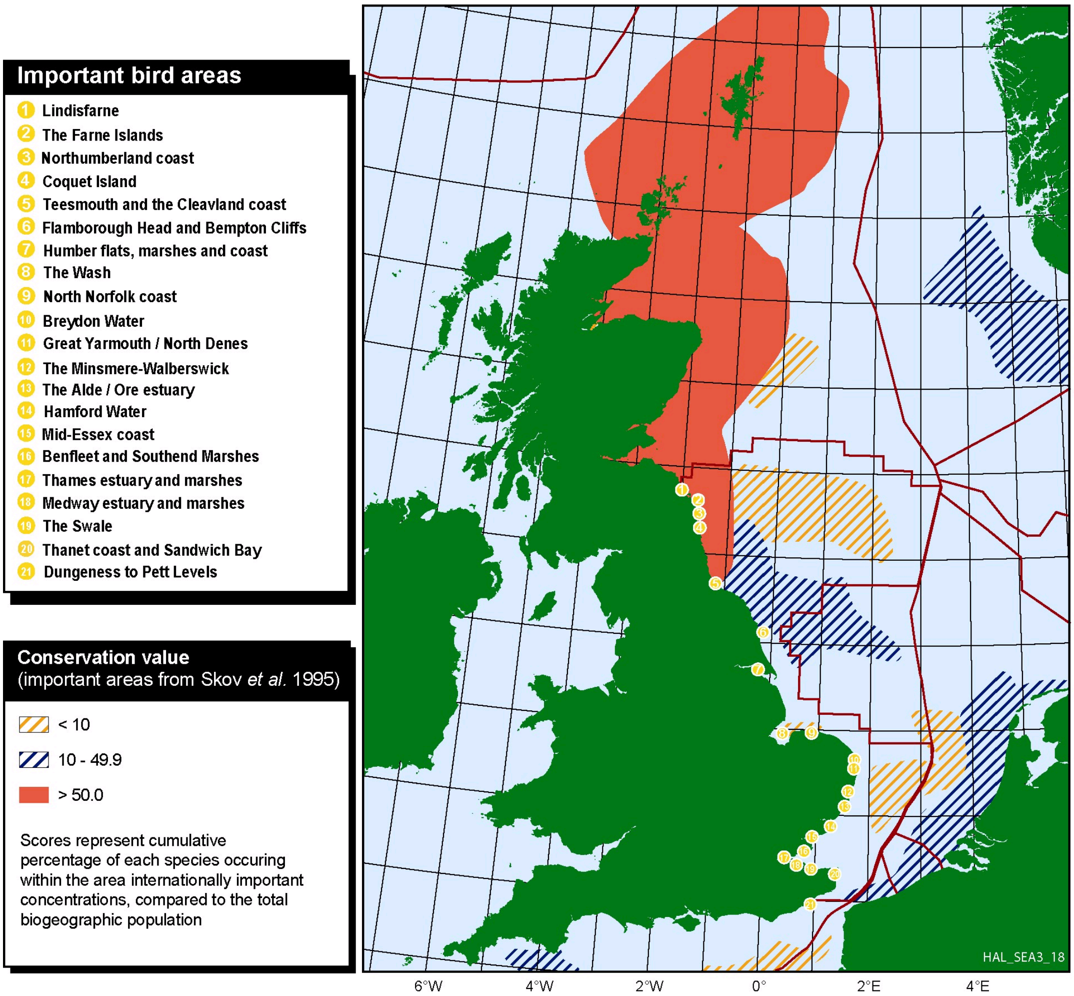


Figure 5.10 Important areas for birds in the North Sea (after Skov *et al.*, 1995, Stone *et al.*, 1995, Heath and Evans, 2000, sourced from Sea 3, 2002).

4.4 Wadden Sea summary (habitat areas)

In the Wadden Sea (249,998 ha; 53º14'N 005º14'E) some 6–12 million birds of more than 50 different species may be present at certain times of the year (OSPAR, 2000). Currently the Trilateral Wadden Sea Plan is in force. This is a cooperative plan between the Netherlands, Germany and Denmark aimed at protection and conservation of the entire Wadden Sea by a series of nature reserves and national parks. Parts of the area have been designated as Ramsar sites, Natura 2000 sites and as Man and Biosphere (MAB) Reserves (Figure 5.11). The Marine Environment Protection Committee (MEPC) of the International Maritime Organization (IMO), which is the UN organization responsible for the world-wide regulation of shipping, agreed to designate major parts of the Dutch, German and Danish Wadden Sea as a Particularly Sensitive Sea Area (PSSA) in 2002. The PSSA covers an area of approximately 15,000 km^2. The designation of the region as a PSSA has not resulted in additional protections, but is seen as a recognition of the regime of protective measures already in place, e.g. the international Convention for the Prevention of Pollution from Ships, 1973/98 (MARPOL, Annexes I and V), as a result of national, EU and IMO measures.

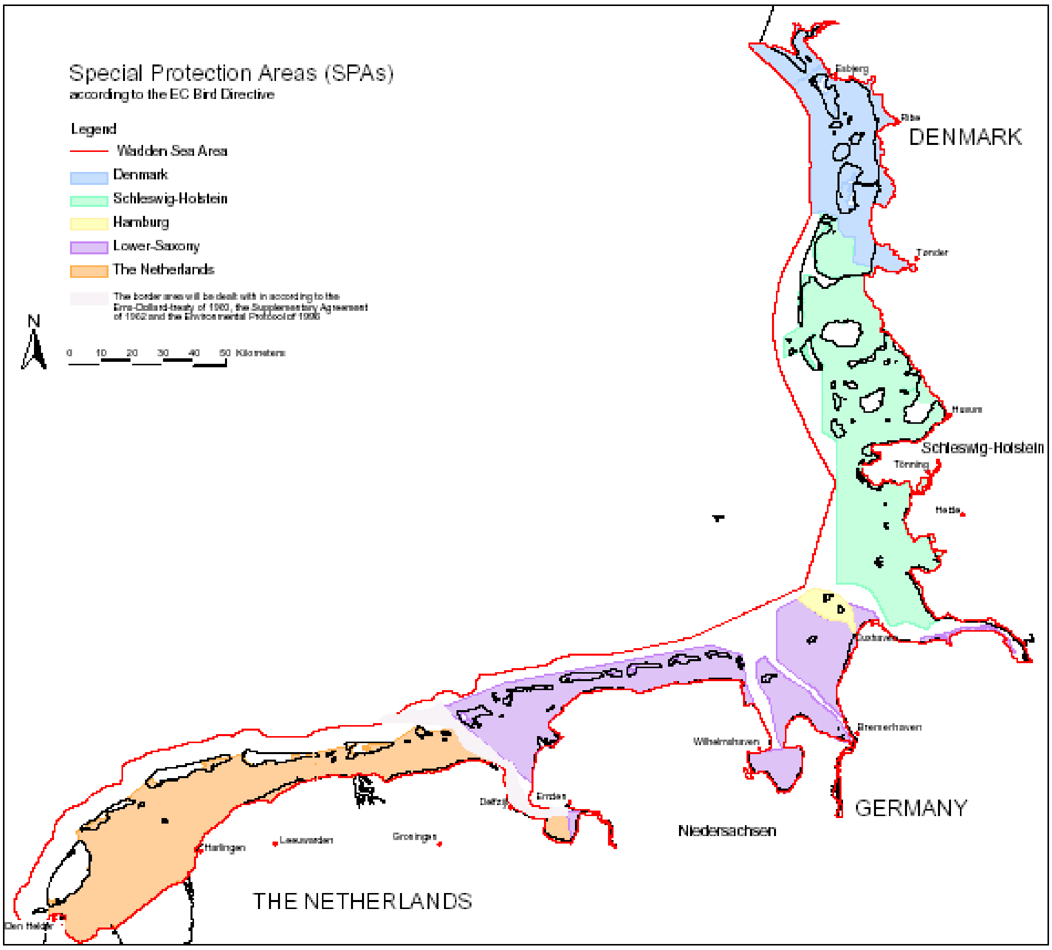


Figure 5.11 Special Protection Areas (SPA) in the Wadden Sea. Coloured areas denoted conservation areas relevant to each country.

5. Site assessments leading to habitat area ramifications for marine mammals in WP3

5.1 Special Areas of Conservation for marine mammals

The identification and protection of the habitats of species deemed in need of conservation are essential for their effective conservation. The creation of SACs requires an assessment of the human activities, plans or projects that are likely to impact the species in the proposed (candidate), and a monitoring programme be undertaken at each site. However, the designation of areas as SACs will be affected by economic, cultural, social and recreational constraints.

Assessment and selection of SACs by EU Member States is divided into two stages:

STAGE 1: Assessment at a national level of the relative importance of sites for each natural habitat type in Annex I and each species in Annex II (including priority natural habitat types and priority species) of the EU Species and Habitats Directive

A. Site assessment criteria for a given natural habitat type in Annex I

(a) Degree of representativity of the natural habitat type on the site.

(b) Area of the site covered by the natural habitat type in relation to the total area covered by that natural habitat type within national territory.

(c) Degree of conservation of the structure and functions of the natural habitat type concerned and restoration possibilities.

(d) Global assessment of the value of the site for conservation of the natural habitat type concerned.

B. Site assessment criteria for a given species in Annex II

(a) Size and density of the population of the species present on the site in relation to the populations present within national territory.

(b) Degree of conservation of the features of the habitat which are important for the species concerned and restoration possibilities.

(c) Degree of isolation of the population present on the site in relation to the natural range of the species.

(d) Global assessment of the value of the site for conservation of the species concerned.

STAGE 2: Assessment of the Community importance of the sites included on the national lists

All the sites identified by the Member States in Stage 1 which contain priority natural habitat types and/or species will be considered as sites of Community importance.

The assessment of the Community importance of other sites on Member States' lists, i.e. their contribution to maintaining or re-establishing, at a favourable conservation status, a natural habitat in Annex I or a species in Annex II and/or to the coherence of Natura 2000 will take account of the following criteria:

(a) relative value of the site at national level;

(b) geographical situation of the site in relation to migration routes of species in Annex II and whether it belongs to a continuous ecosystem situated on both sides of one or more internal Community frontiers;

(c) total area of the site;

(d) number of natural habitat types in Annex I and species in Annex II present on the site;

(e) global ecological value of the site for the biogeographical regions concerned and/or for the whole of the territory referred to in Article 2, as regards both the characteristic of unique aspect of its features and the way they are combined.

5.2 Pinniped SACs

The grey and common (harbour) seal are listed under Annex II of the Habitats Directive under which member countries of the EU are required to consider the establishment of SACs. There are currently no marine candidate SACs. A number of terrestrial candidate SACs have been established for grey and common seals around the coast of the UK, although these areas include regions of the sea around the breeding sites. These terrestrial candidate SACs have been established for grey and common seals including the Berwickshire and North

Northumberland cSAC (grey seal breeding site) and The Wash and North Norfolk cSAC (common seal breeding site).

Common seal SACs in the UK

In the North Sea, common seals haul out on tidally exposed areas of rock, sandbanks or mud. Pupping occurs on land from June to July. The moult is centred around August and extends into September. Thus from June to September common seals are ashore more often than at other times of the year. SAC site selection has therefore favoured sites that are important both as general haul-out sites and for moulting and pupping (Figure 5.12). See the excel file: 'SAC marine mammals.xls' for more information.

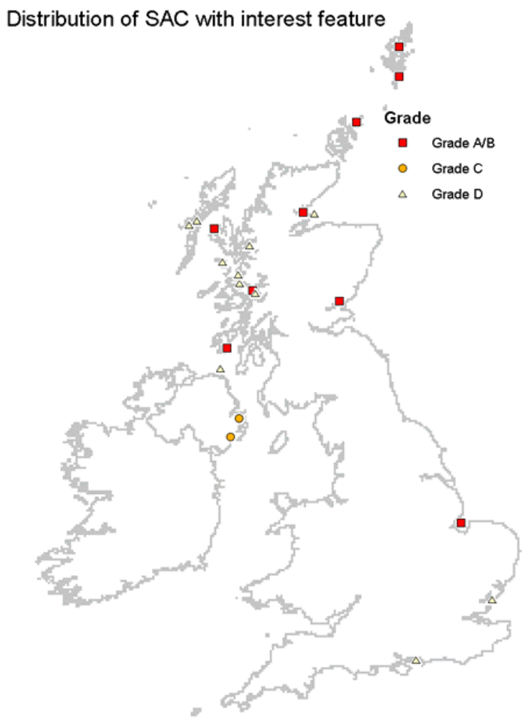


Figure 5.12 Distribution of common seal (*Phoca vitulina*) SACs in the UK.

Explanation of grades

a) Outstanding examples of the feature in a European context.
b) Excellent examples of the feature, significantly above the threshold for SSSI/ASSI notification but of somewhat lower value than grade A sites.

c) Examples of the feature which are of at least national importance (i.e. usually above the threshold for SSSI/ASSI notification on terrestrial sites) but not significantly above this. These features are not the primary reason for SACs being selected.

Grey seal SACs in the UK

The sites recommended as SACs in the UK contain a significant proportion of the UK breeding population of grey seals. Given that UK waters host 40% of the world population and 95% of the EU population of grey seals (JNCC, 2003); these sites are of considerable importance (Figure 5.13). See the excel file 'SAC marine mammals.xls' for more information.

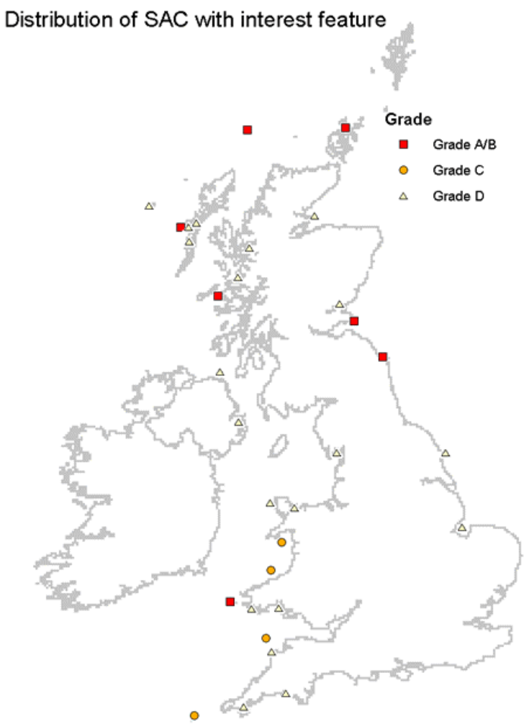


Figure 5.13 Distribution of grey seal (*Halichoerus grypus*) SACs (JNCC, 2003).

Explanation of grades

a) Outstanding examples of the feature in a European context.

b) Excellent examples of the feature, significantly above the threshold for SSSI/ASSI notification but of somewhat lower value than grade A sites.

c) Examples of the feature which are of at least national importance (i.e. usually above the threshold for SSSI/ASSI notification on terrestrial sites) but not significantly above this. These features are not the primary reason for SACs being selected.

d) Features of below SSSI quality occurring on SACs. These are non-qualifying features (‘non-significant presence’), indicated by a letter D, but this is not a formal global grade.

Other sites in the North Sea (pertinent to grey and common seals)

The UK population of grey seals is globally significant in terms of total numbers. The grey seal and the common seal are considered indigenous in the Wadden Sea area and haul out sites have been identified. Two grey seal breeding sites exist in the Wadden Sea area. One near the island of Vlieland in the Netherlands with about 315 animals, where at least 30 pups are born each year, and one small reproductive colony of about 30 to 40 animals in Schleswig-Holstein, Germany (TWSP, 2003).

At this time, the common seal population is regarded as viable in the Wadden Sea Region (Figure 5.14). However, juvenile mortality is very high (over 40% rather than 20–25%) and the reasons for the high mortality need to be addressed. However, the present grey seal population in the Wadden Sea Area cannot be regarded as viable (TWSP, 2003).

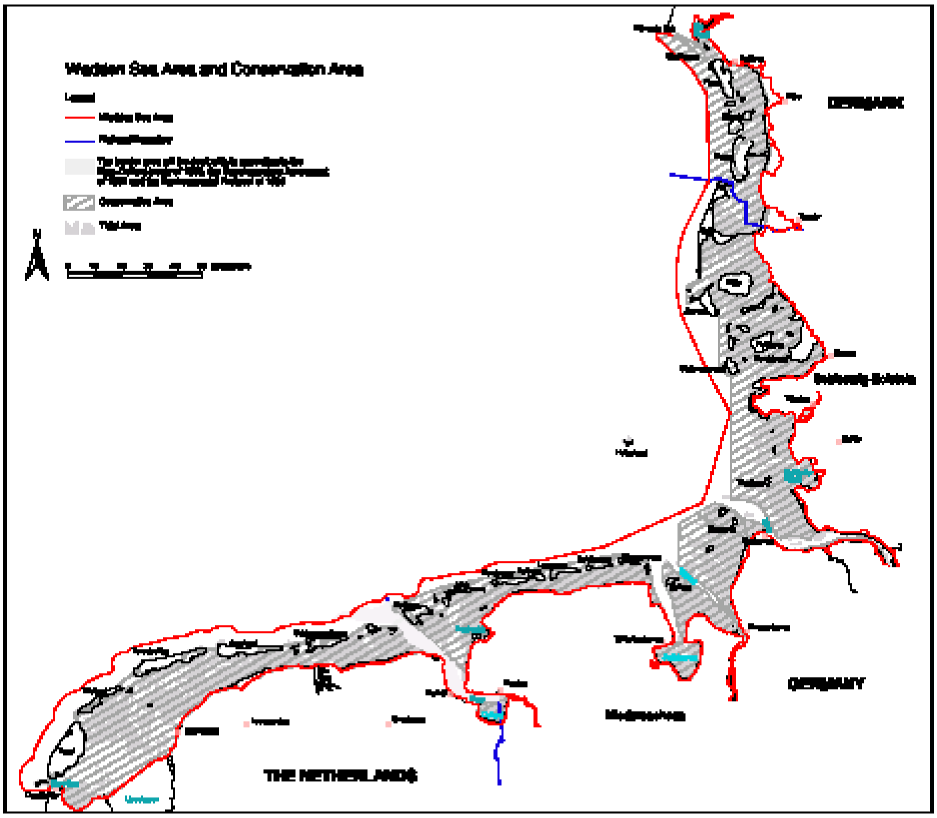


Figure 5.14 Wadden Sea Area and Conservation Area (TWSP, 2003).

5.3 Cetacean SACs

The harbour porpoise and the bottlenose dolphin are listed in Annex II of the EU Habitats Directive.

Bottlenose dolphin SACs in the North Sea

The Joint Nature Conservation Committee (JNCC) of the UK has identified candidate SACs (cSACs) for the bottlenose dolphin under the criteria as 'essential for life and reproduction' for Annex II species as part of Natura 2000. Criteria listed by the JNCC for identifying areas of importance to cetaceans include:

- continuous or regular presence,
- elevated population density,
- good adult to young ratio.

Given the low abundance of these cetaceans in the North Sea, any site should be considered as sites requiring special protection. Candidate SACs have been established for the bottlenose dolphin in the Moray Firth (North east Scotland), Cardigan Bay (Wales) and Sarnau (Wales). The Moray Firth cSAC is a large part of the inner Moray Firth, west of a line from Helmsdale to Lossiemouth (Figure 5.15).

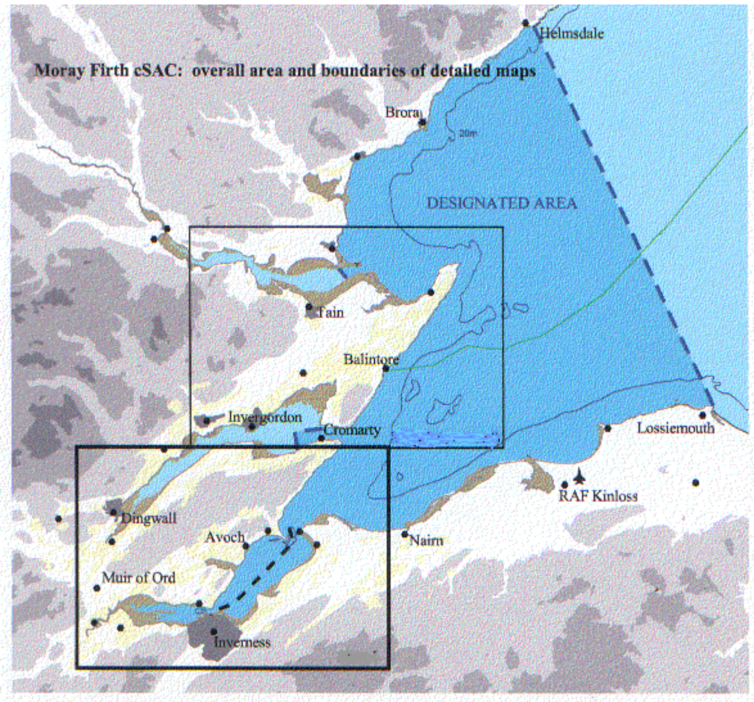


Figure 5.15 Moray Firth cSAC.

Analysis of the genetic diversity within the population of dolphins in the Moray Firth and its genetic relatedness to neighbouring populations have been carried out (Parsons *et al*., 2002). Interestingly, the analysis of molecular variance suggests that the Moray Firth population more closely related genetically to the dolphins in Wales, rather than the nearest population in west Scotland (Figure 5.16). More importantly, however, measures of within-population genetic diversity in the Moray Firth population are lower than any other sampled populations. Thus the low levels of mitochondrial DNA genetic variability observed coupled with its apparent geographic isolation further support the precautionary approach currently being applied to the management of this population.

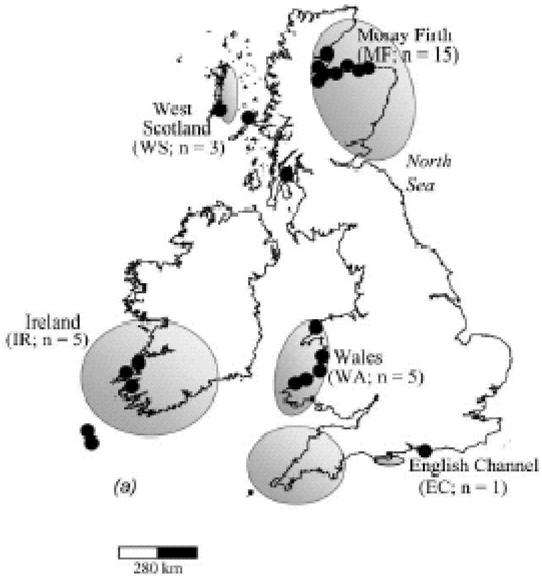


Figure 5.16 Bottlenose dolphins in the UK and Ireland, ellipses indicate core areas of dolphin ranges. (Parsons *et al*., 2002).

Harbour porpoise SACs in the North Sea

The JNNC has identified one cSACs for the harbour porpoise in the North Sea at the same site as for the bottlenose dolphin (Figure 5.17). Sonntag *et al*. (1999) investigated the occurrence of harbour porpoises in the North Sea by Schleswig-Holstein (Figure 5.17). The authors consider that the Natura 2000 criteria (‘essential for life and reproduction’) are satisfied, indicating that this region of coastal waters is used as a preferred calving ground for harbour porpoises. Thus, Sonntag *et al*. (1999) recommend that the area should be protected. However, some marine mammal researchers consider that the area is not marked by a high level of calves compared with other sites (Hammond, pers. comm. 2003). Despite this ambiguity regarding the importance of the area to harbour porpoises, the region is within the Wadden Sea PSSA. Prochnow and Kock (2000) assessed the usage in the PSSA area by different stakeholders and concluded that at that time the local population of harbour porpoises were not threatened.

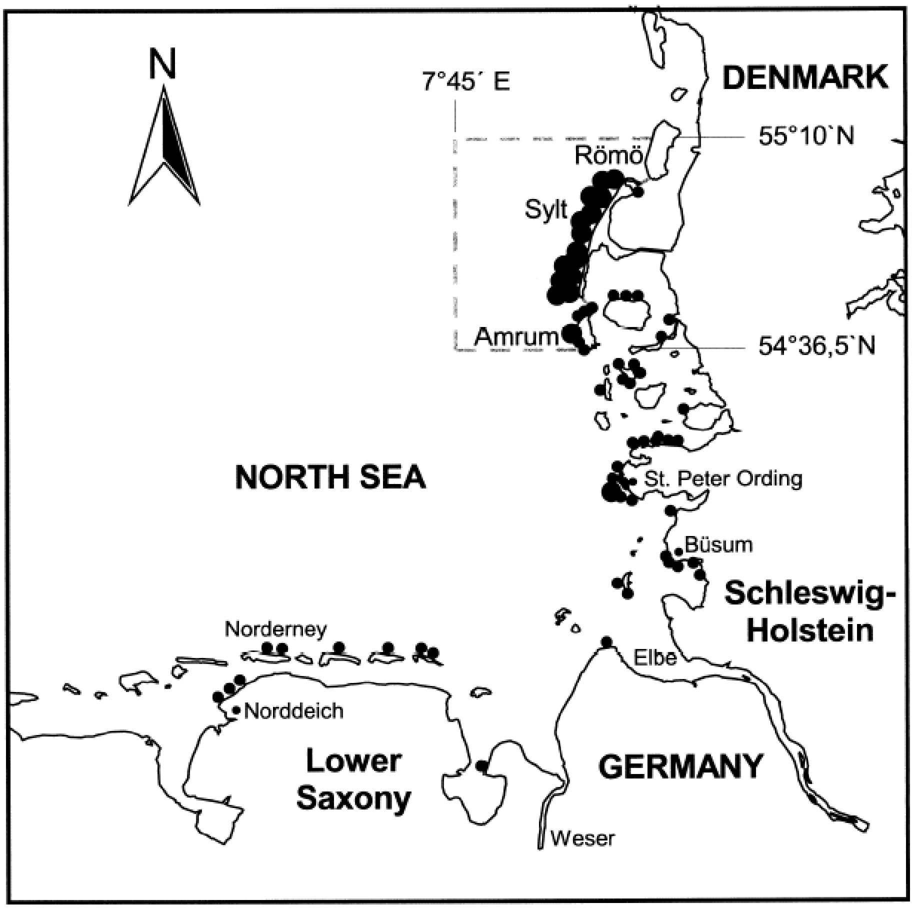


Figure 5.17 The North Sea coast of Germany showing the investigated area and the harbour porpoise calves stranded between January 1990 and January 1997.

5.4 Offshore SPAs

No member state of the EU has yet to designate SPAs outside territorial waters. However, the UK Government is currently taking steps to implement the Habitats Directive in its offshore waters which includes the identification of areas that may qualify as possible offshore SACs and SPAs. The European Commission is encouraging Member States to follow the UK lead. Data are, for the most part, insufficient to identify possible offshore SPAs at this time (Johnston *et al.*, 2002; Turnbull *et al.*, 2002).

6. Fish

Target fish boxes

Figure 5.18 shows the EU regulated areas for fish.

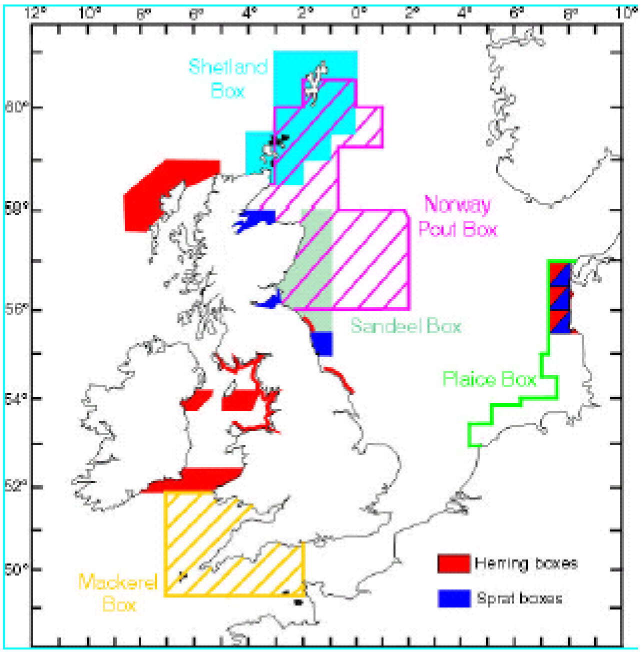


Figure 5.18 EU regulated areas.

The sandeel box

Industrial fishing for sandeels in the 'sandeel box', which covers the inshore area from eastern Scotland down to NE-England (Figure 5.18), is closed if the breeding success of kittiwakes in the nearby colonies falls below 0.5 chicks per pair for 3 successive years. The fishery does not reopen until breeding success has been above 0.7 for 3 consecutive years. A 3-year closure, from 2000 to 2002, was decided upon and the Commission was requested to produce annual reports to the Council on the effects of the restrictions in the sandeel fishery in the Firth of Forth area. As of 2003, the restrictions on the sandeel box, were continued and in the future the area may become a permanent conservation area.

The Norway pout box

Currently industrial fishing for Norway pout is not allowed in the area shown in Figure 5.18. The aim of the Norway pout box is to protect juvenile stocks of haddock and whiting from industrial fishing for Norway pout (EC Regulation No 3094/86).

The plaice box

This area is approximately 38,000 km^2 and is an extension of the 12-mile zone north of the Netherlands, in the German Bight and along the coast of Jutland. The 'plaice box' was established in 1989 to reduce the effort of large beam trawlers (>300 hp) off the coasts of Denmark, Germany and the Netherlands to protect the main nursery area of juvenile plaice (*Pleuronectes platessa*). It is an area with high densities of young plaice and sole. Towed gear is prohibited, but there are derogations for shrimp- and small beam-trawlers.

Sprat and herring restrictions

There are seasonal restrictions on herring, with reference to the retention of herring on a vessel which are caught within certain geographic areas in the North Sea. These areas include:

- from 1 July to 31 October, within the geographical area bounded by the following coordinates:
  - the west coast of Denmark at latitude 55° 30' N,
  - latitude 55° 30' N, longitude 7° 00' E,
  - latitude 57° 00' N, longitude 7° 00' E,
  - the west coast of Denmark at latitude 57° 00' N,
  - latitude 53° 50' N, longitude 4° 50' W;
- from 15 August to 15 September, within the zone extending from six to 12 miles off the east coast of the United Kingdom as measured from the baselines between latitudes 55° 30' N and 55° 45' N;
- from 15 August to 30 September, within the zone extending from six to 12 miles off the east coast of the United Kingdom as measured from the baselines between latitudes 54° 10' N and 54° 45' N.

Additionally, there are seasonal restrictions on sprat, with reference to the retention of sprat on a vessel which are caught within certain geographic areas in the North Sea. These areas include:

- from 1 January to 31 March, and from 1 October to 31 December, within ICES statistical area 3'E8. For the purpose of this Regulation, this ICES area shall be the area bounded by a line due east from the United Kingdom east coast along latitude 55° 00' N to a point at longitude 1° 00' W, from there due north to a point at latitude 55° 30' N and from there due west to the United Kingdom coast;

- from 1 January to 31 March, and from 1 October to 31 December, within the inner waters of the Moray Firth west of longitude 3° 30' W, and in the inner waters of the Firth of Forth west of longitude 3° 00' W;
- from 1 July to 31 October, within the geographical area bounded by the following coordinates:
  - the west coast of Denmark at latitude 55° 30' N,
  - latitude 55° 30' N, longitude 7° 00' E,
  - latitude 57° 00' N, longitude 7° 00' E,
  - the west coast of Denmark at latitude 57° 00' N.

7. Benthos and habitats

Within the North Sea, only one offshore area has been closed for all fishing gears in order to protect benthic habitats, in this case the coral *Lophelia pertusa.* That area is located in the Koster-Vaderfjorden (Sweden) and is 426 km^2, and has been declared as a Special Area of Conservation under the EU Habitats Directive (ICES, 2003e). A large number of sites found intertidally have been protected under various legislation schemes. Around the UK 12 areas have been designated as Special Areas of Conservation (SACs) and from these, five are found within the North Sea (Table 5.2). However, a number of other sites have been proposed to be designated and some others have been listed as being possible canditates. Maerl beds are not found within any of the marine SACs, but are found in Orkney and Shetland.

For other North Sea nations, there is less information available. The Marine Biodiversity Committee of OSPAR reviewed all marine protected areas in the North-east Atlantic (OSPAR 2000, BDC 00/8/2-E). For each country, the number of MPAs is shown as well as summary information such as on their size and distance from coast. However, there is limited information on individual MPAs.

Table 5.2 Benthic species and habitats found within the UK Marine SAC's within the North Sea. SBB= Seapens and burrowing megafauna biotopes, Ss=*Sabellaria spinulosa*, Zo=*Zostera* biotopes; Mod=*Modiolus modiolus* biotopes.

Location of the SAC	SBB	Ss	Zo	Mod
Papa Stour, Shetland	absent			?present
Berwickshire and North Northumberland Coast, NE-England	present	present	present	present
The Wash and North Norfolk Coast, E-England	absent	present	present	
Chesil and the Fleet, Channel	present		present	
Plymouth Sound and Estuaries, Channel	present		present	
References	Hughes, 1998a	Holt *et al.*, 1998	Davison and Hughes, 1998	Holt *et al.*, 1998

In the Netherlands, a large number of saltmarsh areas have been designated as RAMSAR sites. Of these, *Zostera* beds are found in Oosterschelde and Markiezaatmeer (Zeeland, Noord Brabant) (http://www.ramsar.org/profiles_netherlands.htm). In Denmark, a large number of RAMSAR sites have been designated. In total, seven RAMSAR sites contain reefs (undefined), 14 sites are with saltmarsh habitats and one site is with a limestone habitat. (http://www.ramsar.org/profiles_denmark.htm).

In Sweden, the Gullmarn area (100–1000 km^2) is protected for 'other benthic species' under the national legislation. Currently, Sweden is proposing to protect several offshore areas under the EU Habitats Directive (OSPAR, 2000, BDC 00/8/2-E). The World Wildlife Fund for Nature (WWF) has provided suggestions for potential MPAs in the North East Atlantic (http://www.ngo.grida.no/wwfneap/Projects/MPAmap.htm). Within the North Sea, these include the Dogger Bank, waters west of Amrun/Sylt (Germany), Little Middlegrund (on the border between the North Sea and the Kattegat) and Fladen (Kattegat), Kosterfjorden/Ytre Hvaler (transboundary MPA between Norwegian and Swedish waters).

8. Discussion

Habitat Issues SPAs and SACs for seabirds and marine mammals

Throughout Europe, Special Protection Areas (SPA) have been designated, or are pending, to ensure the survival or viability of bird species listed under the

Birds Directive. Similarly, Special Areas of Conservations (SAC) have been designated, or are pending, under the 1994 Habitats Regulations for areas supporting rare, endangered or threatened species of plant or animal (other than birds) and important habitats. Where areas are designated both as a SAC and SPA, they are called European Sites. Where a European site includes an area of sea or shore, it is termed a European marine site. SACs (Special area of Conservation, identified under the EU Habitats Directive), together with SPAs (Special Protection Areas, identified under the Wild Birds Directive), are also collectively known as Natura 2000 network of sites. They are considered an important approach in conservation management. These SPAs, SACs and combined European marine sites areas are not exclusion zones where, for example, fishing is forbidden, but rather are areas which are subject to site management.

European marine site key requirements:

1) Management of the sites should contribute to maintaining or achieving favourable conservation status of their natural habitats and species.
2) Steps must be taken to avoid the deterioration or disturbance of the habitats and species for which the site has been designated.
3) Monitoring must be undertaken to assess the conservation status of the site interest features and to assess the effectiveness of management.
4) Management of the site must take into account the economic, social, cultural and recreational needs of the local people.
5) Activities, plans or projects, whether inside or outside the site, which are likely to have a significant effect upon the site features, must be subject to an assessment.

As such, existing activities are monitored and potential new activities in SPA and SACs are subject to assessment to ensure that the features of the site are not adversely affected by the proposed operations, plans or projects.

The scenarios identified in WP3 for assessment in WP5 refer to habitats, seabirds and marine mammals, therefore, with regard to the EFEP, the identified SPA and SAC areas will need to be considered. So, for example, it has been advocated that all ‘terrestrial’ SPAs relevant to seabirds (and waterbirds) should be extended beyond the intertidal zone. In one study, approximately 900 auks were caught, as by-catch, over eight days in nets set below seabird colonies in the UK (Robins, 1991). Generally aggregations of seabirds are found within 1–2 km of the colony shore (e.g. Wanless *et al*., 1985). Thus at this time a 1–2 km extension to existing SPAs could be considered by the EFEP for modelling purposes, e.g. as fishery exclusion zones. This may also protect identified significant habitat features (see Chapter Three, Section 5 ‘Benthos and habitats’) in addition to considering impacts on birds.

CHAPTER SIX

Metrics

1. Introduction

Workpackage 3 aims to rationalise the selected food web-based models into a 'significant web' model or suite of models. These models will have to be able to answer the questions posed by the proposed scenarios, and show the potential change any given scenario will have on the identified ecosystem components (benthos, zooplankton, fish, marine mammals and birds). These models must consider the key species, their life history stages and habitat interactions. In order to quantify some changes already developed, metrics may be of use. Here we will review and compare metrics that have already been developed to measure the state/health of the ecosystem. We will consider which of them provide useful information and what the necessary input parameters are. If needed, new metrics can be developed and/or existing ones can be modified.

The term *metric* has several definitions. In 2001, the ICES Working Group on the Ecosystem Effects of Fishing (ICES, 2001c) defined the term *metric* as referring to the biological attribute that is being considered as an indicator of an ecological quality of the system. They further observed that *indicator* and *metric* are routinely used interchangeably. However, *indicator* sometimes carries a specific meaning such as an *indicator species*.

Many reviews of metrics exist which assess changes in a given property of an ecosystem. Early reviews include Gauch (1982). More recent, numerous reviews specifically evaluate the impact of fishing on the marine ecosystem in different geographical areas and for different purposes (Anon., 2000b; Gislason *et al.*, 2000; Jackson *et al.*, 2000; Rice, 2000; Link, 2002b; Link *et al.*, 2002; Rochet and Trenkel, 2003; Trenkel and Rochet, 2003). This project will not repeat work that has already been conducted.

Furthermore, the SCOR/IOC Working Group 119 has been created to establish an international network of scientists interested in developing ecosystem indicators in different fields and disciplines for the marine environment (see http://www.ecosystemindicators.org). This working group has the following terms of reference:

⇒ to review the current state of knowledge in different marine and terrestrial disciplines relevant to the development of indicators for marine ecosystems (environmental, ecological and fisheries);

⇒ to review ecological theories (e.g. hierarchy, cascade) and indicators that have been developed in terrestrial ecology and to assess their suitability and usefulness in marine ecosystems;

⇒ to develop new indicators to study the functional role of species in ecosystems, the effects of exploitation, and the state of the environment using output of multi-species models or available time series (e.g. fish catch statistics), and satellite information, GIS (Geographic Information System);

⇒ to apply these indicators in a comparative way to characterise ecosystem states, changes and functioning;

⇒ to assess the value of these indicators for management purposes and for the sustainable utilisation of renewable resources.

Thus, in this review we shall consider the metrics that exist which answer the specific questions we are asking, based on the scenarios developed elsewhere in the project. We shall consider how well they can quantify or measure the changes that are of interest and evaluate their applicability based on data requirements and availability. The types of scenarios to be considered, that have been identified following consultation with stakeholders and in the other work packages of the project, include an increase or decrease in the populations of certain species, a change in a given community or assemblage, the protection of the extension of certain habitat types and of benthos.

2. Criteria for the selection of metrics

All biological populations are influenced by competition and predation and by environmental variability. Habitat availability also influences populations, and this may differ according to the life stage and distribution of the species. An effective metric must consider all these factors, or a compilation of metrics must be used to assess the effects of fishing and other anthropogenic activities on the ecosystem. However, specific questions must be posed, as each metric is limited in the breadth of its application. For this work package, any metric chosen must work with aggregate data sets, although aggregating data can be dangerous as functionally different species or age groups may be grouped together.

More generally any metric must be capable of communicating the state of the ecosystem or ecosystem component and be able to detect changes in this ecosystem; it must be sensitive to changes in ecosystem properties, directional, general enough to be useful, feasible to measure, and able to incorporate uncertainty. Furthermore the properties being described must be relevant; the meaningfulness of any differences among the values of the metric must be determined objectively and it should be possible to partition causality among the effects being investigated (e.g. fishing, other forcing factors and the inherent variability of ecosystems). Above all the chosen metric or suite of metrics must be informative. If there is no link between the response measured by the metric and human activity, the metric cannot be considered as being a useful indicator (Frid *et al.*, in press). Furthermore, in order for a metric to be informative when replying to management requirements, it must answer specific objectives. Simply increasing the understanding of the ecosystem dynamics and functioning is rarely an objective (Frid *et al.*, in press).

To summarise, in order to be of use any metric should meet the following four criteria (Rice and Rochet, SCOR WG119 Cape Town meeting presentation, December 2002 – Jake Rice, pers. comm.):

⇒ it should be meaningful,

⇒ it should be affordable and effective,

⇒ it should use available (historical) data,

⇒ it should show a response.

The ICES Working Group on Ecosystem Effects of Fishing (WGECO) proposed eight criteria in their 2002 report (ICES, 2002d) that should be met in order for Ecological Quality (EcoQ) metrics to be useful. These eight criteria are all encompassed in the four broader criteria above. EcoQ metrics form the basis of Ecological Quality Objectives (EcoQOs). The concept of EcoQOs was introduced by OSPAR and the North Sea Task Force as a framework for ecosystem based management in the North Sea (Kabuta and Laane, 2003).

Finally, the results of any metric or suite of metrics should be communicable to all relevant user groups. A US study observed that in general, stakeholders did not want to know about the 'technicalities' of the metrics used to assess environmental conditions, but rather what the metrics could tell them (Schiller *et al.*, 2001). These authors developed 'Common Language Indicators' to communicate with different user groups based on suites of metrics. These are similar to the 'headline indicators' developed by the European Environment Agency (EEA) to track the environmental performance of European marine fisheries and aquaculture, according to the DRSIR (driving forces-pressure-state-impact-response) framework which has already been successfully used for other environmental indicators (Figure 6.1) (Zenetos *et al.*, 2002).

An example of the successful use of metrics as a tool to drive ecosystem based management is the Chesapeake Bay Program (Environmental Protection Agency, 1999). Here a multidisciplinary, far reaching program has been developed since 1983. Metrics are used: to inform the public about the environment's state; to establish measurable restoration goals and to inform stakeholders and the public about other management decisions. The success of this program lies in the partnership approach and the willingness to set bold long-term objectives.

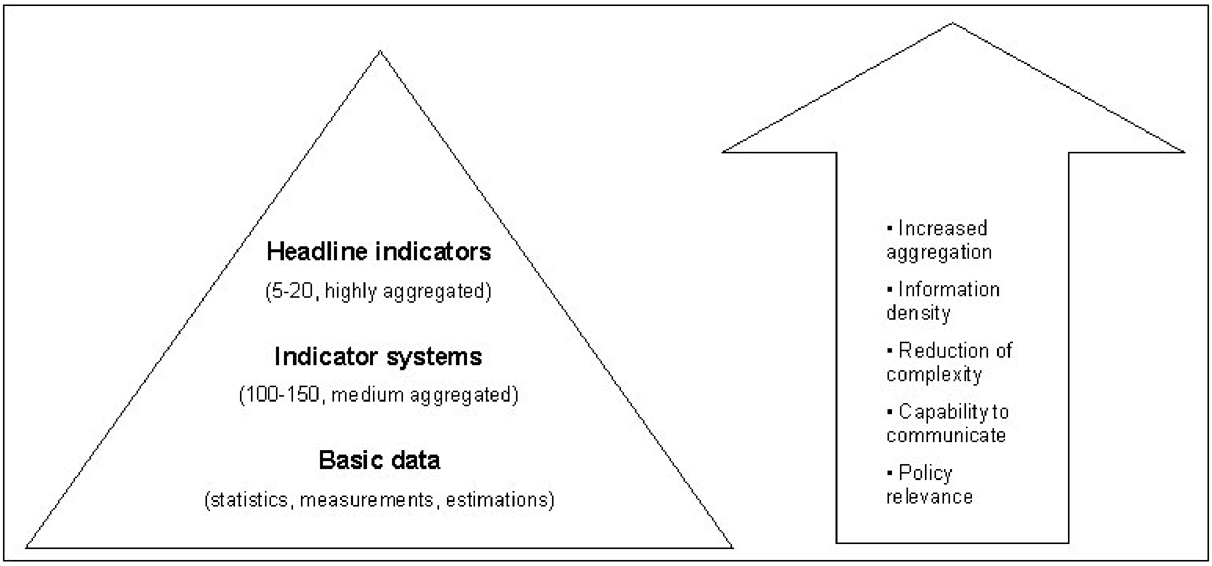


Figure 6.1 A multipurpose hierarchy scheme of environmental indicators proposed by the EEA (in Zenetos *et al.*, 2002).

3. Available types of metrics

Many different metrics exist, each of which considers a different component or set of components in the ecosystem, and each of which provides a specific type of information to answer a specific question. Many classifications of these metrics exist as reviews, and different authors have classified metrics using very different sets of criteria. These range from classifications based on the organisation level under consideration, along the gradient from single-species to ecosystem considerations (Link, 2002b; Rochet and Trenkel, 2003) to classifications based on their properties (Rice, 2000) or nature (Link *et al.*, 2002) or ecosystem objectives (Gislason *et al.*, 2000). Furthermore Frid *et al.* (in press) developed a two-level system of metrics with large-scale routinely measured descriptive metrics that are not tightly linked to specific management activities, but when a change in one of these is observed a more detailed study is initiated using performance metrics. These are smaller-scale more sensitive metrics that are closely linked to an impacting activity.

Much research has been carried out on the use of metrics for the different ecosystem components. Examples for each component will be reviewed here in the context of their applicability to the questions we are asking.

3.1 Metrics for fish

Many different types of metrics have been developed to measure changes in fish populations. These metrics assess the effects of different extrinsic factors on fish populations or assemblages. Here we shall provide examples of metrics taken from published works, especially for the North Sea, that could be used to quantify the objectives for the scenarios for fish.

Increase or decrease in the size of a population or species

To assess the change in the population of a single species, for example, one of particular concern in the ecosystem, single species metrics can be used. Generally these are measures that are used in single species stock assessment, such as recruitment, Spawning Stock Biomass (SSB), Yield Per Recruit (YPR) or total mortality (Z) (Link, 2002b). Other metrics such as exploitation rate (F/Z) has a clear meaning and several targets have been proposed (review in Rochet and Trenkel, 2003). This indicator is almost only influenced by fishing.

Pope and Macer (1996) analysed the time series data of recruitment, spawning-stock biomass and fishing mortality rate estimates for as far back as 1921 for North Sea cod, and 1920 for North Sea haddock and whiting. The authors examine the ability of various factors (both physical and biological) to explain the changes in biomass and recruitment of these stocks.

The effort deployed to catch a single species may also be a means of measuring the predicted change in a population of a given species. Jennings *et al.* (1999) described trends in beam and otter trawling effort (in terms of total hours fishing) in the North Sea from 1977 to 1995. Analyses of temporal trends showed that total international trawling effort in the entire North Sea increased during the study period. The study showed that assessments of the average area swept by trawls in the North Sea are a poor indicator of the direct impacts of trawling on the biota. The authors emphasize that due to many changes in the procedures for recording effort data, any apparent changes in the intensity and distribution effort have to be interpreted with care.

Greenstreet *et al.* (1999a) analysed North Sea fishing effort data, expressed as hours fishing, for UK vessels landing in Scotland over the period 1960–1994. Pelagic fishing effort trends were related to changes in the target species. Total demersal fishing effort varied little during the study period with marked changes in the type of gear used.

Finally, certain species' success is related to environmental conditions. Reproduction may be constrained by temperature or oxygen levels (Van der Kraak and Pankhurst, 1996; Dutil *et al.*, 1999; Planque and Frédou, 1999; Brander, 2000), upwelling can affect the success of recruitment (Santos *et al.*, 2001b), etc. Environmental metrics such as the NAO index or an upwelling index provide a means of predicting these effects.

Change in community or assemblage

Extensive work has been carried out world wide testing and developing metrics to quantify and record changes in fish communities and assemblages. These range from simple metrics such as the mean length in the population to changes in species composition, diversity or richness over time and through to changes in the size structure of the assemblage.

A decrease in mean length in the population can indicate a decreasing population. However, it is difficult to define a reference point in this case. An alternative indicator can be the mean length in the catch. These two indicators can be influenced indirectly by environmental factors affecting growth and longevity; hence, they are not regarded as indicators exclusive to fishing effects (Rochet and Trenkel, 2003). In 2003 the Working Group on Fish Ecology (WGFE) tested using the proportion of large fish in the assemblage as a metric for data sets from six geographical areas. The trends in the metric were generally negative for the longer time series while absent in the shorter series (ICES, 2003g). Another simple metric is the total fish biomass (or abundance) (Link, 2002b, Rochet and Trenkel, 2003). This is a simple and obvious indicator of changes in the community, but how it will be affected by fishing pressure is difficult to predict due to indirect effects along food webs (Rochet and Trenkel, 2003).

More complex metrics include analyses of species composition and diversity indices. Generally, species composition analyses are carried out using multivariate methods. Unless large changes occur, the evaluation of change using multivariate methods may be difficult (Rochet and Trenkel, 2003). Diversity indices, including diversity, richness, evenness, and dominance (Rice, 2000; Link, 2002b; Rochet and Trenkel, 2003) have been widely used for the assessment of aquatic environments. However, in many cases their meaning is unclear. They may be insensitive to some stress types. They are more influenced by natural factors than by human impacts, hence the effect of fishing on them cannot be predicted (Gislason and Rice, 1998; Rochet and Trenkel, 2003). *k*-dominance curves (Rice, 2000; Rochet and Trenkel, 2003) have been tentatively used for fisheries, but they share the deficiencies of diversity indices in that they most often fail to describe fishing induced changes in the ecosystem (Rochet and Trenkel, 2003).

Some of the first analyses of long-term changes of species diversity in the North Sea were conducted by WGECO (ICES, 1994), for the period 1978–1992. The observed changes appeared to be subtle.

Piet and Rijnsdorp (1998) studied the effect of the reduction in trawling effort in south-eastern North Sea on the size distribution and species composition in the demersal fish assemblage. They used MANOVA to study the size distribution, and PCA, MDS and MANOVA to study the species composition. The overall size structure of the commercially exploited species was affected by the change in fishing effort (the abundance of smaller length-classes of commercial fish increased with the reduction of fishing effort), whereas that of the non-target species was unaffected. MANOVA showed that the species composition was not significantly affected by the change in fishing effort.

Rogers *et al.* (1999) described patterns in the abundance of commercially important and non-target demersal fish species, without historical perspective, from the coastal waters of the northeast Atlantic (including the North Sea). Renyi's diversity index was used to rank the diversity of coastal sectors throughout the region. The samples from the continental coast of the North Sea had lower diversity compared to those in the Channel and west of the UK. In addition, *k*-dominance curves were used to provide information on the size of the most dominant species.

Greenstreet *et al.* (1999b) analysed long-term changes in the structure and composition of the groundfish species assemblages in the northern North Sea during the period 1925–1996 and compared them with trends in fishing effort. Species diversity in the whole groundfish assemblage declined and that in the non-target species showed a tendency to increase in the areas where fishing pressure was greatest. No trend in species diversity was detected where fishing pressure was least. Multivariate analyses (MDS and cluster analysis) indicated long-term changes and between-area differences in the species composition of both the whole groundfish assemblage and the non-target component. Species aggregated length-frequency distributions indicated a shift towards an assemblage dominated by smaller fish in the whole assemblage, but not in the non-target species.

Greenstreet and Hall (1996) studied changes in the north-western North Sea groundfish assemblage between the two periods: 1929–1953 and 1980–1993. They used species diversity indices and *k*-dominance curves to examine variation in species richness and species relative abundance, multivariate techniques to explore changes in species composition, and variation in length-frequency distributions. They found an increase in dominance in the groundfish assemblage between the two periods, but these changes were mostly related to changes in relative abundance among the commercially exploited species and not in the non-target groundfish assemblage, which appeared to remain largely unchanged.

Rijnsdorp *et al.* (1996) found higher diversity and evenness in data from trawl surveys in the southern North Sea, in the period 1990–1995 compared to the period 1906–1909, suggesting a response to the change in fishing intensity. However, the different survey gear used in the two periods may have influenced these results. Furthermore Gislason and Rice (1998) were unable to detect such a response with their single and multispecies fisheries models.

Still more complex metrics of change in community or assemblage are size spectra. These are indicators based on the assumption that predation is size-dependent rather than species-dependent. Aggregated length distributions may serve as indicators for exploited communities (review of examples in Rochet and Trenkel, 2003), but they require more theoretical work and examination of data (Rochet and Trenkel, 2003). Rice and Gislason (1996) analysed trends in the size spectra of numbers and diversity in the North Sea fish assemblages over a period of two decades (1977–1993). In the abundance spectrum, the slope decreased and the intercept increased correspondingly, reflecting the effects of fishing. The diversity spectrum remained relatively stable, suggesting stability in the fishing community.

Bianchi *et al.* (2000) analysed data sets from different regions of the world and compared the differences in size spectra and *k*-dominance curves in these areas. Trends in the size spectra in the North Sea were analysed during the period 1973–1993. The results were consistent with those obtained by Rice and Gislason (1996). The changes in size spectra were subsequently compared with exploitation indices.

Change in population traits or life history characteristics

The metrics reviewed above each use a single characteristic to quantify the status and change in status of a fish community over time. However, in certain situations, a single characteristic may not capture all relevant change, and thus using a number of characteristics together may give a better picture of any change. Thus, metrics based on a series of hypotheses about how the life history characteristics of individual fish species determine their sensitivity to fishing have been developed. These include measures such as average length at age, weight at age, fecundity and length at first maturation.

De Veen (1976) analysed biological parameters such as length and weight at age, fecundity and length at first maturation of the North Sea sole landed in the period 1957–1973. Changes in these parameters were found to be correlated with fishing effort and with indices of the disturbance of bottom layers by active gears.

Rijnsdorp (1991) studied variations in size-specific fecundity in North Sea plaice over the period 1977–1985 and fecundity-body length relationships between three periods: 1900–1910, 1947–1949, and 1977–1985. Significant differences were observed between years and areas. Generally, fecundity showed a tendency to increase with time.

Rijnsdorp and Van Leeuven (1996) found changes in the growth of North Sea plaice from the mid-1950s to the 1980s. Growth changes of the smaller size classes were significantly correlated with indices of plaice density, eutrophication, and seabed disturbance by beam trawling. These authors suggest that eutrophication and beam trawling have both affected the growth rate of plaice.

Hubold (1978) analysed length at age and age at maturity in herring from the northern North Sea during the years 1955 to 1973. A general increase of mean lengths at age was observed during this period. Also age at maturity decreased. These changes are suggested to be related with the decreasing stock biomass.

3.2 Metrics for benthos

The benthos is an important component of the ecosystem that may be influenced directly or indirectly by fishing activities. The effects range from direct mortality due to contact with fishing gear to habitat disturbance. Benthic organisms are an important component of the food web, and also play significant roles in creating and maintaining habitat structure (bioturbators and biogenic organisms).

Most of the metrics that exist for fish assemblages also apply to benthic organisms. However, considerably less data exist for benthos making the application of such metrics difficult or impossible.

Many benthic species and populations can be used as indicator species due either to their vulnerability or resistance to disturbance. There has however been some debate about the validity of using indicator species (Pearson and Rosenberg, 1978). While mobile scavenger species may respond positively to fishing, large sessile species such as bivalves may be affected negatively. Benthos that filters plankton and organic particles from the water column are excellent indicators of pollution and low dissolved oxygen levels. For example, some benthic macroinvertebrates, such as certain polychaetes, are one of the most tolerant marine organisms to stressors (e.g., low oxygen, organic contamination of sediment, and sewage pollution) so they are typically used as biological indicators. In addition, some macroinvertebrates have limited mobility and a long enough life span to both avoid pollutants and accurately assess environmental stressors (http://www.epa.gov/bioindicators/html/marinetidal.html). In their review of metrics that were considered appropriate descriptors of Ecological Quality (EcoQ) the ICES Working Group on the Ecosystem Effects of Fishing (ICES, 2001c) chose the 'Presence of indicator/charismatic species' as the only suitable metric for benthos. Before reaching this conclusion they reviewed a number of other metrics and work that has been carried out in the North Sea (see ICES, 2001c).

Other metrics that have been used to measure the impacts of man's activities on benthos include the composition of benthic fauna and the ecological functioning of the benthos (Frid *et al.* in press). The composition of the fauna can be studied by the measurement of total biomass at a given site, the species richness and diversity or the distribution and density of species. The state of ecological functioning of the system can be considered to be the balance between trophic or functional groups, the presence of habitat forming species or the mix of life history strategies. These metrics are all community metrics. Other metrics based on life history or trophic groups may become more important in the future (S. Ragnarsson, pers. comm.).

In the Chesapeake Bay monitoring program, the metrics for benthos that were examined at each of the monitoring sites and compared to several reference sites include:

- benthic biodiverstiy measures,
- measures of assemblage abundance and biomass,
- life history strategy measures,

- activity beneath the sediment surface and
- feeding guild measures

(http://www.chesapeakebay.net/status/benthic-habitat.cfm?SUBJECTAREA=indicators%20).

3.3 Metrics for zooplankton

Zooplankton have been used as indicators of changes in environmental conditions in both fresh water and marine ecosystems. Zooplankton have rich species diversity, they are ubiquitous and easily sampled using, for example, fine mesh WP2 nets (UNESCO, 1968). Large scale sampling programs exist, such as the Continuous Plankton Recorder (CPR), which has been operating for decades across vast geographical areas (Warner and Hays, 1994). Zooplankton are useful indicators that can be included when monitoring and assessing biodiversity. GLOBEC (Global Oceans Ecosystem Dynamics) aims to understand how global climate changes can affect the abundance, diversity and productivity of marine ecosystems. In order to do this, they focus primarily on zooplankton population dynamics (Ambar, 2003). Since many zooplankton are relatively short-lived and are capable of high growth rates, they respond quickly to environmental perturbations that influence diversity, such as point-source pollution (Gee *et al.*, 1985), competition and predation pressure (Pakhomov, 2002; Shiganova, 2002). Crustacean zooplankton growth and development rates are well known to depend strongly on water temperature (McLaren, 1963; Vidal, 1980a, b). Zooplankton species richness is reduced under chemical stress (Baker and Christensen, 1991) and certain species can be used as indicators.

Zooplankton are an essential trophic link between primary producers and finfish, shellfish, birds and mammals. Mesozooplankton consume phytoplankton before being preyed on by higher consumers, and are thus important in the energy economy of the sea. Zooplankton are important prey species for many larger animals, some of which are of commercial importance, such as cod (Sundby, 2000). Thus, changes in zooplankton communities are an indication of imminent change in the food conditions for fish, birds and mammals.

The zooplankton communities of the central and southern North Sea regions are dominated in terms of biomass and productivity by copepods, particularly *Calanus* species (Department of Trade and Industry, 2002). Copepod growth and development rates are influenced by temperature and so life history stage diversity of copepods may be a sensitive early warning of temperature increases in the ocean in response to global atmospheric warming (Johns and Reid, 2001; Department of Trade and Industry, 2002). For example, Beaugrand *et al.* (2002) noted that there has been a strong biogeographical shift in copepod distribution in the North Atlantic, with a northward expansion of warm water species and a decrease in the number of cold water species.

Many potential metrics exist for zooplankton and some are listed in Table 6.1. Measurements of trophic structure require an understanding of the food web.

Table 6.1 Potential zooplankton metrics (taken from Gerritsen *et al.*, 1998).

Metric	Response to stress
% large Daphnia (>1 mm)	Low under plantivorous fish predation
No. of taxa	Reduced under contamination or stress
% dominance	High under stress
Trophic structure measurements - No. of trophic links - Complexity measures - % large predators - No. of predator species	Simplified trophic structure under stress

Link and Brodziak (2002) describe a number of metrics using zooplankton that have been applied in the northeast United States. These are:

- ⇒ Central Gulf of Maine *Calanus finmarchicus*, c. 1–4, c. 5–6 anomalies. Data were collected between 1961 and 1990, in the Central Gulf of Maine using the CPR. Abundance values for zooplankton were gridded in time and space and grids of long term medians, means and standard deviations; and single year conditions, anomalies, and standardized anomalies were produced. These data showed a biphase pattern and also an uptrend for the adult stages of *Calanus finmarchicus*. Furthermore, the adult stages of this taxon exhibited a positive (with lag) correlation with the winter North Atlantic Oscillation.

- ⇒ Anomalies of major zooplankton during spring. Data were collected each spring between 1977 and 1996 on Georges Bank. Zooplankton and larger phytoplankton were captured, identified and enumerated.

Abundance values were gridded in time and space (distance along transect). Single year conditions, anomalies, and standardized anomalies were produced. These data showed that community composition has changed notably over time, although there were no apparent trends in total zooplankton abundance and no major departures from zero even though predator biomass changed greatly during the time period.

⇒ Time and space conditions of *Centropagus typicus* across the continental shelf. Data were collected between 1976 and 1990 on a transect from New York to Bermuda by the CPR. Zooplankton and larger phytoplankton were captured, identified and enumerated. Abundance values were gridded in time and space. The grids of long term medians, means and standard deviations, single year conditions, anomalies and standardized anomalies were produced. From this information, seasonal and local spatial dynamics can be observed.

⇒ *Calanus* abundance by day of year over time. Data were collected between 1961 and 1998 on a transect from Boston to Cape Sable by the CPR. Zooplankton and larger phytoplankton were captured, identified and enumerated. Abundance values were gridded in time and space and in time (years) *vs.* time (days of year). This portrayal showed changes of seasonality for the Gulf of Maine as a whole during the 38 year time span. From these data it could be seen that during the mid 1980s, *Calanus finmarchicus* showed up later and left earlier. In the early 1990s this species appeared even earlier. It must then be determined whether these timing changes are related to the changing oceanographic conditions over this time period.

⇒ The overall zooplankton biomass and abundance trends of two dominant copepods: *Calanus finmarchicus* and *Centropages typicus*. Data were collected approximately bimonthly between 1977 and 2000 on Georges Bank and in the Gulf of Maine. Biomass was measured by displacement volume and individual species were sorted and counted. Departures from the time series monthly means was ranked with a fourth order polynomial fit to the data. Zooplankton trends in both regions were similar. Biomass was usually high in the late seventies, low throughout most of the eighties, and highly variable during the 1990s. The biomass trend line on Georges Bank during the 1990s is higher because of high values recorded in 1989 and 1990, years where budget constraints prevented sampling in the GOM. *Calanus finmarchicus* abundance was high in the late seventies and highly variable during the past two decades with no persistent long-term trend. *Centropages typicus* density was high from 1978–82, low throughout the remainder of the 1980s, and above average during the past decade.

⇒ Total Zooplankton Biomass. Data were collected approximately bimonthly between 1977 and 2000 across the whole shelf. Biomass was measured by displacement volume and individual species were sorted and counted from sub samples. Departures from the time series monthly means was ranked with a fourth order polynomial fit to the data. Biomass was generally higher in the late 1970s, with no persistent long-term trend during the past two decades.

Thus, it can be seen that zooplankton are easily measurable and are sensitive to changes in water quality (temperature, toxic pollution, excess nutrients, low oxygen, etc.), many of which are caused by anthropogenic activities. Their responses to these changes mean that they are indicators of changes in the ecosystem. Zooplankton composition may also offer an indication of the state of future fisheries as many species are important food items for larger organisms.

3.4 Metrics for marine mammals and seabirds

Marine mammals

There are four resident species of marine mammals in the North Sea and a further fifteen species that are considered visitors. Marine mammals have high societal importance. They are charismatic species and their ‘well being’ is closely monitored by conservation groups and the general public. Furthermore, they are important top predators, feeding on commercial and/or on forage fish species that are also prey for commercial fish species. They are therefore competing with fisheries. In a report by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration[1] it is estimated that the consumption of fish by cetaceans is 3 to 5 times the amount of marine resources harvested for human consumption.

One of the main problems encountered when assessing the effects of fishing on marine mammals is the lack of data about most species. Fishing affects mammals both directly and indirectly. Direct affects include bycatch, indirect effects include competition. Different species have different life histories and are thus affected differently.

Work has been carried out on the development of metrics for marine mammals, in particular by the ICES Working Group on Marine Mammal Population Dynamics and Habitat (ICES, 2001b). The metrics that have been developed, largely within the framework of EcoQOs, are listed in Table 6.2. Marine mammal metrics are largely species specific, community metrics are not so common.

The main features of marine mammal management relate to population size and distribution, which are regarded as important aspects for their conservation in the North Sea. In recent years the populations of grey seals (Reijnders and Lankester, 1990) and common seals (Gislason, 1994) exhibit increasing trends. ‘Seal population trends in the North Sea’ was one of the three EcoQOs approved in the Ministerial Declaration of the Fifth International Conference on the Protection of the North Sea, from Bergen, Norway 20–21st March 2002. The other two EcoQOs were ‘utilisation of seal breeding sites in the North Sea’ and ‘by-catch of harbour porpoises’.

Seabirds

Over seven million seabirds (24 species) breed in the coastal regions of the North Sea (Paramor *et al.*, 2002). Fishing activities can be either beneficial or harmful for birds. Direct effects include death in fishing gear, and to a lesser extent, some fishing activities may cause disturbance to the bird population. The indirect effects occur mainly through the alteration in food supplies (Furness,

[1] The Facts About Whales and Fish Stocks. U.S. Department of Commerce, National Oceanic and Atmospheric Administration (undated pamphlet) quoted at http://www.iwmc.org/whales/011018/011018e-04.htm

2000; Tasker *et al.*, 2000). Some species are charismatic, and so monitored by conservation groups.

Seabirds are important top predators, competing with fisheries for the same species. For example, sandeels are major prey for top-predators including seabirds. The industrial sandeel fishery is the largest single fishery in the North Sea. Extensive work has been carried out studying the interactions between sandeel population size and kittiwake (*Rissa tridactyla*) populations (e.g. Bailey *et al.*, 1991; Rindorf *et al.*, 2000; Lewis *et al.*, 2001). Variations in prey availability have profound effects on the population parameters of seabirds, including breeding success and overwintering survival.

Work has been carried out on the development of metrics for seabirds, in particular by the ICES Working Group on Seabird Ecology (ICES, 2003a). The metrics that have been developed, largely within the framework of EcoQOs, are listed in Table 6.2.

Table 6.2 Possible Ecological Quality Objectives (EcoQOs) for marine mammals and seabirds (source: ICES, 2001c).

Theme	Category	EcoQ/EcoQ metric	Current level	EcoQO Reference level	Target level
Pollution	Oil contaminants	Proportion of oiled guillemots among those found dead or dying on the beach	12–85%	0%	10%
	Mercury	Mercury concentrations in eggs of selected seabird species	Various	no	no
		Mercury concentrations in body feathers of selected seabird species		Possibly for situation in 1900	Suggested reference level
	Organochlorines	Organochlorine concentrations in seabird eggs	Various	zero	zero
Eutrophication					
Litter	Plastic particles	Number of plastic particles in gizzards of North Sea fulmars	Various, not well-known	0%	10 particles within any fulmar of a sample of 40
Fisheries	By-catch				
	Harvesting food and predators	Index of breeding productivity of black-legged kittiwake as index for sandeel stocks	0.97	not known	LRP=0.5
	Increase in food supply				
	Mariculture				
	Habitats and ecosystem health				LRP more than20% decrease within 20 years
Threatened and declining					
Hunting/harvesting					
Disturbance					
Introduced/conflicting species					
Climate change					
Community health	Harbour/grey seal	Population size	Increasing	0% increase	More than 10% decrease within 10 years
	Bottlenose dolphin	Population size in NW North Sea		Stable at a higher level than currently	>2% increase per annum over at least 10 years
	Harbour / grey seal	Abandonment of breeding sites	Needs research	zero	Loss of more than10% of breeding sites within 10 years
	Harbour / grey seal	Number of births	Needs research	Current level	More than 10% decrease within 10 years
	Harbour porpoise and other small cetaceans	No appropriate EcoQ selected	Needs research		
Contaminants	Seals	Concentrations of PCB, DDT, OC in body fat	Available	zero	Limit Reference Points are given
	By-catch of harbour porpoise	Percentage of population killed (incidental by-catch)	Available	zero	<1.70%
	By-catch of seals	Percentage of population killed (incidental by-catch)	Available	zero	<1%

Furthermore, in the Ministerial Declaration of the Fifth International Conference on the Protection of the North Sea, from Bergen, Norway 20–21 March 2002, the following EcoQOs were approved for seabirds:

- proportion of oiled common guillemots among those found dead or dying on beaches,
- mercury concentrations in seabird eggs and feathers,
- organochlorine concentrations in seabird eggs,
- plastic particles in stomachs of seabirds,
- local sand-eel availability to black-legged kittiwakes,
- seabird populations trends as an index of seabird community health.

4. Applications and summary

In the above sections, we have reviewed the metrics that have already been developed to measure the state/health of the ecosystem for each of the ecosystem components. In general, the metrics considered have met the four key criteria proposed by Rice and Rochet, (SCOR WG119 Cape Town meeting presentation, December 2002 – Jake Rice, pers. comm.):

1) they are meaningful,
2) they are affordable and effective,
3) they use available (historical) data,
4) they show a response.

It can be seen that fishing activities affect each ecosystem component both directly and indirectly, and that several metrics exist to measure each of these effects. However, not all of them are easily applicable to all components. Very often the necessary data are scarce, and may only exist for commercial or other species considered important by society. The data requirements and applicability of the main metrics reviewed during this paper are summarised in Table 6.3.

It can be seen that no one metric will answer all questions, and, similarly to Rice (2000), no single metric can be endorsed without reservation. Although many ecosystem metrics are partially redundant and may have a degree of overlap, few are identical. Several authors have promoted the idea of using multiple metrics in a single study to assess the changes in the ecosystem (e.g.: ICES, 1998; Rice, 2000). Nevertheless, the problem still exists how to interpret the results of multiple metrics. Many factors influence the ecosystem, and rarely, if ever, do data sets exist that precede fishing activities. Separating the different effects is a problem. Despite these limitations, metrics can assist to focus the overall management objectives of a resource and also help to protect and restore the habitats and populations.

Specific cases, illustrating the uses of metrics in three management approaches, have been reviewed:

1. To drive ecosystem management in a programme such as the Chesapeake Bay Program (Environmental Protection Agency, 1999) where metrics have been used: to inform the public about the environment's state; to establish measurable restoration goals and to inform stakeholders and the public about other management decisions.
2. In the 'headline indicators' developed by the European Environment Agency (EEA) to track the environmental performance of European marine fisheries and aquaculture, according to the DRSIR (driving forces-pressure-state-impact-response) framework.
3. Recently, an innovative, and cost efficient approach to applying several metrics has been proposed by Frid *et al.* (in press), who propose the use of 'performance' and 'descriptive' metrics. 'Performance' metrics are closely linked to the impacting activity. Thus changes in the metric can immediately trigger a management response, while 'descriptive' metrics, such as diversity indices, can be used to identify patterns in community structure and to assess the potential consequences of impacts. With this system, general trends are observed, and when a change is recorded, smaller scale metrics can be used to identify the potential causes of the change.

It can thus be seen that metrics play a significant role in measuring the state/health of the marine ecosystems and in the sustainable management of this resource.

Table 6.3 Summary of the main metrics reviewed their data requirements and applicability.

Ecosystem component		**Metric**	**Examples**	**Data required**	**Applicability**
Fish	Single species	Recruitment		Survey data	Data available for commercial species and other well studied species
		Spawning Stock Biomass (SSB)		Catch at age, maturity at age	- *Idem* -
		Yield per Recruit (YPR)		Growth parameters	- *Idem* -
		Total mortality (Z)		Catch at length	- *Idem* -
		Exploitation rate (F/Z)		Catch at length and age	- *Idem* -
		Fishing effort		Example: number of days fishing	Not always available for all fleets
	Environmental conditions	NAO index			Readily available http://www.cpc.ncep.noaa.gov/data/teledoc/nao.html
		Upwelling index			
	Community metrics	Mean length in population/catch		Survey data, length distributions	Usually available. Global L_{max} values may also be used.
		Changes in species composition	Diversity indices Measures of species richness *k*-dominance curves	Survey data	Available
		Size structure metrics	Size distribution Size spectra	Survey data, length distributions	Usually available. Global L_{max} values may also be used
	Life history characteristics	Length or weight at age		Length/weight at age	Data available for commercial species and other well studied species
		Fecundity		Fecundity	- *Idem* -
		Length at first maturation (L_{mat})		Length at first maturity	- *Idem* -
		Growth		Growth parameters	- *Idem* -
Benthos	Community metrics	Presence of charismatic/ indicator species		Species composition	
		Assemblage abundance or biomass		Survey data	
		Composition of benthic fauna	Species richness Species diversity Distribution of individuals between taxa Balance between groups	Survey data	
	Life history characteristics	Ecological functioning of the benthos	Presence of habitat forming species Mix of life history stages	Survey data	
		Feeding guild measures		Trophic data	
Zooplankton	Community metrics	Presence of indicator species	Species anomalies	Survey data	
		Zooplankton composition	Species diversity Species richness Number of taxa Life history stage diversity	Survey data	
	Life history characteristics	Growth and development rates			
		Trophic structure	Number of trophic links Measures of complexity Proportion of large predators / predator species		

Table 6.3 Continued.

Ecosystem component		**Metric**	**Examples**	**Data required**	**Applicability**
Marine mammals	Single species	Population trends	Population size and distribution		Data scarce for many species
		Bycatch		Fisheries data / on-board-observer projects	- *Idem* -
	Life history characteristics	Use of breeding sites			- *Idem* -
Seabirds	Single species	Population trends Concentration of contaminants in eggs and feathers			
		Bycatch		Fisheries data / on-board-observer projects	Data scarce for many species
		Trophic interactions			

CHAPTER SEVEN

Conclusions

The primary aim of WP3 was to identify the 'significant web' of the North Sea. Importance was determined on the basis of four criteria. The species and habitats selected for inclusion in the 'significant web' had to be considered important under at least one criteria of importance: in providing important functions to the ecosystem (functional importance), important as a predator or prey (ecological importance), of monetary value (economic importance) or of conservation value (societal importance). The former two criteria apply to those species and habitats which provide important goods and services to the ecosystem while the latter two are important to humans. A species or habitat needs to fulfil at least one or more criteria of importance in order to be included to the 'significant web'. In this chapter, the species and habitats which were selected to the 'significant web' are shown.

One of the obstacles in attempting to evaluate the importance of species and habitats is the large gap in the understanding of the biology and population dynamics within and among ecosystem components. In general, the species and habitats which are of societal value (protected), monetary value (harvested) or are found on locations which are easily accessible (e.g. intertidal areas and bird cliffs) have been, in general, relatively well studied. This includes most of the mammal and bird species, habitats which are obviously threatened due to their fragility and fish. However, most benthos and zooplankton species are found in offshore waters and therefore are more difficult to sample and monitor. Basic knowledge of these components is often lacking. One of the disadvantages with our approach, when evaluating importance, was that species which are well studied are overrated at the expense on those which are less studied. However, this is unavoidable as the evaluation is based on the best knowledge currently available. For the application of ecosystem-based management, we need to understand the role of the lower trophic levels (zooplankton and benthos) for ecosystem functioning.

Due to the dissimilarity among some ecosystem components, there were some unavoidable differences in approaches when importance was evaluated. For example, benthic invertebrates species were aggregated to the taxonomic resolution of a family. Such aggregation was necessary due to the high number of species (>1000) found within the North Sea. Similarly, the importance of fish species in predator-prey relationships was influenced largely by their size. For that reason, species selected in the significant web were separated into size or age classes.

The 'significant web' of the North Sea

Seabirds

Table 7.1 Bird species selected in the 'significant web'. 0= no importance, 0.5= medium importance, 1= high importance, ?= importance could not be determined.

Species	Importance			
	Economic	Societal	Functional	Ecological
Northern fulmar *Fulmarus glacialis*	1	0.5	0.5	1
European storm petrel *Hydrobates pelagicus*	0	1[a]	0.5	0
Leach's storm-petrel *Oceanodroma leucorhoa*	0	1[a]	0.5	0
Northern gannet *Morus bassanus*	0	0.5	0.5	1
Great cormorant *Phalacrocorax carbo*	?	1[a]	0.5	0.5
Black-headed gull *Larus ridibundus*	?	1[b]	0.5	0.5
Lesser black-backed gull *L. fuscus*	?	1[b]	0.5	1
Herring gull *L. argentatus*	0.5	1[b]	0.5	1
Great black-backed gull *L. marinus*	0.5	1[b]	0.5	1
Black-legged kittiwake *Rissa tridactyla*	0.5	0.5	0.5	1
Sandwich tern *Sterna sandvicensis*	?	1[a]	0.5	0
Roseate tern *S. dougallii*	0	1[a]	0.5	0
Common tern *S. hirundo*	?	1[a]	0.5	0
Arctic tern *S. paradisaea*	?	1[a]	0.5	0
Little tern *S. albifrons*	?	1[a]	0.5	0
Common guillemot *Uria aalge*	1	0.5	0.5	1
Razorbill *Alca torda*	0	0.5	0.5	1
Eider *Somateria mollissima*	1	1[b]	0.5	1
Oystercatcher *Haematopus ostralegus*	1	1[b]	0.5	1

[a] Annex I species
[b] Annex II species.
Note: Annex I and II species are protected under the Birds Directive 79/409/CEE.

Annex I bird species require special conservation measures to be taken. There is a need to classify their most suitable territories as Special Protection Areas.

Annex I species are:

- species in danger of extinction;
- species vulnerable to specific changes in their habitat;

- species considered rare because of small populations or restricted local distribution;
- other species requiring particular attention for reasons of the specific nature of habitat.

Annex II bird species may be hunted under national legislation but EU Member States must ensure that hunting does not jeopardise conservation efforts. The practice of hunting must comply with the principles of wise use and ecologically balanced control of the species of birds concerned. For example, species which may be hunted, are not hunted during the various stages of the breeding season, including the period during which the young birds are still dependent on the adults.

Annex I and Annex II seabird species are included in the significant web due to their charismatic status. The inclusion of the other species is driven by their ecological and functional importance as predators in the North Sea ecosystem; this, for the most part, is a function of the species' high abundance and biomass.

Cetaceans

Table 7.2 Cetacean species selected in the 'significant web'. 0= no importance, 0.5= medium importance, 1= high importance, ?= importance could not be determined.

Species	Importance			
	Economic	Societal	Functional	Ecological
Bottlenose dolphin *Tursiops truncates*	0	1[a c d]	0	1
Common dolphin *Delphinus delphis*	?	1[b c d]	0	1
Risso's dolphin Grampus griseus	?	1[b c d]	0	1
White-beaked dolphin *Lagenorhynchus albirostris*	?	1[b c d]	0.5	1
White-sided dolphin *L. acutus*	?	1[b c d]	0.5	1
Harbour porpoise *Phocoena phocoena*	1	1[a b c d]	1	1
False Killer whale *Pseudorca crassidens*	?	1[b c]	0	1
Fin whale *Balaenoptera physalus*	?	1[b]	0	1
Killer whale *Orcinus orca*	?	1[b c d]	0.5	1
Long-finned pilot whale *Globicephala melaena*	?	1[b c d]	0	1
Minke whale *Balaenoptera acutorostrata*	?	1[b]	0.5	1[b]
Sperm whale *Physeter catodon*	?	1[b]	0	1

[a] IIa,
[b] IVa,
[c] Bern Convention,
[d] Bonn Convention.

All cetaceans are protected under EU Directive 92/43/EEC IIa and/or IVa, while some are protected under other conventions (Bern and Bonn).

Annex II – Animal and plant species of community interest whose conservation requires the designation of special areas of conservation.

Annex IV – Animal and plant species of community interest in need of strict protection.

Similar to the seabird species, the inclusion of cetacean species is driven by their charismatic status. Unlike seabird species all cetaceans are protected by legislation, necessitating the inclusion of all cetaceans observed in the North Sea in the significant web. However, the focus species in subsequent analyses and treatment during the next phase of development of the EFEP will be those cetaceans which are ecologically, socially, economically and functionally important, e.g. the abundant harbour porpoise.

Pinnipeds

Table 7.3 Pinniped species selected in the ‘significant web’. 0= no importance, 0.5= medium importance, 1= high importance.

Species	Importance			
	Economic	Societal	Functional	Ecological
Grey seal *Halichoerus grypus*	0.5	1[a]	1	1
Common seal *Phoca vitulina*	0.5	1[a]	1	1

[a] IIa

Annex II – Animal and plant species of community interest whose conservation requires the designation of special areas of conservation.

The inclusion of the grey seal and the common seal is based on their social, functional and ecological importance as abundant, top-predators in the North Sea, for example, both species consume significant quantities of fish, many of which are commercially important.

<u>Zooplankton</u>

Table 7.4 Zooplankton species selected in the 'significant web'. 0= no importance, 0.5= medium importance, 1= high importance.

Species	Importance			
	Economic	Societal	Functional	Ecological
Calanus finmarchicus	0	0	1	1
Calanus helgolandicus	0	0	1	1
Acartia spp.	0	0	1	1
Temora spp.	0	0	1	1
Oithona spp.	0	0	1	1
Evadne spp.	0	0	0.5	1
Euphausiids	0	0	1	1
Thaliacea	0	0	1	1

Zooplankton are of significant ecological importance in the North Sea ecosystem and fundamental in the lower trophic position of many marine food webs. However, zooplankton have no direct economic or social importance as they are neither harvested nor protected. Zooplankton suffer no direct mortalities due to fisheries. The indirect effects of top-down control of zooplankton by predators (whose abundance is affected by fisheries) has been demonstrated/hypothesised (e.g. Reid *et al.*, 2000; Lindley *et al.*, 1995), but their abundance is predominantly driven by extrinsic factors. Zooplankton should be considered in subsequent work packages as essential prey items. However, as zooplankton cannot be managed, a more effective strategy for EFEP is to the focus on the elements of the significant web which can be managed, and where changes in management practices can be quantified.

Fish

Table 7.5 Fish species selected in the 'significant web'.

Common name	Scientific name	Sub-groups
Cod	*Gadus morhua*	ages 1–4+
Haddock	*Melanogrammus aeglefinus*	ages 1–4+
Whiting	*Merlangius merlangus*	ages 1–4+
Saithe	*Pollachius virens*	ages 1–4+
Norway pout	*Trisopterus esmarki*	ages 1–4+
Sandeel	*Ammodytes* spp.	ages 1–4+
Plaice	*Pleuronectes platessa*	ages 1–4+
Sole	*Solea vulgaris*	ages 1–4+
Herring	*Clupea harengus*	ages 1–4+
Sprat	*Sprattus sprattus*	ages 1–4+
Mackerel	*Scomber scombrus*	ages 1–4+
Non-target demersal		0–10, 10–20, 20–30 and 30+
Non-target pelagic		0–10, 10–20, 20–30 and 30+
Elasmobranchs (skates and rays)		none
Elasmobranchs (sharks)		none

Benthos and habitats

Table 7.6 shows those benthic organisms and habitats which were selected to comprise the 'significant web' of the North Sea. Note that, in contrast to evaluation of marine mammals, birds and zooplankton, the scoring of importance ranges from 0 to 2 (sometimes 3).

In total, 27 benthic invertebrate families and habitats were selected out of 63 families and habitats which were evaluated (see table 3.16). Benthic families and habitats were selected for the 'significant web' if they had a score of two or higher in any of the importance categories. However, several families (Arenicolidae, Nephtyidae, Nereidae, Orbinidae) and three habitats (Laminariaceae, Salicornidae and Zosteracea) were removed from the list even though they were evaluated to be important. Many of these are predominately found in the intertidal zone and it was considered that they were unlikely to be affected by fishing activities and were therefore of minor importance in Fisheries Ecosystem Plans.

Table 7.6 Benthos and habitats selected in the 'significant web'. 0= no importance, 1= medium importance, 2(3)= high importance, ?= difficult or not possible to determine importance.

Family	Key species	Importance				
		Economic	Societal	Functional	Ecological	Functional group
Annelida						
Chaetopteridae	*Chaetopterus variopedatus*	0	0	2	2	6
Sabellariidae	*Sabellaria* spp.	0	2	2	1	3
Serpulidae	*Serpula vermicularis*	0	2	2	1	3
Pectinariidae	*Lagis koreni*	0	0	1	1	5
Terebellidae	*Lanice conchilega*	0	0	2	2	6
Arthropoda						
Callianassidae	*Callianassa subterranea*	0	0	2	1	7
Crangonidae	*Crangon crangon*	3	0	0	2	7
Laomediidae	*Jaxea nocturna*	?	0	2	?	7
Nephropidae	*Nephrops norvegicus*, *Homarus gammarus*	3	0	2	1	7
Pandalidae	*Pandalus borealis*	2	0	0	2	2
Portunidae	*Carcinus maenas*, *Liocarcinus* spp.	1	0	?	2	2
Upogebiidae	*Upogebia deltaura*	0	0	2	1	7
Cnidaria						
Caryophyllidae	*Lophelia pertusa*	1	2	2	1	3
Pennatulacea	*Pennatula phosphorea*	1	2	1	1?	
Echinodermata						
Amphiuridae	*Amphiura filiformis*	0	0	1	2	5
Asteriidae	*Asterias rubens*	1	0	0	2	2
Ophiotrichidae	*Ophiotrix fragilis*	0	0	2	1	1
Ophiuridae	*Ophiura* spp.	0	0	?	2	2
Spatangidae	*Brissopsis lyrifera*, *Echinocardium cordatum*	0	0	2	1	7
Echiura						
Echiuridae	*Maxmuelleria lankesteri*	0	0	2	1	7
Mollusca						
Buccinidae	*Buccinum undatum*	1?	0	?	2	2
Cardiidae	*Cerastoderma edule*	3	0	2	2	4
Mytilidae	*Mytilus edulis*	3	1	2	2	3
Mytilidae	*Modiolus modiolus*	1?	2	2	1	3
Ostreidae	*Ostrea edulis*	3	2	1	1	3
Pectinidae	*Pecten maximus*	3	0	?	1	1
Tellinidae	*Macoma balthica*	0	0	2	2	5
Vegetative habitats						
Rhodophyceae	*Lithothamnium* spp.	2	2	2	0	3

The habitats and benthic families selected often share characteristics (e.g. life history traits, body structure, vulnerability to disturbance) which allows them too be grouped into functional groups. Below, we propose one approach on how to aggregate benthic families and habitats into functional groups using a three-level classification system (see also Figure 7.1).

First level:

Benthic families and habitats were divided into those living on the sediment surface (epibenthos) and those which are buried in sediments (infauna).

Second level:

<u>Epifauna</u>

Mobile: Applies to those species for which adult stages are capable of some movement. This does not include species for which movements are extremely restricted or infrequent (e.g. mussels).

Sessile: Species and habitats which are entirely non-mobile (see comments above).

<u>Infauna</u>

Shallow burrowing: Organisms found within the upper sediment layers (1–≈5 cm). Note that species which are found at the sediment-water interface where categorised as shallow burrowers.

Deep burrowing: Organisms which burrow deeper than ≈5 cm into the sediment.

Third level:

<u>Epifauna</u>

Mobile

Scavenger/predators: Many species are both scavengers and predators (carnivores). For that reason, no attempts were made to distinguish between the two feeding modes.

Other feeding types: This includes omnivory, suspension feeding (passive and active), herbivore and deposit feeding.

<u>Infauna</u>

Shallow burrowing

Fragile: Species of fragile body structure.

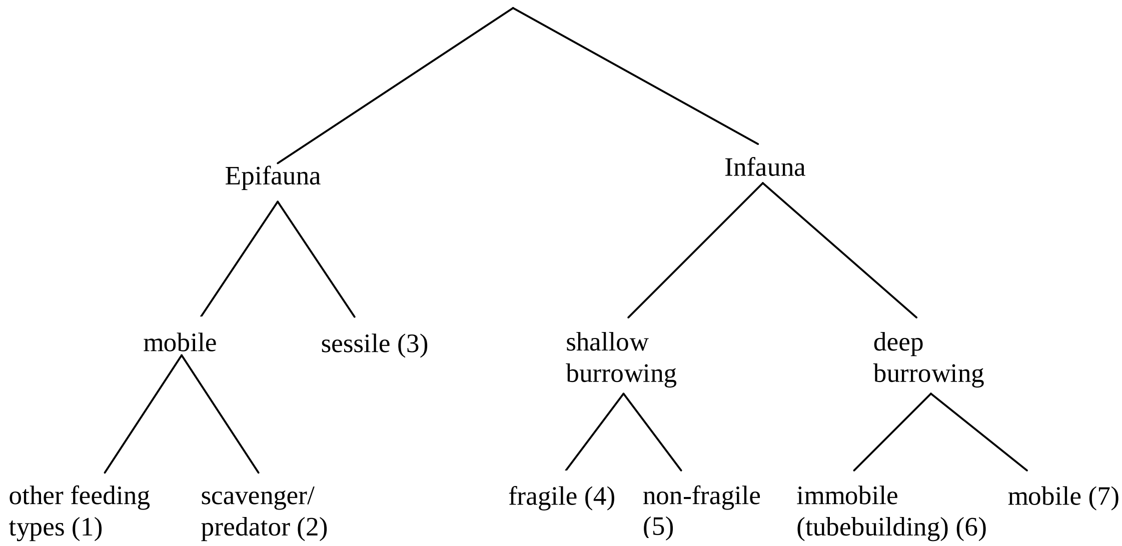
Non-fragile: Species which are robust and are able to re-generate missing body parts.

Deep burrowing

Immobile: Immobile tube-building species (tubes penetrate to greater depths than ≈5 cm).

Mobile: This includes species which are able to move within sediments, e.g. crustacean megafaunal burrowers.

Figure 7.1 An overview over the classification system used to aggregate benthic families and habitats into functional groups.

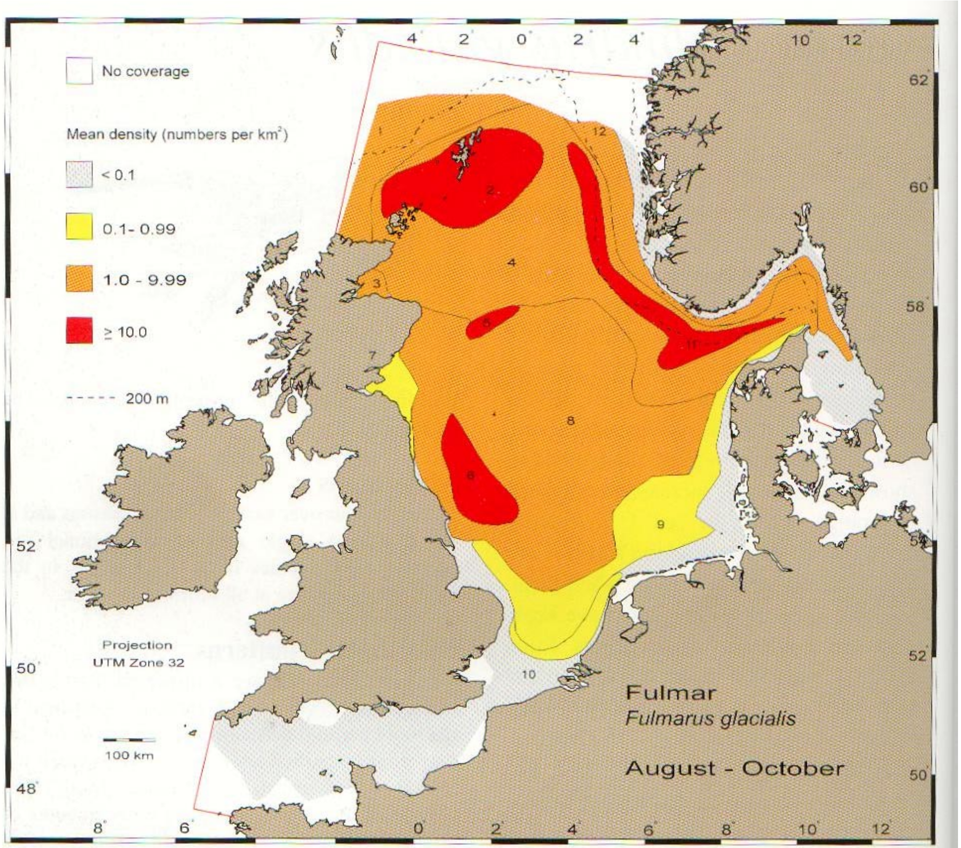


APPENDICES

APPENDIX 1. Distribution of the fulmar, eider and kittiwake within the North Sea.

Bird distribution maps to support data on the bird data base table (selected from Skov *et al*., 1995).

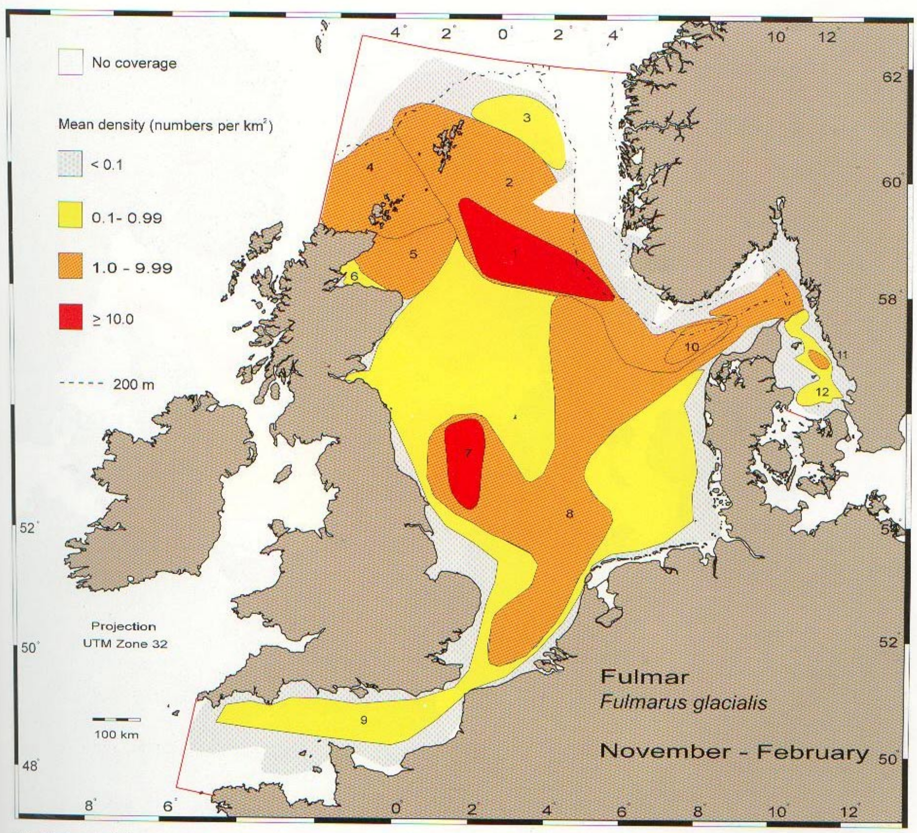
Northern fulmar (*Fulmarus glacialis*) distribution August through to July.



Distribution and density of Fulmar Fulmarus glacialis *in the North Sea, the Channel and the Kattegat from August to October 1980-1994.*

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Orkney – Shetland northwest	1.85	44,500	82,000
2	Shetland Fair Isle Channel	16.9	37,500	63,400
3	Moray Firth	1.16	2,750	3,200
4	Northern North Sea	6.99	118,000	825,000
5	Aberdeen Bank	21.17	7,300	155,000
6	North East Bank – Hills	8.21	23,600	194,000
7	Firth of Forth	0.45	6,500	2,900
8	Central North Sea	2.7	206,000	556,000
9	Southeastern North Sea low	0.72	45,000	32,000
10	Southeastern North Sea very low	0.18	8,750	1,600
11	Southwest Norwegian Trench	25.68	27,300	701,000
12	Northeast Norwegian Trench	11	32,400	36,000
	Residual			12,000
	Total			3,234,70

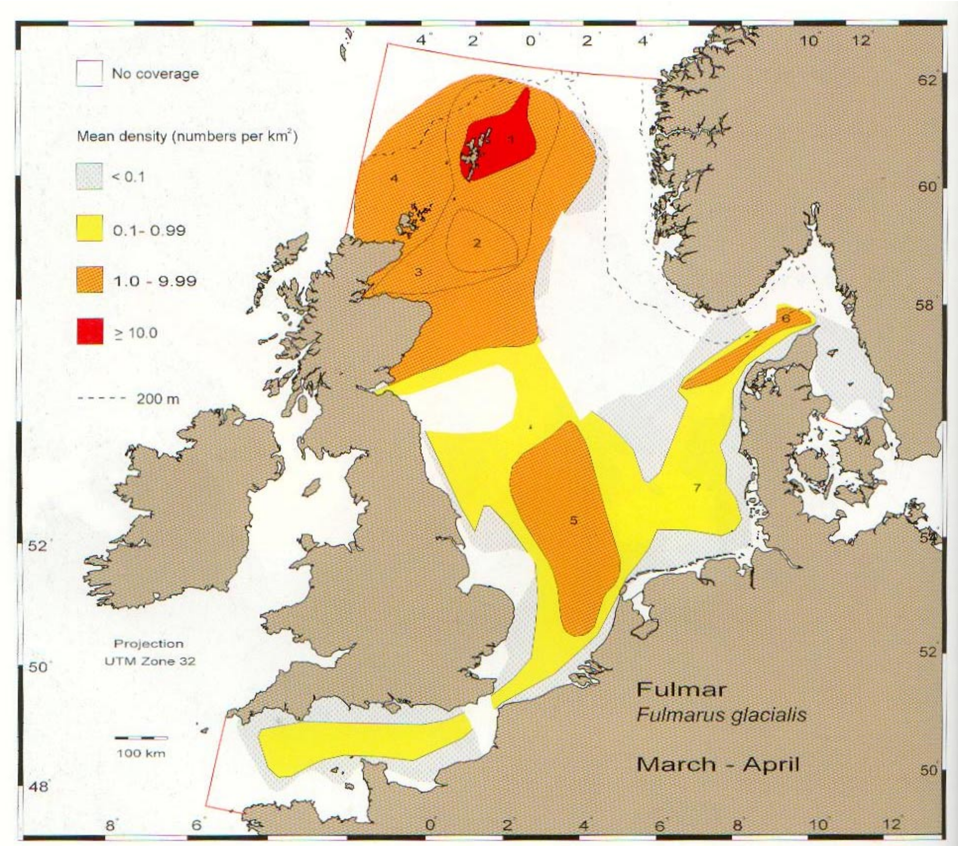
Fulmar distribution at specific sites November to February.



Distribution and density of Fulmar Fulmarus glacialis *in the North Sea, the Channel and the Kattegat from November to February 1980-1994.*

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Bressay Bank – Norwegian Trench	23.6	34,285	810,000
2	Northern North Sea, medium	3.36	80,685	217,000
3	Halibut Bank	0.95	2,930	13,000
4	Orkney	1.3	33,600	44,000
5	Moray Firth – Little Halibut Bank	2.43	20,350	50,000
6	West Moray Firth	0.38	2,050	800
7	North East Bank – Hills	28.66	13,490	387,000
8	North Sea Low	1.4	141,000	197,000
9	Channel – North sea	0.25	76,390	19,000
10	Little Fisher Bank – Skagerrak	9.51	7,030	67,000
11	Middelgrundene	1.56	1,315	2,000
12	Kattegat	0.19	7,735	1,500
	Residual			500
	Total			1,808,80

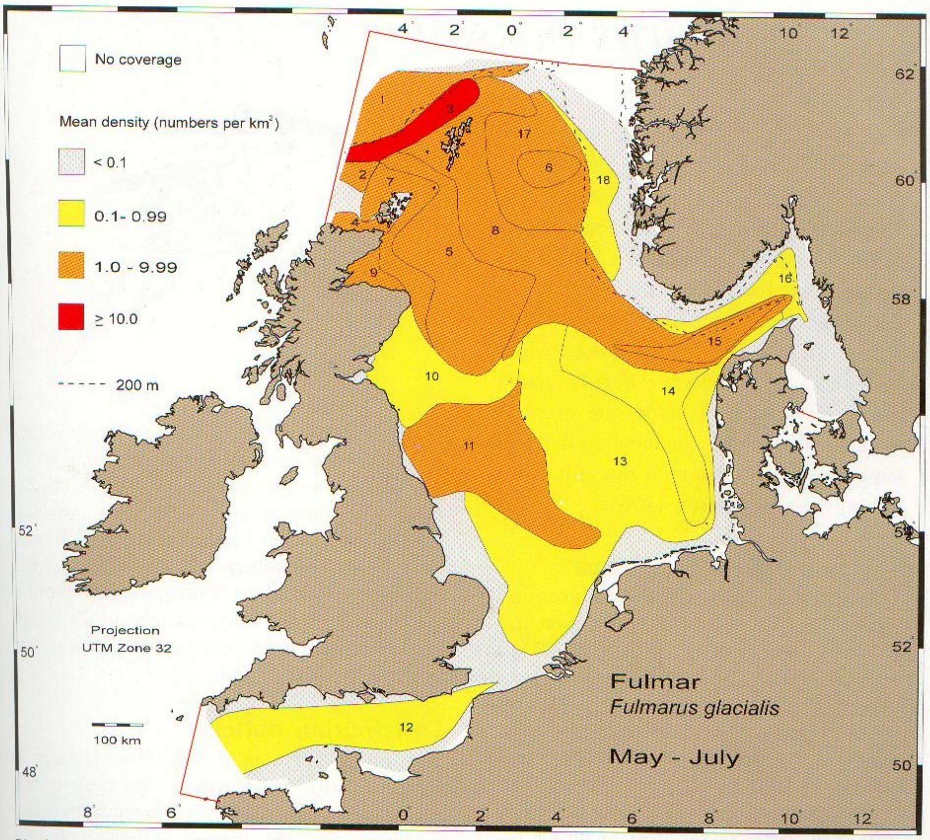
Fulmar distribution at specific sites March to April



Distribution and density of Fulmar Fulmarus glacialis *in the North Sea, the Channel and the Kattegat from March to April 1980-1994.*

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Shetland	25.66	18,640	478,000
2	Little Halibut Bank	9.3	15,500	144,000
3	Northern North Sea, medium	1.76	43,860	7,700
4	Northern North Sea low	1.06	123,600	131,000
5	Brown Ridge – Dogger Bank	1.63	58,880	96,000
6	Little Fisher Bank – Skagerrak	1.35	10,500	14,000
7	North Sea – Channel	0.29	280,000	81,000
	Residual			1,000
	Total			952,700

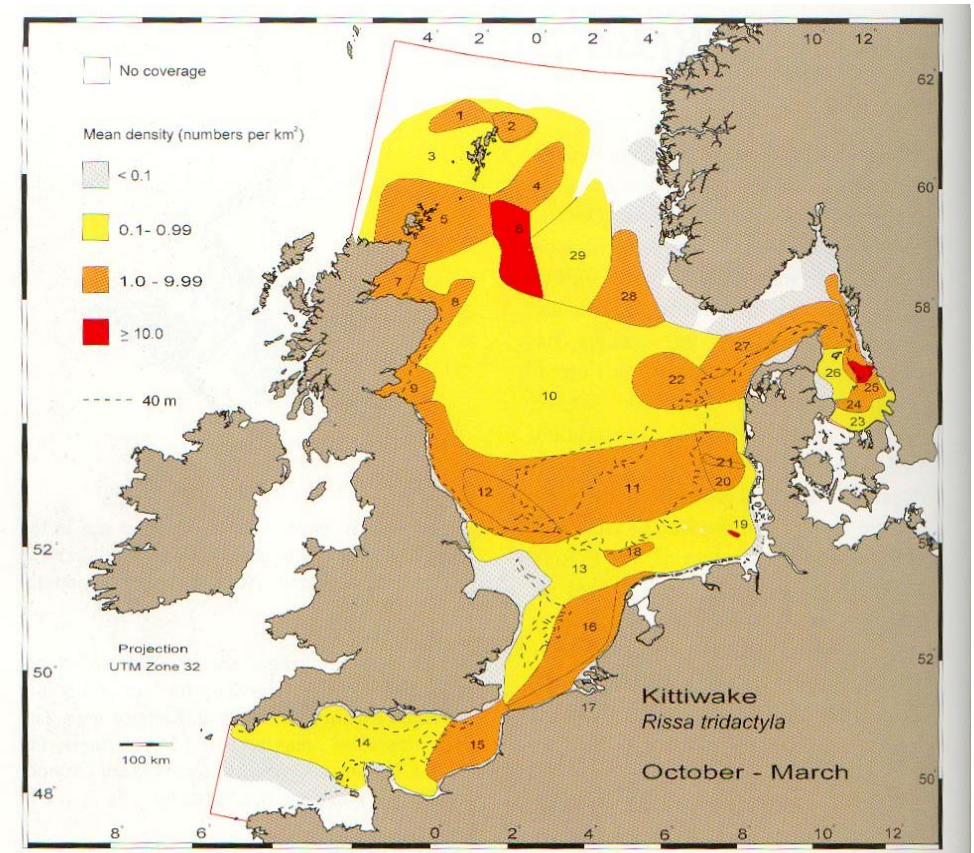
Fulmar distribution at specific sites May to July.



Distribution and density of Fulmar Fulmarus glacialis *in the North Sea, the Channel and the Kattegat from May to July 1980-1994.*

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Shetland – Faroe Channel	1.67	40,000	67,000
2	Papa Bank	1.03	3,600	3,700
3	Northwest Continental Shelf	30.66	17,000	521,000
4	Pentland Firth – Cape Wrath	2.85	3,370	10,000
5	Fiar Isel Channel – Aberdeen Bank	5.59	53,430	299,000
6	Bergen Bank	5.08	9,700	49,000
7	Orkney – Bosies Bank	4.01	20,300	81,000
8	Shetland – Skagerrak	3.05	103,000	314,000
9	Moray Firth	1.1	4,200	4,600
10	Firth of Forth – Devils Hole	0.79	27,800	22,000
11	Dogger Bank	1.5	54,800	82,000
12	The Channel	0.28	53,000	15,000
13	North Sea, low	0.47	92,660	43,550
14	German Bight – Great Fisher Bank	0.83	34,800	44,000
15	Little Fisher Bank	8.25	13,600	29,000
16	Skagerrak, low	0.98	11,400	112,000
17	Utsira Hole – Viking Bank	1.52	29,850	45,000
18	Norwegian trench, Low	0.36	14,350	5,000
	Residual			3,000
	Total			1,749,85

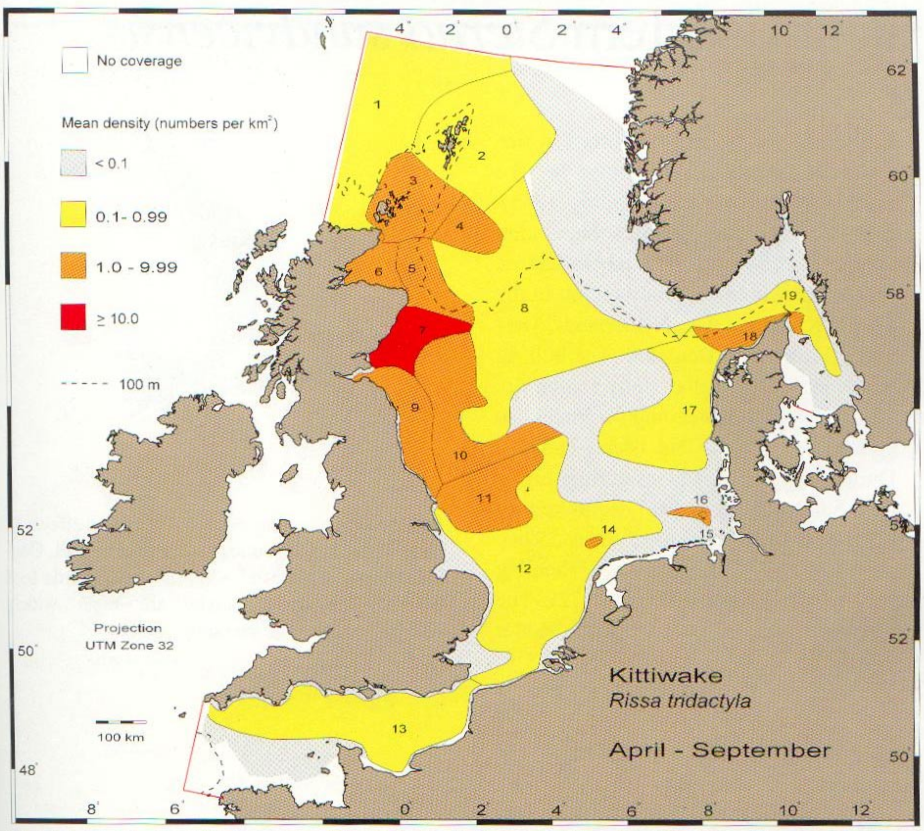
Black-legged kittiwake (*Rissa tridactyla*) distribution October through to September



Distribution and density of Kittiwake Rissa tridactyla *in the North Sea, the Channel and the Kattegat from October to March 1980-1994.*

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Northwestern Shetland	1.18	5,200	6,100
2	North Shetland	6.31	3,300	21,000
3	Cape Wrath – Viking bank	0.22	58,000	12,500
4	Forty Mile Ground	1.06	9,600	10,000
5	Orkney	1.62	27,000	44,000
6	Fladen Ground	10.86	12,000	130,000
7	Moray Firth west	3.6	3,800	13,500
8	North east Scotland	1.15	7,500	8,500
9	Firth of Foerg	1.4	4,600	6,500
10	Central North Sea	0.5	138,000	69,000
11	Dogger Bank	1.6	66,000	106,000
12	Barnade Bank – Silver pit	8	12,000	96,000
13	Southern North Sea	0.47	63,000	30,000
14	Cahnnel	0.43	38,000	16,000
15	Dover Straite	1.42	12,500	17,500
16	Brown Ridge	2.24	17,600	39,000
17	Cap Gris Nez – Ameland	1.13	6,600	7,500
18	Terschelling Bank	2.38	2,300	5,500
19	Helogoland	10.84	190	2,100
20	Horns Rev	1.27	6,900	8,800
21	Blavandshuk	9.6	900	8,700
22	Jutlan Bank – Skagerrak	2.23	21,500	48,000
23	Kattegat, low	0.61	4,300	2,600
24	Kattegat	2.04	7,600	15,500
25	Middelgrundene	59.26	1,300	77,000
26	Alborg Bay	0.18	4,400	790
27	Central Skagerrak	7.18	15,000	108,000
28	The Reef	6.79	14,400	98,000
29	Bergen Bank	0.17	2,700	4,600
	Residual			2,000
	Total			1,014,690

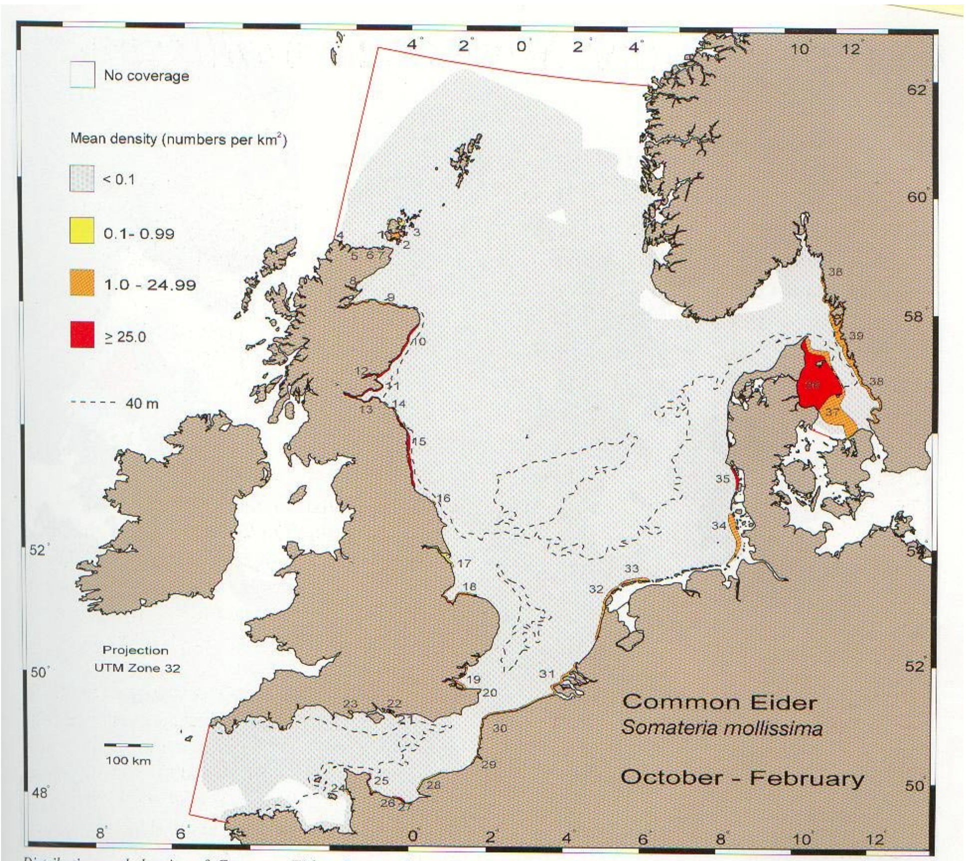
Kittiwake distribution April to September



Distribution and density of Kittiwake Rissa tridactyla *in the North Sea, the Channel and the Kattegat from April to September 1980-1994.*

	Area	Density	Area (km^2)	Average no' estimate
1	Northwestern Continental Shelf	0.51	55,000	28,000
2	Shetland	0.54	46,000	25,000
3	Orkney	2.69	20,000	54,000
4	Fladen Ground	1.11	9,500	10,500
5	Bosies Bank	3.34	12,800	43,000
6	Moray Firth	7.33	6,700	49,000
7	Aberdeen Bank	12.12	11,000	133,000
8	laden Ground – East Bank	0.32	87,000	28,000
9	Farn Deeps – Barmade Bank	3.99	15,700	63,000
10	Eat Bank	1.08	31,500	34,000
11	Outer Silver Pit	2.28	20,400	47,000
12	Southern North Sea	0.27	76,000	21,000
13	Channel	0.14	46,000	6,500
14	Terchelling Bank	1.45	500	700
15	Helgoland, medium	6.5	160	1,000
16	Helgoland, low	1.56	1,430	2,200
17	Monkey Bank – Horns Rev	0.28	35,400	9,900
18	Jammer Bugt	1.45	6500	9,400
19	Skagerrak – Kattegat	0.1	14,000	1,400
	Residual			10,000
	Total			576,600

Eider (*Somateria mollissima*) distribution data October to September

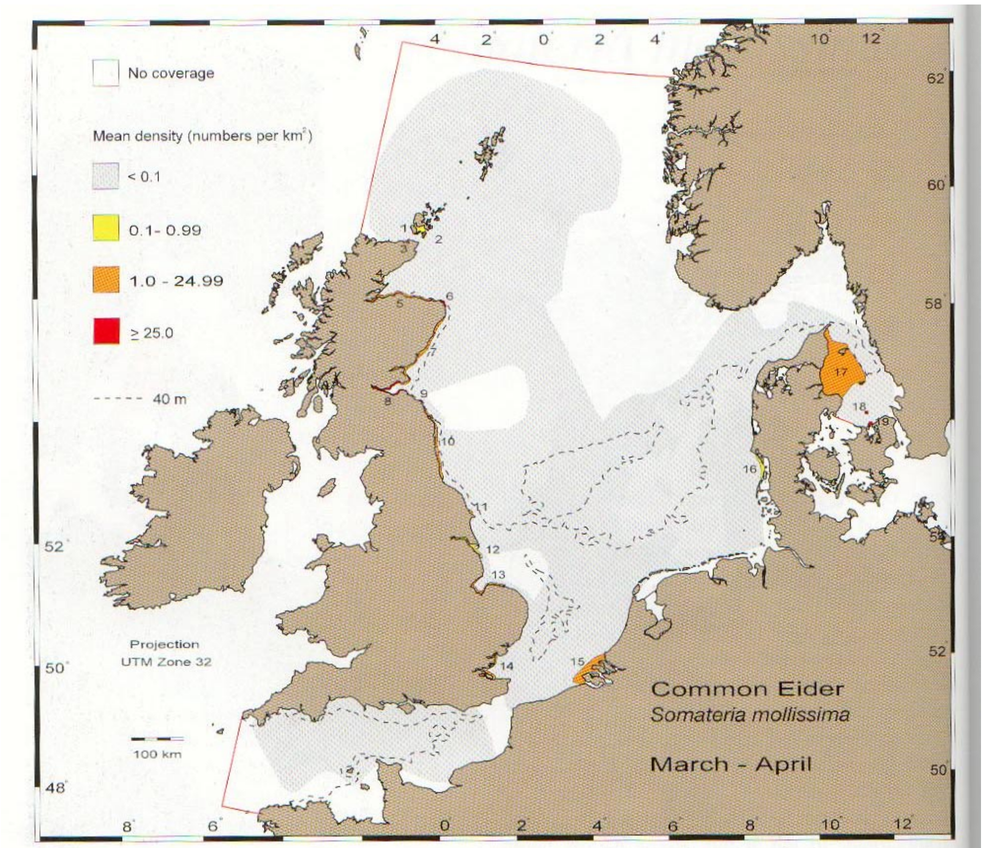


Distribution and density of Common Eider Somateria mollissima *in the North Sea, the Channel and the Kattegat from October to February 1980-1994.*

Eider (*Somateria mollissima*) distribution data October to September (*continued*)

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Scapa Flow	3.79	210	795
2	Newark Bay	6.25	4	25
3	Eynhallow Sound – Markwick	0.75	160	120
4	Faraid Head	54	1	55
5	Kyle of Tongue	1	20	20
6	Sandside Bay	80	2	160
7	Thurso Bay	3.75	12	45
8	Dornoch Firth and Embo – Brora	21	60	1,260
9	Moray Firth	1.97	150	295
10	Collieston – Montrose	65.58	95	6,230
11	Montrose – Firth of Forth	33.13	80	2,650
12	Firth of Tay	363.64	55	20,000
13	Firth of Forth – Tyninghame	66.67	144	9,600
14	Eyemouth	163.33	3	490
15	Berwick upon Tweed – Tees	28.57	140	4,000
16	Whitby	3.75	8	30
17	Humber Estuary	0.14	145	20
18	Wash	3.12	125	390
19	Thames Estuary	1.55	210	325
20	Pegwell Bay	5	6	30
21	Pagham Harbour	5	6	30
22	Chichester Harbour	2.5	20	50
23	Poole Harbour	0.88	40	35
24	Cotentin, west coast	12.39	23	285
25	Cotentin, east coast	9.73	110	1,070
26	Rade de Caen	3.44	16	55
27	Courseulles – Arro manches	54.38	8	435
28	Baie de Seine – Dieppe	0.64	55	35
29	Baie de la Somme	3.3	50	165
30	Nord pas de calais coast	3.2	125	400
31	Voordelta	6.25	800	5,000
32	Vlieland – Ijmuiden	3.45	580	2,000
33	Juist – Terschelling	20	250	5,000
34	Wangerooge – Amrum	5.92	845	5,000
35	Gradyb – Lister Deep	85.71	350	30,000
36	Northwestern Kattegat, high	40.66	6,500	264,270
37	Northwestern Kattegat, medium	7.91	11,600	91,700
38	Swedish westcoast, medium	4.78	1,050	5,020
39	Goteborg Archipelago	11.43	350	4,000
	Residual			1,500
	Total			462,590

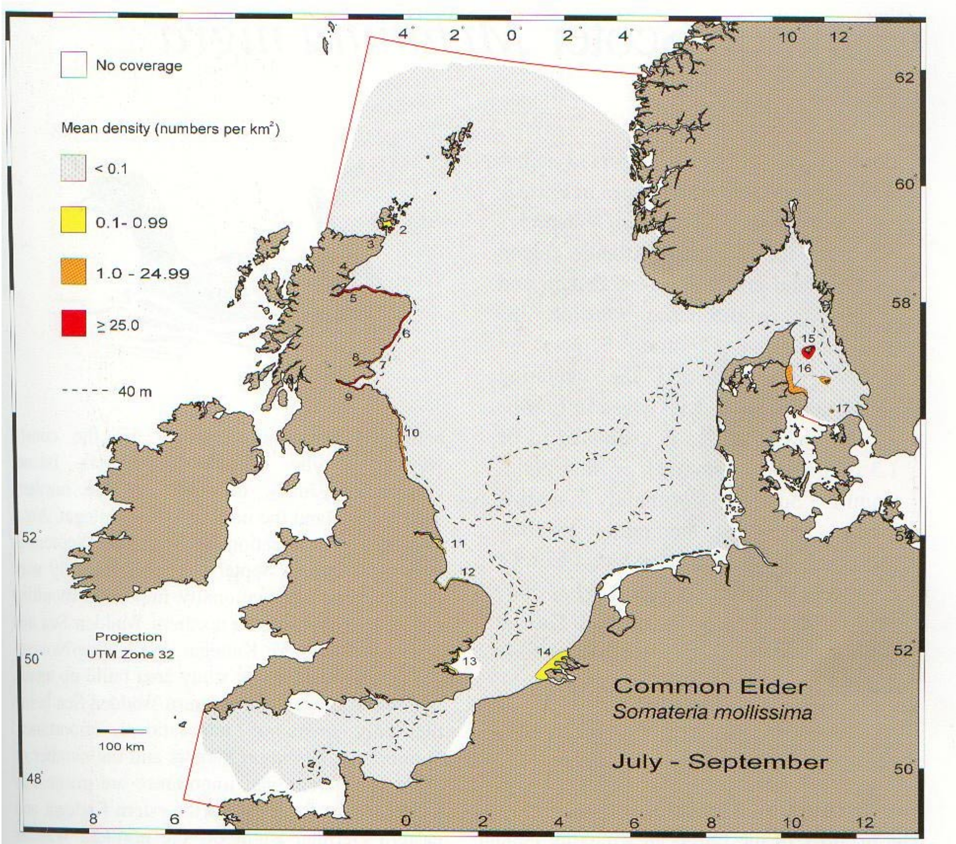
Eider distribution March to April



Distribution and density of Common Eider Somateria mollissima *in the North Sea, the Channel and the Kattegat from March to April 1980-1994.*

	Abundance locality	Density	Area (km^2)	Average no' estimate
1	Scapa flow	0.88	210	185
2	Newark Bay	17.5	4	70
3	Thurso Bay	2.08	12	25
4	Dornoch Firth and Embo Brora	10.83	60	650
5	Moray Firth	9.27	150	1,390
6	Fraserburgh – Peterhead	80	15	1,200
7	Collieston Montrose	10.87	230	2,500
8	Firth of Forth Tyninghame	55.46	144	8,000
9	Eyemouth	43.33	3	130
10	Berwick upon Tweed	11.43	140	1,600
11	Filey	5	8	40
12	Humber Estuary	0.17	145	25
13	Wash	1.84	125	230
14	Thames Estuary	1.12	210	234
15	Voordelta	2.08	1,200	2,500
16	Grådvb	0.71	350	250
17	Northwestern Kattegat	12	6,500	78,000
18	Hesselø	500	40	20,000
19	Hesselø Bay	70	50	3,500
	Residual			4,300
	Total			124,829

Eider distribution July to September



Distribution and density of Common Eider Somateria mollissima *in the North Sea, the Channel and the Kattegat from July to September 1980-1994.*

	Abundance locality	Density	Area (km²)	Average no' estimate
1	Scapa flow	0.19	210	40
2	Newark bay	32.5	4	130
3	Thurso Bay	4.17	12	50
4	Dornoch Firth and Embo Brora	20	60	1,200
5	Moray Firth	33.33	150	5,000
6	Collieston Montrose	68.42	95	6,500
7	Montrose – Firth of Forth	5	80	400
8	Firth of Tay	12.73	55	700
9	Firth of Forth Tyninghame	55.56	144	800
10	Berwick upon Tweed	18.57	140	2,600
11	Humber Estuary	0.17	145	25
12	Wash	0.8	125	100
13	Thames Estuary	0.43	210	90
14	Voordelta	0.75	1,200	900
15	Laesø	81.58	380	31,000
16	Northwestern Kattegat	3.88	1,030	4,000
17	Hesselø	10	40	400
	Residual			450
	Total			54,385

APPENDIX 2. Possible management scenarios for each component of the ecosystem.

Fish	Habitat and benthos	Charismatic and functionally important Change in population – % B_{2003}
Management drivers Increase in fish biomass Maintain target yields in fisheries[b] Objective drivers Maintain B_{2003} Return to B_{1993} All stocks + Metrics	Biogenic Protection of impact on n%[a] of current extent [5, 10 + 50%] Non-biogenic Protection of impact on n%[a] of current extent	Cetaceans[c] Rare: +5, +1, 0 Abundant: +1, 0, –1, –5 Seals[d] Rare: +5, +1, 0 Abundant: +1, 0, –1, –5 Birds[e] Rare: +5, +1, 0 Abundant: +1, 0, -1, –5, –10 Population increase by 50% in past 50 years: 0, –15, –40 Population decrease by 50% in past 50 years: +5, +1, 0, –1, –5

[a] n% will depend on area.
[b] This is not functionally all that different than managing to maintain some particular biomass (like B2003). The nuance is that one estimates the biomass necessary to produce the target yield at a sustainable fishing mortality – and then keep removing that yield while the model allows all the stochastic variation to play out.
[c] the figure of 1% take of the estimated abundance of a population follows the precautionary guidelines of the International Whaling Commission (IWC) and ASCOBANS. The other figure of –/+5% offers a scale comparison.
[d] the potential rates of population decrease/increase for seals will be further refined (using scientific literature by M. Borges).
[e] the potential rates of population decrease/increase for birds will be further refined (using via scientific literature by M. Borges).

APPENDIX 3. Sampling methods and analysis of zooplankton.

Access to databases

The Sir Alister Hardy Foundation for Ocean Science (SAHFOS) which operates the Continuous Plankton Recorder (CPR) survey), kindly released four sets of data:

Jutland:
latitude 57°00' N, longitude 6°30' E
latitude 57°00' N, longitude 8°00' E
latitude 56°30' N, longitude 6°30' E
latitude 56°30' N, longitude 8°00' E
[Filename: 'Jutland_zooplankton.xls']

Wee Bankie:
latitude 56°00' N, longitude 2°00' W
latitude 56°00' N, longitude 1°00' W
latitude 56°30' N, longitude 2°00' W
latitude 56°30' N, longitude 1°00' W
[Filename: 'Wee Bankie_zooplankton']

Dogger:
latitude 55°30' N, longitude 1°30' E
latitude 55°30' N, longitude 3°30' E
latitude 54°30' N, longitude 1°30' E
latitude 54°30' N, longitude 3°30' E
[Filename: 'Dogger_zooplankton']

Fladen:
latitude 59°00' N, longitude 0°00' E
latitude 59°00' N, longitude 1°30' E
latitude 58°00' N, longitude 0°00' E
latitude 58°00' N, longitude 1°30' E
[Filename: 'Fladen_zooplankton']

However, only a small body of data was available from SAHFOS and data was released for only a few species: *Acartia* spp., *Calanus finmarchicus*, *Calanus helgolandicus*, *Calanus* I–IV, *Calanus* Total Traverse, *Calanus* V–VI Total, *Euphausiacea* adults, *Euphausiacea* eggs, *Euphausiacea* juveniles, *Euphausiacea* nauplii, *Euphausiacea* total, fish larvae, *Hyperiidea*, *Oithona* spp., *Para-pseudocalanus* spp. and total copepods for modelling purposes. These datasets are available as excel files with the report ('dogger1_zooplankton.xls', 'Dove_zooplankton.xls', 'Fladen1_zooplankton.xls', 'jutland_zooplankton.xls', 'weeBankie1_zooplankton.xls').

CPR method

CPRs are towed in the surface mixed layer. Water enters the CPR through a 1.27 cm square entrance aperture and travels down a tunnel which expands to cross-sectional dimensions of 5 cm × 10 cm where it passes through a silk filtering mesh (mesh size 270 µm) before exiting via a rectangular exit aperture (dimensions 10 cm × 3cm) at the back of the CPR. The silk moves across the aperture at a rate of approximately 10 cm per 10 nautical miles of tow.

Zooplankton traverse

The silk is viewed under ×48 magnification (field of view 2.05 mm diameter) a traverse of both the filtering and covering silks is made during which approximately 1/40 of the silk is viewed. Due to the semi-quantitative nature of the count, a corrective multiplication has been carried out (details not available).

<u>Zooplankton eye count</u>

All the organisms larger than >2mm on the filtering and covering silks are removed, counted and identified. A category counting system is employed (Warner and Hays, 1994) which corrects for the frequency distribution of the abundance values. This category counting correction has been carried out.

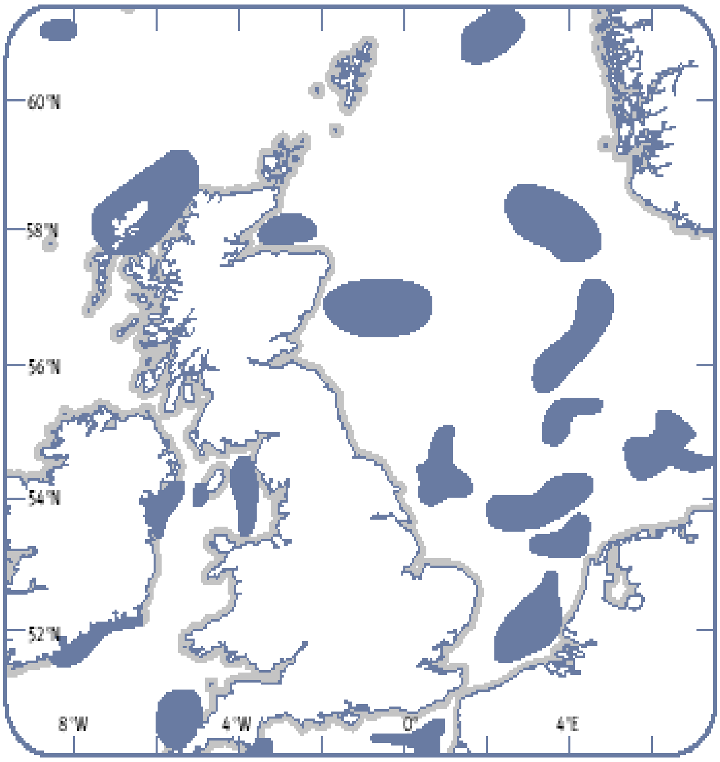
<u>Details of the system used for species or group:</u>

Acartia spp.	TRAVERSE
Calanus finmarchicus	EYECOUNT
Calanus helgolandicus	EYECOUNT
Calanus I–IV	TRAVERSE (juvenile stages of all *Calanus*)
Calanus Total Traverse	TRAVERSE (*Calanus* I–IV and any adult *Calanus* that were seen whilst performing the Traverse scan)
Calanus V–VI Total	EYECOUNT (this is the sum of *C. helgolandicus*, *C. finmarchicus* and *C. glacialis*, but none are present in the areas of interest)
Candacia armata	EYECOUNT
Candacia I–IV	TRAVERSE
Centropages hamatus	TRAVERSE
Centropages typicus	TRAVERSE
Copepod eggs	TRAVERSE
Copepod nauplii	TRAVERSE
Decapod larvae	EYECOUNT
Euchaeta acuta	EYECOUNT
Euchaeta norvegica	EYECOUNT
Euphausiacea adults	EYECOUNT
Euphausiacea calyptopis	TRAVERSE
Euphausiacea juveniles	EYECOUNT
Euphausiacea nauplii	TRAVERSE
Euphausiacea Total	EYECOUNT (this is the sum of adult and juvenile euphausiids)
Fish eggs	EYECOUNT
Fish larvae	EYECOUNT
Gammaridea	EYECOUNT
Hyperiidea	EYECOUNT
Metridia I–IV	TRAVERSE
Metridia lucens	EYECOUNT
Metridia Total Traverse	TRAVERSE
Mysidacea	EYECOUNT
Oithona spp.+	TRAVERSE
Para-pseudocalanus spp.	TRAVERSE (somewhat of a blanket category)
Pseudocalanus elongatus adults	TRAVERSE
Temora longicornis	TRAVERSE
Total copepods	TRAVERSE (this is the sum of all copepods recorded in the Traverse part of analysis).

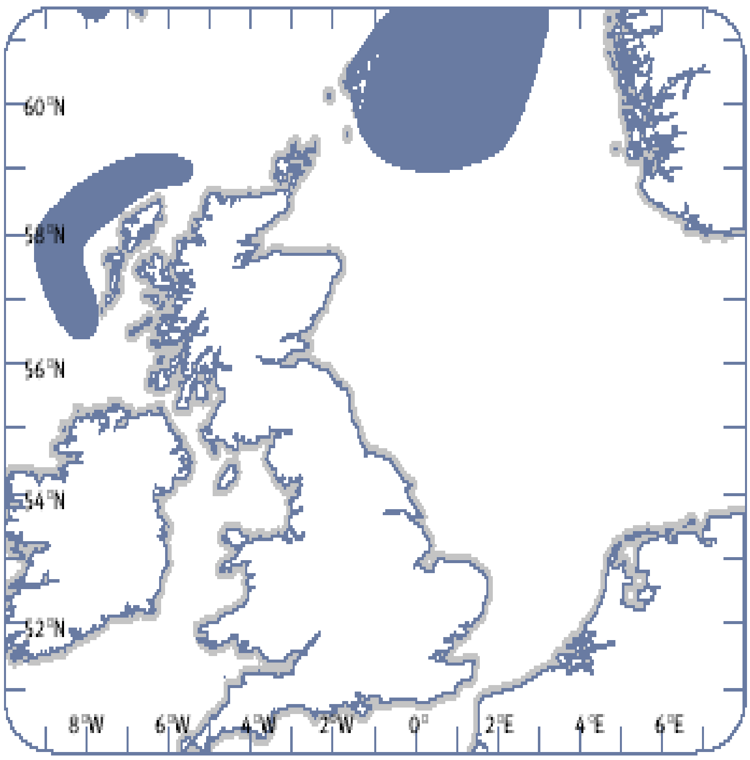
Each sample value represents abundance of the species in question in 3 m^3 of water at the surface mixed layer.
A second database is available from the Dove Marine Laboratory, University of Newcastle, U.K. Monthly sampling has been carried out on the coastal central-west North Sea zooplankton community at a single station (55°07' N, 01°20' W) since 1969 by the Dove Marine Laboratory using a combination of WP2 and WP3 nets. Monthly and yearly abundance of zooplankton sampled at the station are available (data are available in the file ‘Dove_zooplankton.xls’).

APPENDIX 4. Fish spawning grounds in the North Sea.

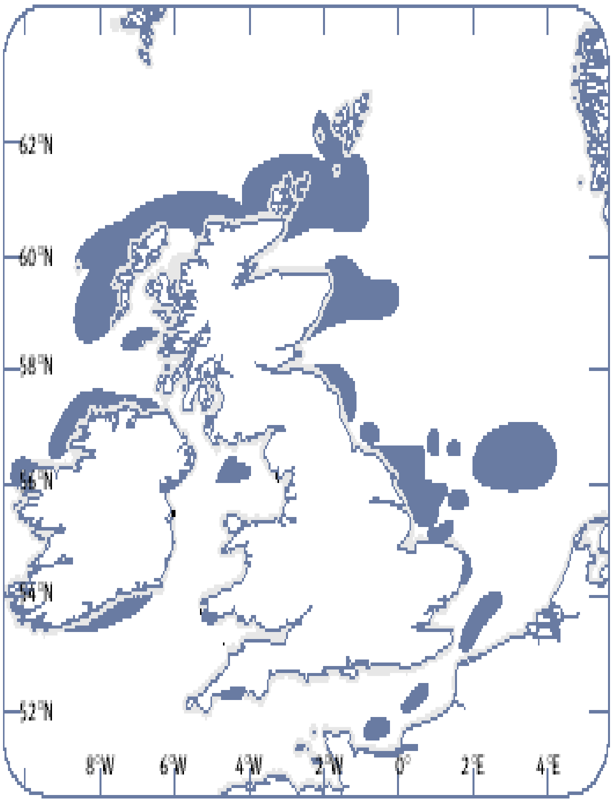
Cod spawning grounds in the North Sea.



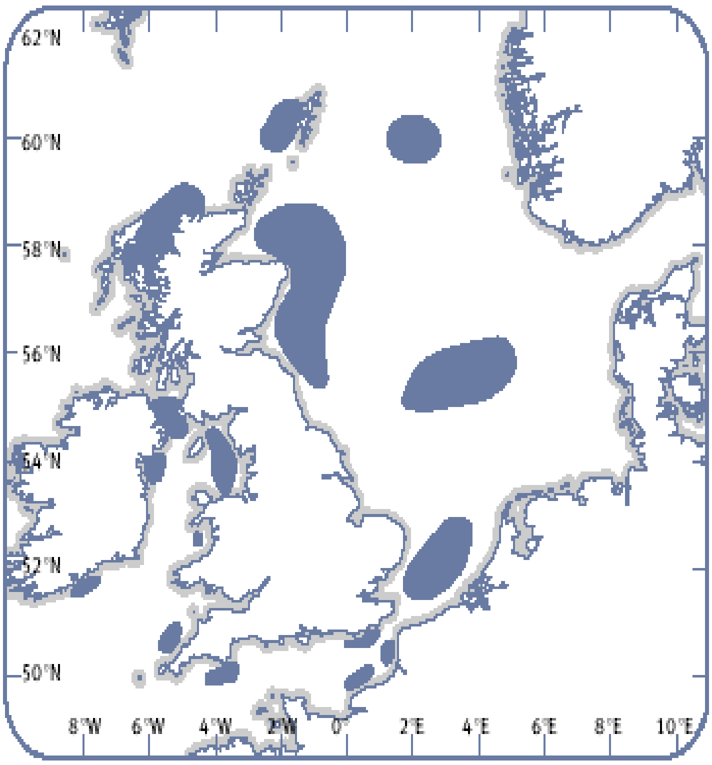
Haddock spawning grounds in the North Sea.



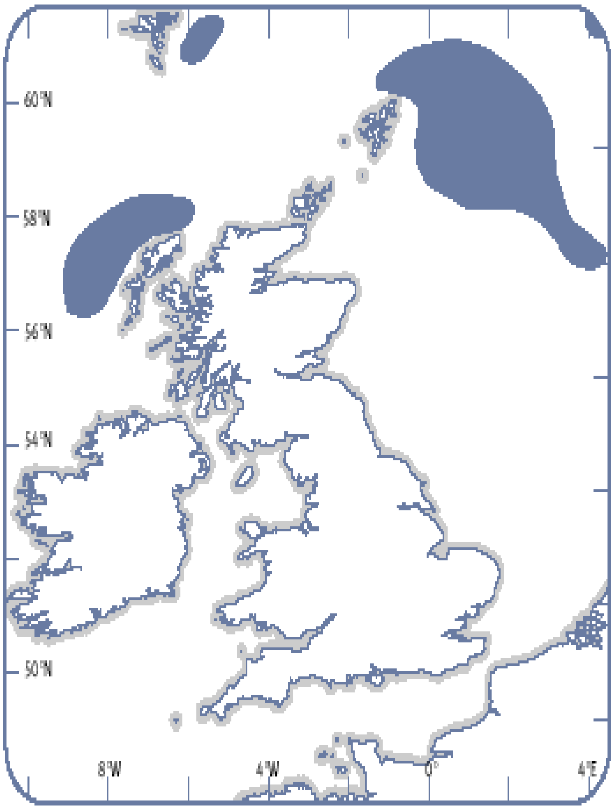
Herring spawning grounds in the North Sea.



Whiting spawning grounds in the North Sea.



Saithe spawning grounds in the North Sea.



Source: www.marlab.ac.uk

APPENDIX 5. Benthic prey items in fish diets in the North Sea.

In this appendix we review all information we found on benthic prey items in the diet of demersal fish. For most species, only the dominant prey items are shown. W%= percentage by weight, F%=frequency of occurrence, N%=percentage by number, av=average.

Plaice *Pleuronectes platessa*

Rijnsdorp and Vingerhoed (2001). Benthic prey items in the diet of plaice in the southern North Sea

Prey	W%	F%
Lagis koreni	31	47
Nereis spp.	9	17
Spisula spp.	9	11
Ensis spp.	7	9
Magelona papillicornis	5	6
Ophitrichidae	3.5	12.2
Echinocardium cordatum	2.5	5.8
Ophiuridae	1.2	5.5

Rijnsdorp and Vingerhoed (2001). Seasonal variation of prey items in the diet of plaice.

Prey	April		June		Aug–Sept	
	W%	F%	W%	F%	W%	F%
Annelida	31.9	86.2	28.7	59.4	66.1	79.8
Bivalvia	28.7	71.7	11.8	30.8	20.5	36.4
Crustacea	17.4	44.8	4.3	8.1	5.1	10.9
Echinodermata	10.8	55.5	20.6	33.2	4.4	10.3
Rest	11.3	34.1	3.9	10	3.9	7.7

Høines and Bergstad (2002). Benthic prey items in the diet of plaice in the SW-Norway.

Prey	Spring				Summer				avW%	avF%
	30–39		40–49		30–39		40–49			
	W%	F%	W%	F%	W%	F%	W%	F%		
Chlamys spp.	19.9	5.9	45.1	17.6			0.4	2.6	16.35	6.52
Ophiura spp.					1.7	13.9			0.425	3.47
Echinus spp.	0	2.9	0.8	11.8	0.3	1.3	0	1.3	0.275	4.32
Ophiura affinis	0.7	20.6	0.1	5.9	0.1	1.3			0.225	6.9
Paguridae	0.3	8.8	0.1	5.9	0.1	2.5	0.2	5.2	0.175	5.6

Høines and Bergstad, (2002). Benthic prey items (>5% of frequency of occurrence) in the diet of plaice in the SW-Norway.

Prey	Spring				Summer			
	30–39		40–49		30–39		40–49	
	W%	F%	W%	F%	W%	F%	W%	F%
Polychaeta	4.1	17.6	8.2	23.5	0.2	5.1	0.6	10.4
Bivalvia	32.8	26.5	92.5	52.9	8.5	34.1	3.1	28.6

Pihl (1993). Benthic prey items in the diet of plaice in the Kattegat.

Prey	W%
Polyphysia crassa	34.8
Abra nitida	8.4
Amphiura spp.	8.2
Amphiura filiformis	5.9
Priapulus caudatus	5.8

Sole *Solea vulgaris*

Rijnsdorp and Vingerhoed (2001). Benthic prey items in the diet of sole in the Southern North Sea.

Prey	W%	F%
Pectinaria koreni	55	52
Macropipus holsatus	18	17
Nereis spp.	8	5
Lanice conchilega	8	5

Prey	April		June		Aug–Sept	
	%W	%F	%W	%F	%W	%F
Annelida	100	100	70.2	85.7	75.9	89.2
Bivalvia	0	0	0.6	4.8	1.3	8.6
Crustacea	0	50	2.5	2.4	20.8	27.5
Echinodermata	0	0	2.5	9.5	1.1	3.7
Rest	0	0	24.2	11.9	0.9	3.7

Dab *Limanda limanda*

Pihl (1994). Benthic prey items in the diet of dab in the Kattegat.

Prey	%W
Amphiura spp.	41.5
Amphiura filiformis	21.5

Høines and Bergstad, (2002). Benthic prey items in the diet of dab in SW Norway in summer.

Prey	20–29		30–39		avW%	avF%
	W%	F%	W%	F%		
Chlamys spp.	0	0	2.6	9.4	1.3	4.7
Paguridae	0.7	6.3	0.4	3.1	0.55	4.7
Ophiura spp.	3.9	25.4	0.3	6.3	2.1	15.85

Long rough dab *Hippoglossoides platessoides*

Klemetsen (1993). Benthic prey items in the diet of long-rough dab in Norway.

Prey	Ramfjordnes	Tennes	avF%
	F%	F%	
Nepthys sp.	18.3	3	10.65
Owenidae	5.2	11.9	8.55
Maldanidae	12.4	1.8	7.1
Ophiuroidea	9.8	1.2	5.5

Ntiba and Harding (1993). Benthic prey items in the diet (>5% of frequency of occurrence) of long-rough dab in the North Sea.

Prey	Jan	Feb	Mar	May	June	Jul	Aug	Nov	Dec	avF%
Pandalus spp.	7.4	13.8	83.9	25.5	0	1.1	0	10.6	14	17.37
Crangon spp.	11.1	46.9	0	2	18.9	2.8	13.6	4.7	22	13.56
Micropipus spp.	0	1.7	0	0	27	0	0	0	0	3.19
Ophiura spp.	0	6.2	0	2	0	0	18.9	0	0	3.01
Tellina spp.	0	0	0	3.9	5.4	5.1	0	2.4	0	1.87

Wolffish *Anarhichas lupus*

Liao and Lucas (2000). Benthic prey items in the diet of wolffish in the North Sea.

Prey	F%
Paguridae	21
Pectinidae	12.8
Buccinidae	10
Aphroditidae	8.1
Echinidae	6.3
Majidae	6

Starry ray *Raja radiata*

Skjæraasen and Bergstad (2000). Benthic prey items in the diet of *Raja radiata* in NE- North Sea and Skagerrak.

Prey	juv F%	med F%	large F%	juv W%	med W%	large W%	avF%	avW%
Polynoidae	0	3	4	4	21	4	2	9.6
Crangonidae	3	1	1	15	0	4	2	6.5
Calocaris macandreae	2	3	4	8	6	2	3	5.2
Pontophilus norvegicus	3	5	13	4	3	1	7	2.9
Munida sarsi	0	0	15	0	0	9	5	2.9
Gammaridae	27	27	7	5	3	0	20	2.5
Isopoda	11	3	0	3	1	0	4	1.2

Cod *Gadus morhua*

Pihl (1993) Benthic prey items in diet of cod in Skagerrak.

Prey	%W
Crangon almani	10.7
Crangon spp.	6.2
Aphrodita acuelata	6.9

Whiting *Merlangius merlangus*

Pihl (1993). Benthic prey items in diet of whiting in Skagerrak.

Prey	%W
Crangon almani	10

Flatfish

Amara *et al.* (2001). Benthic prey items in the diet of juvenile flatfish (0-group). Only prey items with frequency of occurrence >20% are shown.

Prey	May	June	July
Spionidae	x	x	x
Magelona mirabilis	x	x	x
Lanice conchilega		x	x
Bivalvia			
Mysella bidentata	x		
Harpacticoid spp.	x		
Cumacea	x		
Amphipoda			x

Breyst *et al.* (1999) Benthic prey items in the diet of juvenile flatfish (0-group), Belgium. Most important prey items (>20% occurrence) are shown.

Prey	Plaice	Dab	Sole
Polychaeta palp	43.8	29.6	7.4
Polychaeta	70.1		59.3
Harpacticoida	15.3	74.1	16.7
Caridea	40.9	40.7	81.5
Amphipoda	12.4	59.3	48.1

Benthic prey items in fish diet in the North Sea (% by weight) (Greenstreet, 1996)

Prey	Lemon sole	Common dab	Whiting	Haddock	Cod
Amphipoda		9.14	0.77		
Annellida			3.8	10.27	5.39
Anomura			0.97	2.1	3.62
Appendicularia			0.08		
Ascidiae	1.25				
Bivalves		1.1	0.02	3.21	0.82
Brachyrhyncha				0.82	9.04
Brachyura			2.71		
Calanoida				0.28	
Cancridea				0.04	3.78
Caprellidea				0.01	
Caridea			2.84	1.88	
Cephalopoda			2.47	0.91	1.03
Chaetognatha			0.24		
Cnidaria			0.08		0.06
Coelenterates	21				
Copepoda			1.58		
Crangonidae			4.65	0.1	2.43
Crustacea	4.75				
Ctenophora			0.01		
Cumacea		1.7	0.05	0.13	
Decapoda		30.35			
Echinodermata	1.84		0.46	11.65	0.77
Echiura			1.19		0.13
Euphausiacea			9.42	9.21	3.76
Flabellifera				0.74	
Gammaridea				1.02	0.06
Gastropoda			0.52	0.5	0.62
Gephyrea	1.58				
Hydroids		1.9			
Hyperiidea				1.8	0.02
Isopoda			0.07		
Macrura			0.51		
Molluscs	10.7				
Mysidia			0.06	0.05	0.04
Nemertea	0.52				
Nephrops					5.19
Ophiuroids		46.28			
Other Caridea					1.11
Oxyrhyncha				0.76	0.63
Oxystomata					0.02
Pandalidae			0.18		
Polychaetes	57.83	9.53			
Priapulida					0.27
Pycnogonida					0.01
Scaphopoda				0.02	
Tanaidacea				0.02	
Unidentified Crustacea			2.23		
Unidentified Molluscs			0.25		
Urochordata			0.63	0.54	0.01
Valvifera				0.1	0.05
Sum	**99.47**	**100**	**35.79**	**46.16**	**38.86**

APPENDIX 6. List of families in the two studies of in- and epifauna in the North Sea.

We collected information that was available in the literature on distribution, abundance, biology and natural mortality of benthic families considered for inclusion in the 'significant web'. This selection was partly based on data on abundance and frequency of occurrence derived from two sources: (1) Atlas of North Sea Benthic Infauna (Craeymeersch *et al.*, 1997), where we used data on macrobenthos and (2) Monitoring Report on Epibenthos in the North Sea and Skagerrak (Anon., 2001). Information from these two datasets was used to calculate the percentage frequency of occurrence of infauna and epifauna for each family and for the dominant species within each family. In a few cases, a higher taxon than family is specified (as in the original source). Percent of stations in which a taxon was present in the respective study (that of infauna denoted with *i*, and that of epifauna denoted with *e*) is given in the parentheses. Total number of stations in the study of infauna: 231. Total number of stations in the study of epifauna: 270.

Phylum: Annelida

Family: Aphroditidae (*i*: 29, *e*: ?)

Key species: *Aphrodita aculeata* (*i*: 19, *e*: 29), *Gattyana cirrosa* (*i*: 14) (*G. cirrosa* is also classified in the family Polynoidae)

Distribution: *A. aculeata*: most north-west European coasts, Mediterranean (Nelson-Smith *et al.*, 1990); found around the coasts of Britain and Ireland with but rare off southwest coast of England (Hughes, 2003). *G. cirrosa*: on most British coasts; Arctic, north Atlantic, north Pacific (Nelson-Smith *et al.*, 1990).

Depth: *A. aculeata*: sublittoral to depths of over 1000 m (Hughes, 2003).

Substrate type: *A. aculeata*: sand or muddy sand (Nelson-Smith *et al.*, 1990). *G. cirrosa*: in the tube of terebellid or chaetopterid worms (Nelson-Smith *et al.*, 1990).

Coastal/offshore: *A. aculeata*: inshore and offshore (Chambers, 1985).

Natural mortality: *A. aculeata* occurred in more than 20% of plaice stomachs in May (Amara *et al.*, 2001)

Feeding ecology: *A. aculeata*: classified as slow moving carnivores. Prey consists of microscopic animals but if available, sessile or slow-moving organisms (Fauchald and Jumars, 1979).

Life style: free living, epifaunal or sediment-water interface, mobile.

Family: Arenicolidae (not present in the samples)

Key species: *Arenicola marina* (lugworm)

Distribution: *A. marina* has been recorded from shores of western Europe, Norway, Spitzbergen, north Siberia, and Iceland. In the western Atlantic it has been recorded from Greenland, along the northern coast form the Bay of Fundy to Long Island. Its southern limit is about 40°N. Found on all coasts around Britain and Ireland and widely in north-west Europe (Tyler-Walters, 2001a).

Depth: *A. marina*: intertidal, eulittoral, sublittoral fringe (Tyler-Walters, 2001a).

Substrate type: *A. marina*: mixed saltmarsh, sea grass, muddy gravel, sandy mud, muddy sand, fine clean sand (Tyler-Walters, 2001a).

Coastal/offshore: *A. marina*: strait/sound, sealoch, ria/voe, estuary, enclosed coast/embayment, isolated saline water (lagoon) (Tyler-Walters, 2001a).

Densities: *A. marina* reaches high abundances in sheltered estuarine sediments (Tyler-Walters, 2001a). The average density in the Mariager Fjord in 2000 was 41 ind. m^{-2} (Sømod, 2001). Densities of juveniles in the Dutch Wadden Sea (a nursery area for *A. marina*) are highest within 1 km from the mainland (16 ind. m^{-2}). Highest concentrations of adults are found 2 to 4 km from the shore (20–37 ind. m^{-2}). Mean density was 17 ind. m^{-2} (Beukema and De Vlas 1979).

Biomass: *A. marina* in the Marjager Fjord: 0.07095 g DW m^{-2} (Sømod, 2001); in the western part of the Dutch Wadden Sea: between 1.7 and 7.9 g AFDW m^{-2} (Beukema *et al.*, 1978); mean biomass on the tidal flats of the Dutch Wadden Sea: about 5 g AFDW m^{-2} (Beukema and De Vlas 1979).

Natural mortality: *A. marina* is an important food source for wading birds, e.g. curlew (*Numenius arquata*), bar-tailed godwit (*Limosa lapponica*) and oystercatcher (*Haematopus ostralegus*), flatfish, and ragworm (*Nereis virens* and *Hediste diversicolor*) (Tyler-Walters, 2001a). Beukema and De Vlas (1979) suggested an average annual mortality of 22%, an annual recruitment of 20% and reported that the abundance of the population had been stable for the previous 10 years. However, Newell (1948) reported 40% mortality of adults after spawning in Whitstable (Kent, UK).

Life span: *A. marina*: Beukema and De Vlas, (1979) suggested a life span, in the Dutch Wadden Sea, of at least 5–6 years, and cite a life span of at least 6 years in aquaria.

Reproduction: *A. marina*: gonochoristic (separate sexes); reproduction frequency: annual episodic; fecundity (number of eggs): 100,000–1,000,000 (Tyler-Walters, 2001a).

Early development: *A. marina*: eggs and early larvae develop within the female burrow, however post larvae are capable of active migration by crawling, swimming in the water column and passive transport by currents. Günther (1992) suggested that post-larvae of *A. marina* could be transported distances in the range of 1 km.

Feeding ecology: *A. marina*: sub-surface deposit feeder. It makes a non-permanent L-shaped burrow, with the worm head-down. During feeding, the worm ingests the deeper sediment in front of the head, which causes the sediment column above to collapse producing a depression or funnel. The ingested sediment is defecated at the sediment surface at the entrance to the tail shaft as a faecal mound or cast. *A. marina* feeds on material obtained from the sediment surface: micro-organisms (bacteria), benthic diatoms, meiofauna, and detritus (Tyler-Walters, 2001a), and is also capable of absorbing dissolved organic matter (DOM) such as fatty acids through the body wall (Zebe and Schiedek, 1996).

Life style: free living, burrower, slow mobility.

Other information: *A. marina*: an important food source for wading birds, e.g. curlew (*Numenius arquata*), bar-tailed godwit (*Limosa lapponica*) and oystercatcher (*Haematopus ostralegus*), flatfish, and ragworm (*Nereis virens* and *Hediste diversicolor*). Collected, commercially and by individuals for bait; aquaculture use, research use (Tyler-Walters, 2001a).

Family: Magelonidae (*i*: 45)

Key species: *Magelona* spp. (*i*: 45) (probably *Magelona mirabilis*, *M. alleni*, *M. rosea*)

Distribution: *M. mirabilis*: recorded from North Sea coasts, the Baltic Sea, the Atlantic coast of France and the Mediterranean coast of France. Expected to occur all around the coasts of Britain and Ireland where suitable substrata occur. Recorded patchily from all British and Irish coasts (Rayment, 2001a).

Depth: *M. mirabilis*: mid shore to 32 m depth; lower eulittoral, sublittoral fringe, infralittoral, upper circalittoral (Rayment, 2001a).

Substrate type: *M. mirabilis*: coarse clean sand, fine clean sand (Rayment, 2001a). It prefers unstable sedimentary environments (Lackschewitz and Reise, 1998).

Coastal/offshore: *M. mirabilis*: open coast, offshore seabed, strait/sound, enclosed coast/embayment (Rayment, 2001a).

Densities: *M. mirabilis* occurs at high densities where environmental conditions are suitable (Rayment, 2001a). Kuhl (1972) reported *M. papilliformis* at densities of 279 individuals per 0.1 m^2 on sandy muddy ground in the Elbe Estuary. The annual mean density of *M. mirabilis* in the Southern Bight of the North Sea was 214 ind. m^{-2} (Amara *et al.*, 2001).

Biomass: *M. mirabilis*: annual mean biomass in the Southern Bight 27.2 mg AFDW m^{-2} (Amara *et al.*, 2001).

Natural mortality: *M. mirabilis* is an important prey for dab and plaice in the Southern Bight (Amara *et al.*, 2001).

Life span: *M. mirabilis*: 2–5 years (Rayment, 2001a).

Reproduction: *M. mirabilis*: gonochoristic; reproduction frequency: annual protracted (Rayment, 2001a).

Early development: *Magelona* spp.: planktonic larvae; large interannual variability in numbers (Bosselmann, 1989 cited in Rayment, 2001a).

Feeding ecology: *M. mirabilis*: surface deposit feeder; typically feeds on detritus, microalgae, small animals (Rayment, 2001a).

Life style: burrowers.

Other information: *M. mirabilis* does not produce a tube. It is adapted for life in highly unstable sediments, characterized by surf, strong currents and sediment mobility (Rayment, 2001a).

Family: Maldanidae (*i*: 34, *e*: < 1)

Key species: *Rhodine gracilior* (= *R. loveni*) (*i*: 10), *Praxillura longissima* (*i*: 7), *Praxillella affinis* (*i*: 7), *Euclymene droebachiensis* (*i*: 6), *Maldane sarsi* (*i*: 3)

Distribution: *R. gracilior*: north-west Britain, Arctic, North Sea, west Baltic, Atlantic coast of Europe to Mediterranean, often in brackish waters (Nelson-Smith *et al.*, 1990). *Praxillura longissima*: Arctic, North Atlantic to Skagerrak, Kattegat, Belts and northern Baltic. *Praxillella affinis*: North Pacific, eastern Atlantic to Mediterranean and Red Sea, western North Sea, Skagerrak, Kattegat, Belts. *E. droebachiensis*: central and northern North Sea, Skagerrak, Kattegat (Hartmann-Schröder, 1996).

Depth: *R. gracilior*: from upper sublittoral to almost 1000 m; *Praxillura longissima*: from upper sublittoral to a depth of 2000 m; *E. droebachiensis*: from upper sublittoral at about 20 m to upper bathyal at 450 m (Hartmann-Schröder, 1996).

Substrate type: *R. gracilior*: mixed bottoms of mud, sand and shells; *Praxillura longissima*: mud or sandy mud with gravel and *Zostera* debris; *E. droebachiensis*: mainly on muddy bottoms, but also on mixed bottoms with fine sand and gravel (Hartmann-Schröder, 1996).

Densities: *Praxillella affinis*: the average annual population density off the coast of Northumberland (NE England) between 1971–1972 was 26 ind. m^{-2} (Buchanan and Warwick, 1974).

Biomass: *Praxillella affinis*: the average annual biomass off the Northumberland coast between 1971–1972 was 71 mg AFDW m^{-2} (Buchanan and Warwick, 1974).

Reproduction: *M. sarsi*: generative and vegetative reproduction (Hartmann-Schröder, 1996).

Feeding ecology: *M. sarsi*: subsurface deposit feeder (Schäfer, 1962 cited in Hartmann-Schröder, 1996).

Life style: sessile, tube building, slow mobility.

Family: Nephtyidae (*i*: 91, *e*: ≈ 6)

Key species: *Nephtys hombergii* (catworm) (*i*: 61, *e*: < 1), *N. longosetosa* (*i*: 41, *e*: 5), *N. cirrosa* (*i*: 25, *e*: 2), *N. caeca* (*i*: 22, *e*: 3)

Distribution: *N. hombergii*: common and widespread (all around Britain, north-west Europe, Mediterranean); *N. longosetosa*: west coast of Britain, Atlantic coast of Europe; *N. cirrosa*: all around Britain, Atlantic coast of Europe; *N. caeca*: common and widespread (all around Britain; Arctic and north Atlantic) (Nelson-Smith *et al.*, 1990).

Depth: *N. hombergii*: intertidal and at low water to 400 m depth; *N. longosetosa*: sublittoral, in shallow water down to 1000 m depth; *N. cirrosa*: intertidal and at low water to 170 m; *N. caeca*: intertidal and at low water (Nelson-Smith *et al.*, 1990; Hartmann-Schröder, 1996).

Substrate type: *N. hombergii*: mixed bottoms with mud, shells and *Zostera*; *N. longosetosa*: all types of sediments from coarse gravel, shells, mixed bottoms and mud, coral reef and oyster beds, to substrates within rhizoids of *Laminaria* and *Lanice* tubes, in mud of *Mytilus* and oyster beds; *N. cirrosa*: clean to muddy, coarse to fine, sand, e.g. *Amphioxus* sand, less common on sand or shell muddy bottoms; *N. caeca*: all types of sediments from gravel to soft mud, mixed bottoms with shells or other admixture, *Zostera* meadows, oyster beds and coral reef (Hartmann-Schröder, 1996).

Coastal/offshore: *N. hombergii*: open coast, estuary, enclosed coast/embayment (Budd and Hughes, 2003). *N. cirrosa*: coastal; mudflats and open beaches (Hartmann-Schröder, 1996).

Densities: *N. hombergii*: Clay (1967 cited in Budd and Hughes, 2003) lists densities of *N. hombergii* reported by various authors from locations in the British Isles, which range from 2 ind. m^{-2} at a location on the Northumbrian coast (NE England) to 570 ind. m^{-2} in the Tamar Estuary. The average annual population density off the Northumberland coast between 1971–1972 was 10 ind. m^{-2} (Buchanan and Warwick, 1974). Ball *et al.* (2000) reported densities of 58–70 ind. m^{-2} in the northwestern part of the Irish Sea, on *Nephrops* grounds. *N. cirrosa* is one of the most abundant species on the Dogger Bank (Johnston *et al.*, 2002). Mean densities of *N. hombergii* and *N. cirrosa* in the southern North Sea in August 1989: 7 and 3 ind. m^{-2}, respectively (Bergman and Hup, 1992). *N. caeca*: the mean density in southern Kattegat in 2001 was 14 ind. m^{-2} (Frederiksborg Amt, 2001).

Biomass: *N. hombergii*: the average biomass on the tidal flats of Balgzand, Wadden Sea in the 1990s: 0.3 g AFDW m^{-2} (Beukema *et al.*, 2002). Its abundance is controlled by winter temperature; the biomass of *N. hombergii* was <0.1g AFDW m^{-2} during the coldest winters, compared to 1 g AFDW m^{-2} during periods with mild winters (Beukema *et al.*, 2000). *N. caeca*: the mean biomass in southern Kattegat in 2001 was 2.37 g WW m^{-2} (Frederiksborg Amt, 2001). The average annual biomass off the Northumberland coast between 1971–1972 was 23 mg AFDW m^{-2} (Buchanan and Warwick, 1974).

Natural mortality: *Nephtys* spp. occurred in more than 20% of plaice stomachs in July (Amara *et al.*, 2001).

Life span: *N. hombergii*: 2–5 years (Budd and Hughes, 2003).

Reproduction: *N. hombergii*: gonochoristic; reproductive frequency: annual protracted (Budd and Hughes, 2003); spawns mainly in the spring and may more easily colonise areas during this period (Ferns *et al.*, 2000).

Early development: *N. hombergii*: the pelagic life cycle lasts seven to eight weeks at the end of which larvae metamorphose into benthic juveniles (Budd and Hughes, 2003).

Feeding ecology: *N. hombergii*: scavenger, active carnivore; typically feeds on molluscs, crustaceans and other polychaetes (Budd and Hughes, 2003). Two deposit-feeders, *Scoloplos amiger* and *Heteromastus filiformis* were the main prey components in the guts of *N. hombergii* on tidal flats near the island of Sylt in the North Sea (Schubert and Reise, 1986). Beukema (1987) observed a negative relation between abundance of *N. hombergii* and values for biomass and rate of increase in two of its prey species, the polychaetes *Scoloplos armiger* and *Heteromastus filiformis*. In the presence of *N. hombergi*, the density of juvenile *Nereis diversicolor* was significantly reduced (Desroy *et al.*, 1998). *N. caeca*: predator (Hartmann-Schröder, 1996).

Life style: free living, mobile. Swimmer, crawler, burrower (Budd and Hughes, 2003)

Family: <u>Nereidae</u> (*i*: 20, *e*: ≈ 3)

Key species: *Nereis longissima* (*i*: 10), *Nereis (=Hediste) diversicolor* (not present in the samples)

Distribution: *N. longissima*: eastern North Atlantic to Mediterranean, Adriatic and Black Seas, Channel and North Sea (Hartmann-Schröder, 1996). Around most British coasts (Nelson-Smith *et al.*, 1990). *N. diversicolor*: the Arctic, North Pacific, North Atlantic to Mediterranean, Adriatic, Black and Caspian Seas, Channel, North and Baltic Seas (Hartmann-Schröder, 1996). Around most British coasts (Nelson-Smith *et al.*, 1990). Restricted to the shallow marine and brackish waters in the North Temperate Zone (Scaps, 2002).

Depth: *N. longissima*: at low water and in the shallow sublittoral (Nelson-Smith *et al.*, 1990), to about 2000 m (Hartmann-Schröder, 1996). *N. diversicolor*: intertidal (Nelson-Smith *et al.*, 1990), from supralittoral to upper sublittoral, about 40 m (Hartmann-Schröder, 1996).

Substrate type: *N. longissima*: in muddy sand or rich mud amongst eel-grass (Nelson-Smith *et al.*, 1990). *N. diversicolor*: inhabits muddy substrata (sandy mud, muddy sand, mud) in a more-or-less permanent U or J-shaped burrow that may be up to 20 cm in depth. Also occurs under stones on mud where the burrow is adjacent to the stone (Budd, 2001a). Burrow depth varies with body size and seasonal variation in burrow depth is correlated with sea temperature (Esselink and Zwarts, 1989).

Coastal/offshore: *N. diversicolor*: coastal; estuary, enclosed coast/embayment, ria/voe (Budd, 2001a).

Densities: *N. longissima*: mean density in the southern North Sea in August 1989: 1 ind. m^{-2} (Bergman and Hup, 1992). Density of *N. diversicolor* may range from 35–3700 ind. m^{-2} dependant upon environmental factors (Scaps, 2002). Numbers of juveniles may be over 100 000 per m^2 (Clay, 1967 cited in Budd, 2001a). In the Ythan Estuary, Scotland, the density of adult *N. diversicolor* was reported to be 961 ind. m^{-2} (Chambers and Milne, 1975). Mean annual density of *N. diversicolor* at Stiffkey salt-marshes (North Norfolk coast, UK.): 392 ind. m^{-2} (Nithart, 1995).

Biomass: The biomass of *N. diversicolor* may range from 13–39 g DW m^{-2} (Scaps, 2002). Mean biomass of *N. diversicolor* at Stiffkey salt-marshes (North Norfolk coast, UK.): 10.26 g DW m^{-2}, annual production: 17.91 g DW m^{-2} (P/B = 1.8) (Nithart, 1995).

Natural mortality: Overwintering and passage of birds (waders and shellduck) may reduce the population of *N. diversicolor* by up to 90% (Evans *et al.*, 1979). In the presence of *Nephtys hombergi*, the density of juvenile *N. diversicolor* was significantly reduced, although the weight of individual *Nereis* did increase (Desroy *et al.*, 1998).

Life span: *N. diversicolor* are 1–3 years old when they spawn. They die shortly afterwards (Scaps, 2002).

Reproduction: *N. diversicolor*: gonochoristic; reproductive frequency: semelparous (breeding only once then dying); fecundity: 1,000–10,000 (Budd, 2001a).

Early development: *N. diversicolor*: larval development is entirely benthic (Chambers and Garwood, 1992; Hartmann-Schröder, 1996). *N. virens*: benthic development with a brief planktonic phase (Chambers and Garwood, 1992).

Feeding ecology: *N. longissima*: deposit feeder; *N. diversicolor*: deposit feeder (feeds on detritus, diatoms, algae), also carnivorous (feeds on other annelids and occasionally on conspecifics, small molluscs) (Hartmann-Schröder, 1996). *N. diversicolor* may be a key organism in the control of phytoplankton in shallow brackish waters. If phytoplankton concentrations are sufficiently high *N. diversicolor* shifts from predatory and surface deposit-feeding to suspension feeding (Riisgård, 1991).

Life style: free-living, mobile. *N. diversicolor*: burrower, swimmer, crawler (Budd, 2001a).

Other information: *N. diversicolor* is an important prey item for wading birds (avocet *Recurvirostra avosetta*, grey plover *Pluvialis squatarola*, curlew sandpiper *Calidris ferruginea*, bar-tailed godwit *Limosa lapponica* and curlew *Numenius arquata*) because it is common, profitable and detectable as well as accessible (Zwarts and Esselink, 1989). *Nereis diversicolor* is also important food flatfish (sole, dab, flounder and plaice) (Budd, 2001a).

Family: <u>Orbiniidae</u> (*i*: 81)

Key species: *Scoloplos armiger* (bristle worm) (*i*: 71), *Orbinia sertulata* (*i*: 11), *O. norvegica* (*i*: 6)

Distribution: *S. armiger*: cosmopolitan, the Arctic, north-west Europe, Indian Ocean, Pacific, Antarctic; west and north of Britain; *O. sertulata*: west of Britain, North Sea, Channel and Atlantic coasts of Europe, Mediterranean (Nelson-Smith *et al.*, 1990). *O. norvegica*: widely distributed (except Arctic and Antarctic); North Sea, Skagerrak, Kattegat (Hartmann-Schröder, 1996).

Depth: *S. armiger*: at low water or in shallow sublittoral (Nelson-Smith *et al.*, 1990), from eulittoral to 2000 m (Hartmann-Schröder, 1996). *O. sertulata*: at low water and in shallow sublittoral (Nelson-Smith *et al.*, 1990). *O. norvegica*: from upper sublittoral to 2900 m depth (Hartmann-Schröder, 1996).

Substrate type: *S. armiger*: in fine muddy sand, often amongst sea-grasses (Nelson-Smith *et al.*, 1990). *O. sertulata*: in clean sand, mixed substrates of sand and mud, with and without shells; also mud and sediments between brown algae and oyster beds; *O. norvegica*: muddy substrates or mixed bottoms: clean sand less common (Hartmann-Schröder, 1996).

Densities: *S. armiger*: mean density in the southern North Sea in August 1989: 9 ind. m^{-2} (Bergman and Hup, 1992). Mean density at Stiffkey salt-marshes (North Norfolk coast, UK.): 978 ind. m^{-2} (Nithart, 1995).

Biomass: *S. armiger*: at Stiffkey salt-marshes (North Norfolk coast, UK.), biomass: 5.74 g DW m^{-2}, production: 1.5 g DW m^{-2}, P/B = 0.3 (Nithart, 1995).

Natural mortality: *S. armiger* was a major prey item for the polychaete *Nephtys hombergii* on tidal flats near the island of Sylt in the North Sea (Schubert and Reise, 1986). Beukema (1987) found a negative relation between biomass and rate of increase in *S. armiger* and abundance *N. hombergii*. *S. armiger* was reported as a regular prey item for the bar-tailed godwits *Limosa lapponica* in the Wadden Sea (Scheiffarth, 2001).

Life span: *S. armiger*: opportunistic and short-lived species (Kröncke, 1991).

Reproduction: *S. armiger*: spawns in the North Sea from March to May (Hartmann-Schröder, 1996)

Early development: *S. armiger*: pelagic larvae; only benthic development within egg cocoons (Plate and Husemann, 1991). *O. sertulata*: probably no pelagic phase (Thorson, 1946 cited in Hartmann-Schröder, 1996).

Feeding ecology: *S. armiger*: non-selective deposit feeder (Reise, 1979b).

Life style: free-living, burrowers, mobile.

Family: Oweniidae (*i*: 71, *e*: 1)

Key species: *Owenia fusiformis* (*i*: 56, *e*: 1), *Myriochele* spp. (*i*: 52)

Distribution: *O. fusiformis*: cosmopolitan, north-west Europe, North Sea, Mediterranean, Indian Ocean, Pacific; all around Britain (Nelson-Smith *et al.*, 1990). *Myriochele* spp.: Arctic, North Pacific, Northeast Atlantic, North Sea, Skagerrak (Hartmann-Schröder, 1996).

Depth: *O. fusiformis*: at low water and in the shallow sublittoral (Nelson-Smith *et al.*, 1990); from eulittoral to depths of about 5000 m (Hartmann-Schröder, 1996). *M. oculata*: from upper sublittoral to bathyal at about 2800 m (Hartmann-Schröder, 1996).

Substrate type: *O. fusiformis*: muddy sand to coarse sand and gravel, mixed bottoms with or without shells (Hartmann-Schröder, 1996). *Myriochele oculata*: clean fine or coarse sand; mixed bottoms, with or without clay (Hartmann-Schröder, 1996).

Coastal/offshore: *A. aculeata*: inshore

Densities: *O. fusiformis*: mean density in the southern North Sea in August 1989: 23 ind. m^{-2} (Bergman and Hup, 1992).

Life span: *O. fusiformis*: longer than 1 year (Sarda *et al.*, 2000)

Reproduction: *O. fusiformis*: in north-west Europe, spawns from spring to early summer; *M. oculata*: in Øresund (Denmark/Sweden), spawning peaks in spring (Hartmann-Schröder, 1996).

Early development: *O. fusiformis, M. oculata*: planktonic larvae (Hartmann-Schröder, 1996)

Feeding ecology: *O. fusiformis*: surface deposit and suspension feeder; feeds on detritus, and microorganisms (Hartmann-Schröder, 1996).

Life style: sessile, tube building, slow mobility.

Family: Pectinariidae (*i*: 45, *e*: ≈ 2)

Key species: *Amphictene auricoma* (*i*: 35, *e*: 2), *Lagis koreni* (*i*: 19, *e*: 2)

Distribution: *A. auricoma*: Arctic, North Pacific, northeast Atlantic to the Bay of Guinea, Mediterranean, Adriatic Sea, Channel, North Sea, western Baltic Sea. *L. koreni*: eastern Atlantic from the Barents Sea to Namibia, Mediterranean, Adriatic and Black Seas, Channel, North Sea, western Baltic Sea (Hartmann-Schröder, 1996)

Depth: *A. auricoma*: at low water and sublittorally (Nelson-Smith *et al.*, 1990), from upper eulittoral to a depth of 500 m in bathyal (Hartmann-Schröder, 1996). *L. koreni*: at very low water (Nelson-Smith *et al.*, 1990), from eulittoral to 500 m depth (Hartmann-Schröder, 1996).

Substrate type: *A. auricoma*: on mixed bottoms of mud and sand (Hartmann-Schröder, 1996). *L. koreni*: on mixed bottoms of mud and fine sand (Hartmann-Schröder, 1996).

Densities: *L. koreni*: adult densities may exceed 1000 per m^2 (e.g. Eagle, 1975) but numbers characteristically fluctuate widely from year to year, owing to variations in recruitment success and mortality. *L. koreni* often co-occurs with high densities of *Abra alba* (Eagle 1975). Population size in southwestern Kiel Bay varied widely from year to year, from <100 adult ind. m^{-2} in autumn of 1973 and 1975 to > 1000 ind. m^{-2} in 1974 (Nichols, 1976). Mean density in the southern North Sea in August 1989: 1 ind. m^{-2} (Bergman and Hup, 1992).

Biomass: *L. koreni*: biomass and production in southwestern Kiel Bay reached highest levels during late summer of 1974 (from 0.7 to 2.5 g C m^{-2} and from 0.5 to 1.0 g C m^{-2} $month^{-1}$ respectively), with highest values recorded at deeper stations (Nichols, 1976).

Natural mortality: *L. koreni* is a significant food-source for commercially important demersal fish, especially dab and plaice (review in Mayhew, 2002). *L. koreni* constituted about 30% of the total diet of plaice in the North Sea (Greenstreet, 1996).

Life span: *A. auricoma*: life-span longer than one year. *L. koreni*: probably lives not longer than one year, and dies after spawning (Hartmann-Schröder, 1996).

Reproduction: *A. auricoma*: in north-west Europe, spawn from summer to early autumn, probably more than once in their lifetime. *L. koreni*: in north-west Europe, spawns from May to August (Hartmann-Schröder, 1996).

Early development: *A. auricoma*: planktonic larvae. *L. koreni*: planktonic larvae, benthic post-larvae (Hartmann-Schröder, 1996).

Feeding ecology: *A. auricoma*: surface deposit feeder. *L. koreni*: surface deposit feeder, feeds on microorganisms such as ciliates, foraminifers, small crustaceans, one-cell algae (Hartmann-Schröder, 1996).

Life style: tube building, slow mobility.

Family: <u>Sabellariidae</u> (*i*: 3, *e*: ≈ 1)

Key species: *Sabellaria spinulosa* (*i*: 3), *S. alveolata* (*e*: 1)

Distribution: *S. spinulosa*: Arctic, North Sea, Channel, Atlantic (Jackson and Hiscock, 2003); all coasts of Britain; locally abundant (Nelson-Smith *et al.*, 1990). *S. alveolata*: Mediterranean, north Atlantic south to Morocco; the British Isles form the northern limits of the distribution in the north east Atlantic (Jackson, 1999a); west and east coasts of Britain, western Ireland; locally abundant (Nelson-Smith *et al.*, 1990).

Depth: *S. spinulosa*: sublittoral (Nelson-Smith *et al.*, 1990), from lower eulittoral to bathyal to 600 m depth (Hartmann-Schröder, 1996). *S. alveolata*: on lower shore and shallow sublittoral (Nelson-Smith *et al.*, 1990), from lower eulittoral to upper sublittoral, to about 26 m depth (Hartmann-Schröder, 1996).

Substrate type: *S. spinulosa*: on rocks and other hard bottoms such as oyster beds, rhizoids of *Laminaria*, and coral reef, furthermore sandy bottoms with shells and some mud (Hartmann-Schröder, 1996). S. spinulosa often settles on *Pecten maximus* and *Buccinum undatum* and occasionally on *Chlamys opercularis.* It has strong settlement preference for tubes or sites currently or previously used by the species (Jackson and Hiscock, 2003). *S. alveolata*: on rocks and various sediments among algae and *Mytilus* (Hartmann-Schröder, 1996); the larvae preferably settle on tubes or sites currently or previously used by the species (Jackson, 1999a).

Coastal/offshore: *S. spinulosa*: open coast, offshore seabed (Jackson and Hiscock, 2003). *S. alveolata*: open coast (Jackson, 1999a).

Densities: *S. spinulosa* can be found in very high densities, e.g. when forming a reef; typically found in lower densities as a crust or even as individuals (Jackson and Hiscock, 2003).

Natural mortality: *S. alveolata*: one of the main causes of colony destruction is through wave action (Jackson, 1999a).

Life span: *S. spinulosa*: usually 2–5 years, possibly up to 9 years (Jackson and Hiscock, 2003). *S. alveolata*: most individuals have a lifespan of 3 to 5 years but there are records for 7 and even 9 year old individuals (Jackson, 1999a).

Reproduction: *S. spinulosa*: gonochoristic; reproductive frequency: annual protracted; fecundity may be similar to *S. alveolata* (Jackson and Hiscock, 2003). Spawns in the summer in the Channel, in the autumn in Ireland. The fertilisation is external (Hartmann-Schröder, 1996). *S. alveolata*: gonochoristic; reproductive frequency: annual protracted; fecundity: 100,000–1,000,000 (Jackson, 1999a).

Early development: *S. spinulosa*: pelagic larvae metamorphose within several weeks after fertilisation and settle upon suitable benthic substrata (Hartmann-Schröder, 1996). *S. alveolata*: pelagic larvae; a relatively long larval life (2–4 months; Wilson, 1970; Jackson, 1999a).

Feeding ecology: *S. spinulosa*: passive suspension feeder; typically feeds on phytoplankton (Jackson and Hiscock, 2003) by means of ciliated tentacles (Hartmann-Schröder, 1996). *S. alveolata*: passive suspension feeder; typically feeds on seston (Jackson, 1999a).

Life style: sessile, tube building.

Other information: *S spinulosa* and *S. alveolata* are hosts for a variety of associated fauna and flora, particularly mussels, barnacles and ephemeral algae (Jackson, 1999a; Jackson and Hiscock, 2003).

Family: Sabellidae (not present in the samples)

Key species: *Sabella pavonina*, *Chone fauveli*, *Fabriciola baltica*, *Myxicola sarsi*.

Distribution: *S. pavonina*: Arctic, northeast Atlantic to the Gulf of Guinea, Mediterranean, Adriatic Sea, Channel, North Sea; South Africa, southern South America (Hartmann-Schröder, 1996); found on all British coasts, with big populations in Menai Strait, Swansea Bay, and estuaries of Essex and Plymouth rivers (Nelson-Smith *et al.*, 1990). *C. fauveli*: Arctic, North Pacific, North Atlantic, northern North Sea, western Baltic Sea (Hartmann-Schröder, 1996); Clyde Sea, Celtic Sea; locally common (Nelson-Smith *et al.*, 1990). *F. baltica*: head of Loch Etive, west Scotland; very abundant. *M. sarsi*: northern species; north and east coasts of Scotland, north-east England, Isle of Man. Fairly common (Nelson-Smith *et al.*, 1990). *M. infundibulum*: widely distributed, but often locally scarce (Avant, 2002b).

Depth: *S. pavonina*: from lower eulittoral to about 1200 m (Hartmann-Schröder, 1996); sublittoral (Nelson-Smith *et al.*, 1990). *C. fauveli*: from eulittoral to bathyal, to depths of 3500 m; *F. baltica*: to 18 m depth (Hartmann-Schröder, 1996). *M. sarsi*: sublittoral (Nelson-Smith *et al.*, 1990). *M. infundibulum*: down to 30 m (Avant, 2002b).

Substrate type: *S. pavonina*: muddy sand, fine sand with shells or gravel; *C. fauveli*: various substrata, from mud to mixed bottoms with shells, gravel and stones (Hartmann-Schröder, 1996). *F. baltica*: sandy, sandy mud; *M. sarsi*: fine muddy sand (Nelson-Smith *et al.*, 1990).

Coastal/offshore: *M. infundibulum*: wave sheltered habitats; the species has a high salinity tolerance (Avant, 2002b).

Densities: *S. pavonina* can be found in high densities (>100 ind. m^{-2}) within sections of channel in Poole Harbour (natural tidal basin located on the central southern coast of England), where the substrate is formed by fine sand or sand-mud mixtures (Dyrynda, 2003).

Biomass: *S. pavonina*: the average annual biomass off the Northumberland coast (NE England) between 1971–1972 was estimated at 21 mg AFDW m^{-2} (Buchanan and Warwick, 1974).

Reproduction: *S. pavonina, C. fauveli*: no information found on reproduction; *F. baltica* spawns in summer; 4–6 big eggs are laid; brood care (?) (Hartmann-Schröder, 1996).

Feeding ecology: *S. pavonina*: deposit feeder, feeds on detritus (Hartmann-Schröder, 1996) and finely sorted plankton (Lewis, 1980). *Chone* spp.: no information found.

Life style: sessile, tube building.

Family: Serpulidae (*i*: 10, *e*: ?)

Key species: *Hydroides norvegica* (*i*: 5, *e*: 24), *Ditrupa arietina* (*i*: 1, *e*: 9), *Pomatoceros triqueter* (*i*: 3, *e*: 8), *Filograna implexa* (*e*: 7), *Serpula vermicularis* (*i*: < 1, e: *1*)

Distribution: *H. norvegica*: north-east Atlantic to the Mediterranean, Adriatic and Black Seas, Channel, North Sea, Danish Straits (Hartmann-Schröder, 1996); common (Nelson-Smith *et al.*, 1990). *S. vermicularis*: widely distributed (except Arctic and Antarctic) (Hartmann-Schröder, 1996); Shetlands, west and south coasts of Britain, western Ireland, and Channel Isles; often abundant (Nelson-Smith *et al.*, 1990*). P. triqueter*: Arctic, north-east Atlantic to the Mediterranean, Adriatic, Black and Red Seas, Channel, North Sea, Danish Straits to the Kiel Bay (Hartmann-Schröder, 1996); abundant (Nelson-Smith *et al.*, 1990).

Depth: *H. norvegica*: from eulittoral to lower bathyal, to 5000 m depth (Hartmann-Schröder, 1996); usually sublittoral (Nelson-Smith *et al.*, 1990). *S. vermicularis*: from eulittoral to mid bathyal, to about 1400 m depth (Hartmann-Schröder, 1996); sublittoral (Nelson-Smith *et al.*, 1990); sublittoral fringe, infralittoral, circalittoral, circalittoral offshore (Hill, 2003a). *P. triqueter*: from eulittoral to about 5000 m (Hartmann-Schröder, 1996); mainly sublittoral (Nelson-Smith *et al.*, 1990).

Substrate type: *H. norvegica*: various substrata from mud, mixed bottoms of gravel, stones, shells and algae, to sandy bottoms (Hartmann-Schröder, 1996); generally on hard substrata (Nelson-Smith *et al.*, 1990). *S. vermicularis*: hard bottoms, corals, algae, sand and shells, gravel (Nelson-Smith *et al.*, 1990; Hartmann-Schröder, 1996); bedrock, boulders, cobbles, pebbles, other species, biogenic reef, artificial (e.g. metal, wood, concrete) (Hill, 2003a). *P. triqueter*: hard bottoms, rocks, stones, *Sabellaria*-reefs, corals (Nelson-Smith *et al.*, 1990; Hartmann-Schröder, 1996)

Coastal/offshore: *S. vermicularis*: in lagoons, inlets, fjords and natural harbours (Nelson-Smith *et al.*, 1990); open coast, offshore seabed, strait/sound, sealoch, estuary (Hill, 2003a).

Densities: *S. vermicularis*: dense aggregations of *S. vermicularis* tubes occur in enclosed and sheltered locations. In the open marine environment the species is not normally gregarious (Hill, 2003a). *D. arietina*: During a series of North Sea demersal fish surveys in 1978–1980, this serpulid polychaete was found in large numbers off the west coast of Shetland. Some local populations had densities of 1000 ind. m^{-2} (Dyer *et al.*, 1982).

Life span: *S. vermicularis*: life span: 2–5 years (Hill, 2003a)

Reproduction: *S. vermicularis*: reproductive frequency: annual episodic; spawning in summer; age at maturity: 1 year (Hill, 2003a). *P. triqueter*: reproductive frequency: annual protracted; in the Channel, spawning mainly in March and April; in the North Sea, in July (Hartmann-Schröder, 1996).

Early development: *H. norvegica*: planktonic larvae; the pelagic phase lasts about 3 weeks (Hartmann-Schröder, 1996). *S. vermicularis*: the length of the planktonic stage is unknown but comparison with other serpulid species suggests it may be between six days and two months (Holt *et al.*, 1997 cited in Hill, 2003a). *P. triqueter*: planktonic larvae; the pelagic phase lasts 3–6 weeks (Hartmann-Schröder, 1996).

Feeding ecology: *H. norvegica*: suspension feeder (Hartmann-Schröder, 1996). *S. vermicularis*: active suspension feeder; typically feeds on detritus (Hill, 2003a) and microorganisms (Hartmann-Schröder, 1996).

Life style: sessile, tube building.

Family: Spionidae (*i*: 98)

Key species: *Spiophanes bombyx* (bristleworm) (*i*: 78), *Spiophanes kroeyeri* (*i*: 44), *Spio filicornis* (*i*: 38), *Aonides paucibranchiata* (*i*: 34), *Minuspio cirrifera* (*i*: 31), *Scolelepis bonnieri* (*i*: 20), *Prionospio malmgreni* (*i*: 11), *Scolelepis tridentata* (*i*: 11), *Laonice sarsi* (*i*: 10), *Pseudopolydora* cf. *pauchibranchiata* (*i*: 9), *Polydora socialis* (*i*: 8), *Scolelepis squamata* (*i*: 6), *Polydora flava* (*i*: 6), *L. cirrata* (*i*: 5), *Pseudopolydora pulchra* (*i*: 5), *Polydora ciliata* (*i*: < 1), *Pygospio elegans* (not present in the samples)

Distribution: *Spiophanes bombyx*: Arctic, North Pacific, North Atlantic to Mediterranean, Channel, North Sea, Skagerrak, Kattegat, South Atlantic, South Pacific, seldom found in tropics. *Spiophanes kroeyeri*: widely distributed, probably cosmopolitan; North Sea, Skagerrak, Kattegat. *Spio filicornis*: Arctic, North and Central Pacific, Mediterranean, Adriatic, Black and Red Seas, Channel, North Sea, Skagerrak, Kattegat, Small Belt and Öresund to Kiel Bay. *A. paucibranchiata*: North Atlantic, Mediterranean, Black Sea, North Sea, Skagerrak, Kattegat. *M. cirrifera*: Arctic, North Atlantic between Iceland and Biscay Bay, Channel, North Sea, Skagerrak, Kattegat. *Scolelepis bonnieri*: Northeast Atlantic, Channel, North Sea, Skagerrak. *Prionospio malmgreni*: presumably cosmopolitan; Arctic, North Pacific, North Atlantic to Mediterranean, Adriatic and Black Seas, North Sea, Skagerrak, Kattegat, Öresund to Kiel Bay, Indopacific, South Africa, Australia, southern South America. *Scolelepis tridentata*: North Atlantic to Mediterranean, and Black Seas, southern North Sea, Skagerrak, Öresund. *L. sarsi*: Northeast Atlantic (Shetland Islands to North Norway), northern North Sea to Skagerrak and Kattegat (Hartmann-Schröder, 1996). *Pygospio elegans*: Arctic, north Pacific, north Atlantic, Mediterranean, Adriatic and Black Seas, Channel, North Sea, Danish Straits, western and northern Baltic Sea, South Africa, Australia (Hartmann-Schröder, 1996); all around the British coast (Nelson-Smith *et al.*, 1990). *Polydora ciliata*: Arctic, Baltic, Mediterranean, Indo-Pacific; all around Britain (Nelson-Smith *et al.*, 1990).

Depth: *Spiophanes bombyx*: at low water (Nelson-Smith *et al.*, 1990), lower eulittoral, sublittoral fringe, infralittoral, 0–60 m (Ager, 2002a), eulittoral, sublittoral, to 1000 m (Hartmann-Schröder, 1996). *Spiophanes kroeyeri*: from upper sublittoral to hadal (5200 m depth). *Spio filicornis*: from eulittoral to upper bathyal, to 400 m depth. *A. paucibranchiata*: from eulittoral to 495 m depth. *M. cirrifera*: in North Atlantic, to 4165 m depth. *Scolelepis bonnieri*: eulittoral, upper and mid sublittoral to 50 m depth. *Prionospio malmgreni*: from eulittoral to hadal, to over 5000 m depth. *Pygospio elegans*: from upper eulittoral to lower sublittoral (Hartmann-Schröder, 1996).

Substrate type: *Spiophanes bombyx*: fine clean sand, sandy mud (Ager, 2002a). *Spiophanes kroeyeri*: mostly muddy bottom, also sandy mud, sand with shells. *Spio filicornis*: coarse sand and *Amphioxus*-sand, fine sand, mixed bottoms with shells, stones and *Zostera*-debris, clean sand. *A. paucibranchiata*: coarse sand, shells and fine gravel, less common on fine sand and soft bottoms. *M. cirrifera*: soft bottoms with mud and an admixture of fine sand, clay and shells. *Scolelepis bonnieri*: sand, muddy sand and in oyster beds of Helgoland. *Prionospio malmgreni*: all types of sediments from coarse sand with shells, mixed bottoms to clean mud, in sediments among mangroves, algae, *Zostera* and corals. *Pygospio elegans*: on shells, gravel, coarse and fine sand, sandy mud, with or without *Zostera*, with some detritus (Hartmann-Schröder, 1996). *Polydora ciliata*: in limestone rock and stones, old shells, or lithothamnia (Nelson-Smith *et al.*, 1990); classified as: epibenthic, epilithic, epizoic (Hill, 2000a).

Coastal/offshore: *Spiophanex bombyx*: open coast, strait/sound, estuary, enclosed coast/embayment, sealoch, open coast (Ager, 2002a). *Spio filicornis*: open coast, strait/sound, enclosed coast/embayment (Ager, 2003a). *Polydora ciliata*: open coast, offshore seabed, strait/sound, estuary, isolated saline water (lagoon), enclosed coast/embayment (Hill, 2000a).

Densities: *Spiophanex bombyx*: mean density in the southern North Sea in August 1989: 496 ind. m^{-2}; *Spio filicornis*: 69 ind. m^{-2}; *Scolelepis bonnieri*: 51 ind. m^{-2} (Bergman and Hup, 1992). *Spiophanex bombyx*: annual mean density at Gravelines, northern France: 130 ind. m^{-2} (Amara *et al.*, 2001). *Spiophanes kroeyeri* and *Prionospio malmgreni*: the average annual population densities off the coast of Northumberland (NE England) between 1971–1972 were 39 and 47 ind. m^{-2}, respectively (Buchanan and Warwick, 1974). *L. cirrata*: 4–10 ind. m^{-2} in the northwestern part of the Irish Sea, on *Nephrops* grounds (Ball *et al.*, 2000).

Biomass: *Spiophanex bombyx*: the average annual biomass in Carmarthen Bay, S. Wales: B = 0.688 g AFDW m^{-2}; annual production: P = 3.345 g AFDW m^{-2}; P/B = 4.86 (Warwick *et al.*, 1978). Annual mean biomass at Gravelines, northern France: 27.2 mg AFDW m^{-2} (Amara *et al.*, 2001). *Spiophanes kroeyeri*: the average annual biomass off the

Northumberland coast between 1971–1972 was 140 mg AFDW m^{-2}; the total production of *S. kroyeri* in the area was 196 mg AFDW m^{-2} y^{-1} (Buchanan and Warwick, 1974).

Natural mortality: *Pygospio elegans* is known to decline in areas where sediments are unstable, either through sediment deposition (Wilson, 1981) or erosion (Zühlke and Reise, 1994). In addition, larvae of *P. elegans* may show high mortality in highly re-suspensible sediments (Rhoads and Young, 1970). Spionidae species occurred in more than 50% of dab stomachs in May–July at Gravelines, northern France (Amara *et al.*, 2001).

Life span: *Spiophanes bombyx*: short life span (Ager, 2002a). *Spio filicornis*: life span: < 1 year (Ager, 2003a). *Polydora ciliata*: life span: < 1 year (Hill, 2000a).

Reproduction: *Spiophanes bombyx*: gonochoristic; reproductive frequency: annual protracted (Ager, 2002a); larvae in the Gullmarfjord (west coast of Sweden) present from April to December (Hannerz, 1956 cited in Hartmann-Schröder, 1996). *Spio filicornis*: gonochoristic; reproductive frequency: annual protracted, fecundity: 100–1,000 (Ager, 2003a); spawning in Gullmarfjord from February to April (Hannerz, 1956 cited in Hartmann-Schröder, 1996). *Scolelepis squamata*: spawning in late spring and June (Hartmann-Schröder, 1996). *Polydora ciliata*: gonochoristic; reproductive frequency: annual protracted; fecundity: 100–10,000 (Hill, 2000a). Spawning period varies, from February until June in northern England. The number of offspring produced per female varied from 200 to 2200 (Gudmundsson, 1985).

Early development: *Spiophanes bombyx*: planktonic larvae (Hannerz, 1956 cited in Hartmann-Schröder, 1996). *Spio filicornis*: larvae develop in maternal tubes and then burrow into the sand (Srikrishnadhas and Ramamoorthi, 1981 cited in Ager, 2003a). *Scolelepis squamata*: planktonic larvae (Hannerz, 1956 cited in Hartmann-Schröder, 1996). *Polydora ciliata*: pelagic larvae, pelagic life from two to six weeks before settling (Fish and Fish, 1996). *Pygospio elegans*: planktonic or benthic larvae (Bolam and Fernandes, 2002)

Feeding ecology: *Spiophanes bombyx*: surface deposit feeder; typically feeds on sediment particles, planktonic organisms, meiobenthic organisms (Dauer *et al.*, 1981). *Spio filicornis*: surface deposit feeder, typically feeds on detritus (Ager, 2003a). *Scolelepis squamata*: selective suspension feeder, feeds on living or dead plankton (Hartmann-Schröder, 1996). *L. cirrata*: surface-feeding detrivorous (Holte and Gulliksen, 1998). *Polydora ciliata*: surface deposit feeder, active suspension feeder; typically feeds on detritus (Hill, 2000a). *Pygospio elegans*: surface deposit feeder, feeds on dead plankton, diatoms (Hartmann-Schröder, 1996).

Life style: sessile, tube building, slow mobility.

Other information: Spionids can be extremely abundant and are often regarded as opportunistic.

Family: <u>Terebellidae</u> (*i*: 46, *e*: ?)

Key species: *Lanice conchilega* (*i*: 13, *e*: 1), *Polycirrus* spp. (indet.) (*i*: 10), *Pista cristata* (*i*: 9), *Polycirrus medusa* (*i*: 9), *Streblosoma intestinalis* (*i*: 8), *Thelepus cincinnatus* (*i*: 5, *e*: 17), *Amphitrite cirrata* (*i*: < 1)

Distribution: *L. conchilega*: northern hemisphere, the Channel, North Sea, Danish Straits (Hartmann-Schröder, 1996); around all coasts of Britain and Ireland (Ager, 2002b). *Polycirrus medusa*: Arctic, north Pacific, north Atlantic to Mediterranean, North Sea, Danish Straits, western Baltic Sea. *Pista cristata*: Arctic, North Pacific, North Atlantic to Mediterranean, Adriatic and Red Seas, Channel, northern North Sea, Skagerrak, Kattegat, northern Öresund. *S. intestinalis*: north-east Atlantic, northern North Sea, Skagerrak and Kattegat. *A. cirrata*: Arctic, North Pacific, North Atlantic southwards to Azores, Mediterranean, Adriatic Sea, whole North Sea, Skagerrak, Kattegat, western Baltic, South Africa, Antarctic (Hartmann-Schröder, 1996).

Depth: *L. conchilega*: from intertidal to about 1,700–1,900 m depth (Hartmann-Schröder, 1996; Ager, 2002b). *Polycirrus medusa*: from eulittoral to more than 1500 m depth. *A. cirrata*: from lower eulittoral to more than 2700 m depth (Hartmann-Schröder, 1996).

Substrate type: *L. conchilega*: mainly sandy bottoms, also sand with shells, gravel, stones and mud (Hartmann-Schröder, 1996); mud beneath stones or rock-crevices (Nelson-Smith *et al.*, 1990); coarse clean sand, fine clean sand, sandy mud, muddy sand (Ager, 2002b). *Polycirrus medusa*: mud and sand, mixed bottoms with shells, gravel, stones, clay or detritus. *A. cirrata*: mud, sand and mixed bottoms of mud, sand and shells; substratum with *Posidonia* and corals, *Sabellaria*-reef (Hartmann-Schröder, 1996).

Coastal/offshore: *L. conchilega*: open coast, offshore seabed, strait/sound, estuary, enclosed coast/embayment (Ager, 2002b).

Densities: *L. conchilega*: at Gravelines, northern France, density in June 1998: 3592 ind. m^{-2}, annual mean density: 1947 ind. m^{-2} (Amara *et al.*, 2001). Mean density in the southern North Sea in August 1989: 355 and 38 ind. m^{-2}, for small and large *L. conchilega*, respectively (Bergman and Hup, 1992). Average abundance of Terebellidae off the north east coast of Anglesey, Liverpool Bay, was 0 and 10.6 ind. per 100 m^2, in April and October 1993, respectively (Kaiser *et al.*, 1998b).

Biomass: *L. conchilega* at Gravelines, northern France: biomass in June 1998: 11249.6 mg AFDW m^{-2}, annual mean biomass: 6328.4 mg AFD m^{-2} (Amara *et al.*, 2001).

Natural mortality: *L. conchilega* at Gravelines, northern France, occurred in more than 50% of plaice stomachs in May–July, in more than 50% of dab stomachs in June and in more than 50% of sole stomachs in July. (Amara *et al.*, 2001). Sediment movements may have large impact on abundances of *L. conchilega* (Zühlke and Reise 1994). Eagle (1975) showed that dramatic decreases in the numbers of *L. conchilega* and associated fauna coincided with severe storms in the shallow sublittoral.

Reproduction: *L. conchilega*: gonochoristic (Ager, 2002b). Spawning mainly occurs in the spring or autumn and may more easily colonise areas during this period (Ferns *et al.*, 2000). Spawning in the German Bight takes place from April to June (Kessler, 1963 cited in Hartmann-Schröder, 1996).

Early development: *L. conchilega*: planktonic larval stage can last for up to 60 days. The larvae can disperse over a great distance, but the degree of dispersal depends on hydrographical regime (Ager, 2002b).

Feeding ecology: *L. conchilega*: active suspension feeder, surface deposit feeder; typically feeds on detritus (Ager, 2002b). *A. cirrata*: surface deposit feeder; feeds on unsorted or roughly sorted detritus (Blegvad, 1914 cited in Hartmann-Schröder, 1996).

Life style: sessile, tube building.

Phylum: Arthropoda

Family: Ampeliscidae (*i*: 57, *e*: ≈ 7)

Key species: *Ampelisca brevicornis* (*i*: 25, *e*: < 1), *A. tenuicornis* (*i*: 23), *A. macrocephala* (*i*: 14, *e*: 6), *A. spinipes* (*i*: 6), *A. gibba* (*i*: 5), *Byblis gaimardi* (*i*: 5, *e*: < 1).

Distribution: *A. brevicornis*: common around all British coasts (Avant, 2002c). *A. macrocephala*: a northern species that extends southwards into the Irish Sea and Celtic Sea on the west, and to the Yorkshire coast on the east; *A. spinipes*: all British coasts; *A. gibba*: recorded from Moray Firth, Channel Islands, and south and west Ireland (Isaac *et al.*, 1990). *B. gaimardi*: North Pacific, North Atlantic, American and European coasts; southern Africa (Lincoln, 1979).

Depth: *A. brevicornis*: on the lower shore and sublittorally to a depth of 200 m (Avant, 2002c). *A. tenuicornis*, *A. macrocephala*, *A. spinipes*: sublittoral; *A. gibba*: sublittoral, usually below 20 m (Isaac *et al.*, 1990). *B. gaimardi*: littoral, or continental shelf (30 to 200 m), or upper bathyal (Myers *et al.*, 2003).

Substrate type: *A. brevicornis*: most common in fine or muddy sand mixed with shell, but also found in coarse sand and gravel (Avant, 2002c). *A. tenuicornis*: on fine silty sediments; *A. macrocephala*: on muddy sublittoral sands; *A. spinipes*: on coarse sand and mixed bottoms; *A. gibba*: on mud and muddy sand (Isaac *et al.*, 1990).

Coastal/offshore: *A. brevicornis*: coastal (Avant, 2002c).

Densities: *A. brevicornis*: in Hevring Bay, western Kattegat: 1091 m^{-2} in 2001 (Sømod, 2002), 100 m^{-2} in 2002 (Sømod, 2003). The average abundance of *A. spinipes* off the north east coast of Anglesey, Liverpool Bay, varied in 1993 from 0 in April to 5.4 ind. per 100 m^2 in October (Kaiser *et al.*, 1998b).

Biomass: *A. brevicornis*: The annual production at Derbyhaven Beach, Isle of Man, ranged from 1.31 g DW m^{-2} (12.54 kJ m^{-2}) to 1.68 g DW m^{-2} (18.98 kJ m^{-2}) with a *P*:*B* ratio of 2.49 to

3.21 (Hastings, 1981). *A. brevicornis* in Hevring Bay, western Kattegat in 2001: 1.68 g DW m^{-2} (Sømod, 2002).

Natural mortality: *A. brevicornis*: a substantial part of the production at Derbyhaven Beach is probably consumed by young flatfish (Hastings, 1981). *A. tenuicornis*: Sheader (1998) assessed the grazing impact for a population of *A. tenuicornis* off the east coast of the Isle of Wight, England. Although grazing on the population was high, rapid regeneration and compensatory feeding appeared to minimise the impact.

Reproduction: *A. brevicornis* at Derbyhaven Beach was univoltine (producing one generation per year), breeding annually from May to September (Hastings, 1981). *A. brevicornis* in the English Channel showed an intermediate reproductive cycle between univoltism and bivoltism (two generations per year). The reproductive period extended from April–May to October–December (Dauvin, 1988a). *A. tenuicornis* from the English Channel was found to have a bivoltine cycle with breeding extending from June to October (Dauvin, 1988b). Powell and Moore (1991) observed a biennial life cycle in *A. macrocephala* in the Clyde Sea area.

Life style: free-living, highly mobile.

Family: <u>Axiidae</u> (*i*: 1)

Key species: *Calocaris macandreae* (*i*: 1).

Distribution: *C. macandreae*: from Iceland and Norway to Mediterranean; also North America, Arabian Gulf, Indian Ocean, and Pacific; western coasts of British Isles (Moyse and Smaldon, 1990).

Depth: *C. macandreae*: at 35–1400 m (Moyse and Smaldon, 1990).

Substrate type: *C. macandreae*: burrows in muddy sediments with high silt-clay fractions. The species does not occur in sandy substrata (Buchanan, 1963).

Densities: *C. macandreae*: the average annual population density off the coast of Northumberland (NE England) between 1971–1972 was 10 ind. m^{-2} (Buchanan and Warwick, 1974), and was found very stable at about 18 ind. m^{-2} over a period of ten years (Buchanan, 1974). Densities of <0.1–0.4 burrow systems per m^2 were reported by Hughes and Atkinson (1997) in the north-eastern Irish Sea.

Biomass: *C. macandreae*: the average annual biomass off the Northumberland coast between 1971–1972 was 1205 mg AFDW m^{-2}. *C. macandreae* was the single biomass dominant (30% of the total biomass). The total production of C. macandreae in the area was estimated at 142 mg AFDW m^{-2} y^{-1} (Buchanan and Warwick, 1974).

Natural mortality: *C. macandreae*: reduced predation due to deep burrowing. Mortality of a year group is almost wholly confined to the 9th and 10th year (Buchanan, 1974). *C. macandreae* has been found in the stomachs of cod and haddock (Buchanan, 1963). *Nephrops norvegicus* has been observed to prey on *C. macandreae* (Smith, 1988).

Life span: *C. macandreae* are long-lived (9–10 years) and slow growing (Buchanan, 1963; 1974).

Reproduction: *C. macandreae* is a protandrous hermaphrodite (initially male, becoming female in later life) producing eggs between January and February that hatch between September and October. Approximately 100 eggs are produced in each batch. *C. macandreae* does not mature until five years of age, and only produces two or three batches of eggs in a lifetime (Buchanan,1963; 1974).

Early development: *C. macandreae*: the large larvae have no free-swimming phase before settlement (Buchanan,1963; 1974).

Feeding ecology: *C. macandreae* constructs a system of U-shaped tunnels, which may reach a depth of 21 cm (Nash *et al.*, 1984). The shrimp is principally a deposit feeder. The diet consists of a mixture of organic (diatoms, dinoflagellates, algal and terrestrial plant fragments, and material of animal origin) and fine inorganic fragments. *C. macandreae* showed little evidence of food selectivity (Pinn *et al.*, 1998a).

Life style: burrower.

Family: Callianassidae (*i*: 19)

Key species: *Callianassa subterranea* (*i*: 16) (mud shrimp)

Distribution: *C. subterranea*: southern coasts of British Isles, common; elsewhere southwards, probably to Mediterranean (Moyse and Smaldon, 1990); abundant in the southern North Sea (Witbaard and Duineveld, 1989; Rowden and Jones, 1994).

Depth: *C. subterranea*: from low water spring tide down to 20 m (Moyse and Smaldon, 1990). Sublittoral fringe, infralittoral, circalittoral (Hill, 2001). In the North Sea, *C. subterranea* is restricted to water depths of between 30–50 m (Rowden *et al.*, 1998).

Substrate type: *C. subterranea*: burrows in sandy mud (Moyse and Smaldon, 1990).

Coastal/offshore: *C. subterranea* inhabits offshore muddy sands, and is less frequent in coarse sediments closer inshore. Open coast, offshore seabed, strait/sound, sealoch, enclosed coast/embayment (Hill, 2001).

Densities: The density of *C. subterranea* varied between 2 and 60 ind. m^{-2} in the southern North Sea (Künitzer *et al.*, 1992). Rowden and Jones (1994) observed densities from 38 to 59 ind. m^{-2} at a fixed station in the central North Sea. Densities of about 20 ind. m^{-2} were reported for offshore muddy sands, and 4 burrows m^{-2} for inshore muddy sands in the north-eastern Irish Sea (Hughes and Atkinson, 1997).

Life span: *C. subterranea*: 2–3 years (Hill, 2001).

Reproduction: *C. subterranea*: gonochoristic; reproduction frequency: biannual (every second year) episodic (Hill, 2001). Reproduction in the North Sea (based on the presence of ovigerous females) extended from April to September with a peak in July (Rowden and Jones, 1994).

Early development: *C. subterranea*: newly-hatched larvae live for about four weeks in the plankton before being recruited to the benthic population (Hill, 2001).

Feeding ecology: *C. subterranea* is a burrowing sub-surface deposit feeder and typically feeds on organic content of sediment particles (Hill, 2001).

Lifestyle: semimobile burrower.

Other information: *C. subterranea*: builds a complex lattice of horizontal tunnels connected to the surface via one or a few vertical ones (Atkinson and Nash, 1990; Nickell and Atkinson, 1995). Burrows in mud are relatively simple and deep (30–81 cm) (Rowden and Jones, 1997). In coarser North Sea sediments, *C. subterranea* constructs a different burrow with multiple funnel-shaped surface openings (Rowden and Jones, 1995; Witbaard and Duineveld, 1989). These differences may be related to the associated food content of the substratum.

Family: Cancridae (*e*: 3)

Key species: *Cancer pagurus* (*e*: 3) (edible crab, brown crab)

Distribution: *C. pagurus*: north Norway to West Africa, Mediterranean; abundant on all British coasts (Moyse and Smaldon, 1990).

Depth: *C. pagurus*: mid-tide to shallow sublittoral at 100 m (Moyse and Smaldon, 1990). In some years, fishermen report large amounts of edible crab captured in nets at depths of 300–400 m.

Substrate type: *C. pagurus*: rocky (Moyse and Smaldon, 1990) or sandy grounds (Muus and Dahlstrøm, 1985). Juvenile crabs are often found in kelp forests (Woll and Van der Meeren, 1997).

Reproduction: *C. pagurus*: The female lays 0.5–3 million eggs in autumn and carries them during the winter (Muus and Dahlstrøm, 1985).

Early development: *C. pagurus*: The eggs hatch in the summer into pelagic larvae. After 1–2 months they settle on the bottom (Muus and Dahlstrøm, 1985), typically in kelp forests (Woll and Van der Meeren, 1997).

Feeding ecology: *C. pagurus*: scavenger (Nickell and Moore, 1992b), but large individuals seem to prefer soft bottom fauna, such as infaunal mussels and polychaetes (Moen, 2003). *C. pagurus* is a major predator on the scallop *Pecten maximus* and has been identified as the major impediment to the development of scallop seabed cultivation in Norway (Strand *et al.*, 1999). Suspension feeding has been observed in *C. pagurus* from the Swedish west coast (Havsfiskelaboratoriet, 1996).

Life style: free living, mobile.

Family: Corophiidae (*i*: 24)

Key species: *Corophium volutator* (not present in the samples), *Unciola planipes* (*i*: 12)

Distribution: *C. volutator*: North Atlantic (American and European coasts), Norway to Mediterranean, Black Sea, Azov Sea (Myers *et al.*, 2003); all British coasts (Isaac *et al.*, 1990). *U. planipes*: a northern species (Isaac *et al.*, 1990).

Depth: *C. volutator*: intertidal; *U. planipes*: sublittoral (Isaac *et al.*, 1990).

Substrate type: *C. volutator*: burrows in mud (Isaac *et al.*, 1990).

Coastal/offshore: *C. volutator*: mud flats, salt marsh pools and brackish ditches (Avant, 2003).

Densities: *C. volutator*: maximum densities of 2077 ind. m^{-2} were observed in the Humber estuary (Jones and Ratcliffe, 1979). The species may reach densities up to 100,000 ind. m^{-2} on intertidal mudflats during summer period (Flach, 1992b).

Natural mortality: *C. volutator* is the main food of several small shorebird species in the intertidal (Evans *et al.*, 1998). *C. volutator* was found to be extensively preyed by the sand goby *Pomatoschistus minutus*, which occurs seasonally in high densities in shallow water and intertidal sediments in the Ythan estuary, Aberdeenshire, U.K. (Jaquet and Raffaelli, 1989). It was also the main prey item of the flounder *Platichthys flesus* on the mudflats of the upper part of the Ythan estuary (Summers, 1980).

Reproduction: *C. volutator*: Females from the Bay of Fundy, Nova Scotia, can lay between 10 and 172 eggs, depending on their size. The fecundity of *C. volutator* in Europe is generally lower. The eggs are fertilised and develop in brood sacs (Percy, 1999).

Early development: *C. volutator*: ‘direct development’, the newly hatched animals resemble adults (Percy, 1999).

Feeding ecology: *C. volutator*: unselective surface deposit feeder, also suspension feeder, feeding on diatoms and bacteria (Gerdol and Hughes, 1994a, b); occupies semi-permanent U-shaped burrows (Avant, 2003).

Life style: *C. volutator*: burrower, semimobile (Lawrie and Raffaelli, 1998).

Family: Corystidae (*i*: 8, *e*: 24)

Key species: *Corystes cassivelaunus* (masked crab, helmet crab) (*i*: 8, *e*: 24)

Distribution: *C. cassivelaunus*: from Sweden to Portugal, Mediterranean; all British coasts, very common (Moyse and Smaldon, 1990).

Depth: *C. cassivelaunus*: found from the lower shore and shallow sublittoral to about 100 m (Skewes, 2001).

Substrate type: *C. cassivelaunus*: sandy and soft bottoms (Moyse and Smaldon, 1990), typically found in burrows (Skewes, 2001).

Densities: *C. cassivelaunus*: mean density in the southern North Sea in August 1989: 1 ind. m^{-2} (Bergman and Hup, 1992).

Reproduction: *C. cassivelaunus*: breeding season from April to June (Hartnoll, 1972).

Early development: *C. cassivelaunus*: incubation takes up to 10 months; pelagic larvae hatch in March and April (Hartnoll, 1972).

Feeding ecology: *C. cassivelaunus*: the food consists almost entirely of burrowing invertebrates, predominantly lamellibranchs, polychaetes and amphipods (Hartnoll, 1972).

Life style: *C. cassivelaunus*: free living, burrower.

Family: Crangonidae (*e*: ?)

Key species: *Crangon allmanni* (*e*: 46), *C. crangon* (brown shrimp, sand shrimp) (*e*: 14), *Pontophilus spinosus* (*e*: 14)

Distribution: *C. allmanni*, *C. crangon*: all coasts; *P. norvegicus*: northern and western coasts (Moyse and Smaldon, 1990).

Depth: *C. allmani*: sublittoral, 10–250 m, *C. crangon*: from mid-tide level to about 50 m, *P. norvegicus*: sublittoral, 50–500 m (Moyse and Smaldon, 1990).

Densities: *C. allmani* was reported as the most frequent species in the group Natantia during the benthos surveys in the northern North Sea between 1980–1985 (Basford *et al.*, 1989). *C. crangon*: Beyst *et al.* (2001) reported average monthly catches varying from <1 to 649 ind. per 100 m^2 in the surf zone of sandy beaches of the Belgian coast (in the Southern Bight) in the period May 1996–July 1997. Yearly average catches varied from 145 to 249 ind. per 100 m^2 at four different locations (Beyst *et al.*, 2001).

Natural mortality: *C. crangon*: Tiews (1978) found that among the main predators preying on the brown shrimps in the German coastal waters were the armed bullhead, gobies, gastropods, whiting, cod and dab. These species contributed to 93.5% of the total number of prey consumed. Oh *et al.* (1999) estimated the natural mortality in Port Erin Bay (Isle of Man, Irish Sea) at 3.6 $year^{-1}$.

Life span: *C. crangon*: 3–4 years (Muus and Dahlstrøm, 1985). Oh *et al.* (1999) estimated the life span for the population in Port Erin Bay at 3.3 years.

Reproduction: *C. crangon*: protandrous hermaphrodites (initially males, becoming females in later life); the female lays 2,000–14,000 eggs two or three times a year, and carries them attached to the abdomen (Muus and Dahlstrøm, 1985).

Early development: *C. crangon*: the larvae are free-swimming until they are about 10 mm long (Muus and Dahlstrøm, 1985). Recruitment of juveniles in the German and Dutch Wadden Sea occurs in May/June; they are presumed to grow into the exploitable stock by the autumn (Temming and Damm, 2002).

Feeding ecology: *C. crangon*: the diet consists of invertebrates, detritus and algae (Muus and Dahlstrøm, 1985). Mysids and amphipods together constituted the dominant prey in *C. crangon* in Port Erin Bay, accounting for >60% of the diet. Larger shrimps preyed on 0-group fish co-occurring in the study area, mainly plaice *Pleuronectes platessa*, dab *Limanda limanda* and sandeel *Ammodytes tobianus* (Oh *et al.*, 2001).

Life style: free living.

Family: Galatheidae (*i*: 2, *e*: ?)

Key species: *Galathea dispersa* (*e*: 7), *G. intermedia* (*i*: 2, *e*: 7), *Munida rugosa* (squat lobster) (not present in the samples)

Distribution: *G. dispersa*: Norway and south Iceland to Madeira and Canaries, Mediterranean; all British coasts, common. *M. rugosa*: Norway to Madeira, Mediterranean; all British coasts, fairly common. *G. intermedia*: Norway to Dakar and Mediterranean; all British coasts, very common (Moyse and Smaldon, 1990). *G. intermedia* is a very common species in all deeper parts of the German Bight, particularly near the island of Helgoland (Caspers, 1950 cited in Christiansen and Anger, 1990).

Depth: *G. dispersa*: sublittoral, depths of 10–500 m. *G. intermedia*: sublittoral, 15–20 m (exceptionally 35 m). *M. rugosa*: from low water spring tide to 150 m (Moyse and Smaldon, 1990).

Substrate type: *G. intermedia*: often among mollusc shells (Caspers, 1950 cited in Christiansen and Anger, 1990). *M. rugosa*: stony bottoms (Moyse and Smaldon, 1990).

Early development: *G. intermedia*: meroplanktonic stages occur near Helgoland from June through October (Fiedler, 1987 cited in Christiansen and Anger, 1990).

Life style: free living, mobile.

Family: Laomediidae (not present in the samples)

Key species: *Jaxea nocturna*

Distribution: *J. nocturna*: south to the Mediterranean, particularly in the Adriatic (Moyse and Smaldon, 1990).

Depth: *J. nocturna*: sublittoral, 10–50 m (Moyse and Smaldon, 1990).

Substrate type: *J. nocturna*: burrows in mud (Moyse and Smaldon, 1990).

Densities: *J. nocturna*: Densities of <0.1–1.5 burrow systems per m^2 were reported by Hughes and Atkinson (1997) in the north-eastern Irish Sea.

Feeding ecology: *J. nocturna*: re-suspension feeder, i.e. the shrimp-flicks up deposited material ahead of the mouthparts and suspension feeds (Pinn *et al.*, 1998b). The shrimp may also scavenge organic material from the sediment surface (Nickell and Atkinson, 1995).

Life style: free living, burrower.

Other information: The burrow of *J. nocturna* is relatively persistent with a wide spiralling shape. Burrow depths of 92 cm have been recorded (Nickell and Atkinson, 1995).

Family: Majidae (*i*: 3, *e*: ?)

Key species: *Hyas coarctatus* (toad crab) (*i*: 2, *e*: 35), *Macropodia rostrata* (*e*: 16)

Distribution: *H. coarctatus*: Spitzbergen and Norway to Brittany, also Greenland and North America. *M. rostrata*: Norway to West Africa, Azores, Mediterranean. Both are common on all British coasts (Moyse and Smaldon, 1990). *H. araneus* is a more northern species and is less frequent in the North Sea than *H. coarctatus* (Dyer, 1985).

Depth: *H. coarctatus*: from low water spring tide to 50 m. *M. rostrata*: shallow sublittoral, 4–90 m (Moyse and Smaldon, 1990). *H. coarctatus* in the eastern central North Sea was observed attached to the bryozoan *Flustra foliacea* (Dyer, 1985).

Substrate type: *H. coarctatus*: on hard and sandy bottoms. *M. rostrata*: on hard or mixed substrata (Moyse and Smaldon, 1990).

Reproduction: *H. coarctatus* produces a single brood per year. Egg number was found to be positively correlated with maternal body weight (Bryant and Hartnoll, 1995).

Early development: *H. coarctatus* has a life cycle with a planktonic larval phase of several weeks. Larval dispersal can therefore be considerable (Weber *et al.*, 2000).

Life style: free living.

Family: Nephropidae (*i*: < 1, *e*: 11)

Key species: *Nephrops norvegicus* (Norway lobster) (*e*: 11)

Distribution: *N. norvegicus*: Norway and Iceland to Morocco and Mediterranean; all coasts of the British Isles, common (Moyse and Smaldon, 1990).

Depth: *N. norvegicus*: found sublittorally at 200–800 m, occasionally as shallow as 20 m (Moyse and Smaldon, 1990; Hill, 2003b).

Substrate type: *N. norvegicus*: in shallow burrows, in soft sediments, common on grounds with fine cohesive mud which is stable enough to support their unlined burrows (Moyse and Smaldon, 1990, Hill, 2003b).

Densities: *N. norvegicus*: Densities of up to 68 burrows per 100 m^2 were reported by Dyer *et al.* (1982) in deep offshore waters in the North Sea, based on underwater photographs. Densities of about 1 burrow system per m^2 were reported by Hughes and Atkinson (1997) in the north-eastern Irish Sea (0.6–1.6 burrow m^{-2}) and by Tuck *et al.* (1997) in a region of the Firth of Clyde, SW Scotland (0.6–1.3 burrow m^{-2}).

Feeding ecology: Cristo and Cartes (1998) reported the major groups observed in the stomachs of *N. norvegicus* to be decapods, other crustaceans (euphausiids and peracarids) and fish.

Life style: free living, burrower.

Family: Paguridae (*e*: ?)

Key species: *Pagurus bernhardus* (*e*: 87), *Anapagurus laevis* (*e*: 38), *P. pubescens* (*e*: 34), *P. prideaux* (*e*: 24)

Distribution: *P. bernhardus*: from Iceland and Norway to Portugal; very common off all British coasts. *A. laevis*: from Norway to Senegal, Azores, Mediterranean; very common on all British coasts. *P. pubescens*: a northern species; Norway, Iceland, north and west coasts of Britain, including Irish Sea. *P. prideaux*: Norway to Cape Verde, Mediterranean; all British coasts, locally very common (Moyse and Smaldon, 1990).

Depth: *P. bernhardus*: from mid-tide level to 140 m (occasionally 500 m). *A. laevis*: 20–200(400) m. *P. pubescens*: 8–500(1000) m. *P. prideaux*: from low water spring tide to 40 m (exceptionally 400 m) (Moyse and Smaldon, 1990).

Substrate type: *P. bernhardus*: on rocky and sandy substrata. *A. laevis*: on substrata of muddy sand and gravel. *P. pubescens*: sand, mud or rock. *P. prideaux*: on sand, mud or gravel (Moyse and Smaldon, 1990).

Densities: *P. bernhardus* was the most widely distributed decapod crustacean in the northern North Sea during the benthos surveys in 1980–1985 (Basford *et al.*, 1989).

Life style: free living.

Family: <u>Pandalidae</u> (*e*: ?)

Key species: *Pandalus montagui* (*e*: 31), *P. borealis* (*e*: 16), *Dichelopandalus bonnieri* (*e*: 10)

Distribution: *P. montagui*: all British coasts. *P. borealis*: north-east coast of Britain only. *D. bonnieri*: less common in the North Sea, not in the Channel; south and west coasts of Britain (Moyse and Smaldon, 1990).

Depth: *P. montagui*: sublittoral, 5–230 m. *P. borealis*: sublittoral, 20–600 m. *D. bonnieri*: sublittoral, 33–400 m (Moyse and Smaldon, 1990).

Substrate type: *P. boralis*: lives on soft bottoms (Muus and Dahlstrøm, 1985)

Biomass: *P. borealis*: estimates of the total biomass have been done by ICES Pandalus Assessment Working Group, based on the total weight of shrimp caught per hour (ICES, 2003d).

Natural mortality: *P. borealis* are preyed upon by numerous predators, predominantly for fish (Muus and Dahlstrøm, 1985). The main predators in the North Sea are: gadoids, redfishes, halibut, long rough dab, skates, rayfish and dogfish (ICES, 2003d). *P. borealis* was the most important prey for two benthopelagic fish species, roundnose grenadier *Coryphaenoides rupestris* and great silver smelt *Argentina silus*, inhabiting the 300–700 m deep shelf of the central Skagerrak (Bergstad *et al.*, 2001). The natural mortality for *P. borealis* in the North Sea is likely to be substantially higher than the fishing mortality and can fluctuate considerably in relation to predator abundance. It was assumed to be constant at 0.75 in most of the assessments until 1999 (ICES, 2003d).

Life span: *P. borealis*: a short lived species; age groups up to 3 years are found in the catches (ICES, 2003d).

Reproduction: *P. borealis*: a protandrous hermaphrodite that shows a great variation in both age at sex change and in the proportion of males that become females. This plasticity is believed to be a phenotypic response to maximize individual reproductive success (Hansen and Aschan, 2001). In Europe, mating takes place in the autumn. The fertilisation is internal. Fecundity: 1000–3000 eggs (Muus and Dahlstrøm, 1985).

Early development: *P. borealis*: pelagic larvae (Muus and Dahlstrøm, 1985).

Feeding ecology: *P. borealis*: omnivorous. The food is obtained from the macroplankton as well as the macrozoobenthos. Meiofauna and detritus are of less importance in the diet. *P. borealis* have a nocturnal feeding activity phase during which they consume mainly plankton. During the day, they ingest benthic species. The males feed on plankton in the pelagic zone more actively than do females (Winberg, 1981).

Life style: free living, mobile.

Family: Portunidae (*i*: 5, *e*: ?)

Key species: *Liocarcinus holsatus* (*i*: 3. *e*: 53), *L. depurator* (*i*: < 1, *e*: 23)

Distribution: *L. holsatus*: north Norway to Spain and Canaries, not in the Mediterranean; widespread and often very common on all British coasts. *L. depurator*: Norway to West Africa, Mediterranean (Moyse and Smaldon, 1990).

Depth: *L. holsatus*: 6–350 m. *L. depurator*: low water spring tide to 450 m (Moyse and Smaldon, 1990).

Substrate type: *L. holsatus*: on hard and mixed bottoms. *L. depurator*: Norway to West Africa, Mediterranean (Moyse and Smaldon, 1990).

Life style: free living, mobile.

Family: Upogebidae (not present in the samples)

Key species: *Upogebia deltaura*

Distribution: *U. deltaura*: Norway to Spain and Mediterranean, and Black Sea, perhaps all coasts of British Isles, common (Moyse and Smaldon, 1990).

Depth: *U. deltaura*: low water spring tide to 40 m (Moyse and Smaldon, 1990).

Substrate type: *Upogebia* spp. are usually found in sands or muddy sands with mixtures of stones or shell gravel (Hughes, 1998a). *U. deltaura*: uses burrows made by other megafaunal burrowers (Moyse and Smaldon, 1990).

Densities: *U. deltaura*: Densities of 3.3 burrow systems per m^2 were reported by Hughes and Atkinson (1997) in the north-eastern Irish Sea in inshore muddy sands.

Feeding ecology: *Upogebia* spp.: suspension-feeders, actively pumping water through their burrows and filtering out particulate matter (Dworschak, 1981).

Life style: Free living, burrower, semimobile.

Phylum: Bryozoa

Family: Alcyonidiidae (*e*: ?)

Key species: *Alcyonidium diaphanum* (*e*: 24), *A. parasiticum* (*e*: 19)

Distribution: *A. diaphanum*: all coasts, generally common (Ryland, 1990).

Depth: *A. diaphanum*: low water spring tide and shallow water; may be washed up; occasionally present sublittorally in great quantity (Ryland, 1990).

Substrate type: *A. diaphanum*: attached to stones and boulders, or detached (Ryland, 1990).

Life style: sessile.

Other information: *A. diaphanum*: apparently responsible for alergic dermatitis 'Dogger Bank Itch' in the North Sea (Ryland, 1990).

Family: <u>Flustridae</u> (*i*: < 1, *e*: ?)

Key species: *Flustra foliacea* (*i*: < 1, *e*: 32), *Securiflustra securifrons* (*e*: 10)

Distribution: *F. foliacea*: all coasts, common (Ryland, 1990).

Depth: *F. foliacea*: in shallow water (Ryland, 1990).

Substrate type: *F. foliacea*: on stones and shells, dead colonies often washed up (Ryland, 1990).

Densities: During the North Sea demersal fish surveys in 1978–1980, *F. foliacea* was reported in trawl catches throughout the central and northern North Sea. In the region of Forth, the population ranged from 22 to 68 colonies per 100 m^2 (Dyer *et al.*, 1982).

Life style: sessile.

Phylum: Cnidaria

Class: <u>Hydrozoa</u> (*e*: ?)

Key species: *Dicoryne conferta* (*e*: 6), *Obelia longissima* (*e*: 4)

Distribution: *D. conferta*: Barents Sea to southern Africa; scattered records around British Isles, mostly northerly. *O. longissima*: probably near-cosmopolitan; all British coasts (Cornelius *et al.*, 1990).

Depth: *D. conferta*: 5–300 m. *O. longissima*: intertidal pools to about 30 m or more (Cornelius *et al.*, 1990).

Substrate type: *D. conferta*: on shells of living gastropods and empty ones with or without hermit crabs. *O. longissima*: on plant and inert substrata, including rock and sand (Cornelius *et al.*, 1990).

Life style: sessile.

Order: <u>Pennatulacea</u>, families: Pennatulidae, Virgulariidae (sea pens) (Class: Anthozoa) (*i*: 2, *e*: 14)

Key species: *Pennatula phosphorea* (*e*: 14), *Virgularia mirabilis* (not present in the samples)

Distribution: *P. phosphorea*: widespread in north Atlantic; on all British coasts except south, local (Cornelius *et al.*, 1990).

Depth: *P. phosphorea*: below about 15 m (Cornelius *et al.*, 1990).

Substrate type: *P. phosphorea, V. mirabilis*: living erect in mud or sand (Cornelius *et al.*, 1990). They construct large, long-lasting burrows in the bottom sediments (Hughes, 1998a).

Coastal/offshore: *P. phosphorea*, *V. mirabilis*: sheltered inshore waters (e.g. sea lochs) (Hughes, 1998a).

Densities: *P. phosphorea*: Dyer *et al.* (1982) reported that this pennatulid was rarely caught in the trawls during the North Sea demersal fish surveys in 1978–1980. The underwater photographs showed that it was common throughout the northern North Sea at depths > 100 m. Particularly large populations were found in the Norwegian Trench (182 ind. per 100 m^2) and in the Farne Deeps (66 ind. per 100 m^2) (Dyer *et al.*, 1982).

Life span: *P. phosphorea*, *V. mirabilis* are likely to be long-lived, but there are no more details on their life span (Hughes, 1998a).

Reproduction: *P. phosphorea*, *V. mirabilis*: gonochoristic; each colony of polyps is either male or female (Hughes, 1998a).

Feeding ecology: *P. phosphorea*, *V. mirabilis*: suspension-feeders, living on plankton and organic particles captured by the polyp tentacles (Hughes, 1998a).

Life style: sessile; burrower (Hughes, 1998a).

Family: <u>Caryophyllidae</u> (*e*: 6) (Class: Anthozoa)

Key species: *Lophelia pertusa* (not in the samples), *Caryophyllia smithii* (*e*: 6)

Distribution: *L. pertusa*: Patchily distributed in the north-east Atlantic (Wilson, 1979b); records in Britain are from west Scotland and Ireland (Pecket, 2003). *C. smithii*: north-east Atlantic to south-west Europe and Mediterranean; all British coasts except eastern England (Cornelius *et al.*, 1990).

Depth: *L. pertusa*: usually at great depths (>150 m) and occasionally in shallower inshore waters (Pecket, 2003). *C. smithii*: low water spring tide in south and west to about 100 m where often in great abundance (Cornelius *et al.*, 1990).

Substrate type: *L. pertusa*: usually occurs on soft bottoms, rarely found attached to solid substrata; also known from the North Sea attached to oil industry structures (Pecket, 2003). *C. smithii*: on rocks and shells (Cornelius *et al.*, 1990).

Coastal/offshore: *L. pertusa*: mainly off the continental shelf, also in inshore waters in Scotland (Pecket, 2003).

Densities: *L. pertusa*: high densities of up to nine reefs per km^2 were found in areas off the coasts of mid-Norway. The area covered by individual reefs varied between 1,230 m^2 and 37,310 m^2 with a mean of 5,628 m^2 (Mortensen *et al.*, 2001). The density of reefs is dependent on the sea floor topography. The latter has an important effect on current velocity and concentration of food particles (Mortensen, 2000).

Feeding ecology: *L. pertusa*, *C. smithii*: suspension feeders.

Life style: sessile.

Other information: *C. smithii*: an epizoic barnacle, *Megatrema anglicum* is commonly attached to the corallum (Cornelius *et al.*, 1990).

Phylum: Echinodermata

Family: Amphiuridae (*i*: 68, *e*: ≈ 5)

Key species: *Amphiura filiformis* (*i*: 66, *e*: 4), *Acrocnida brachiata* (*i*: 8, *e*: 1), *Amphiura chiajei* (*i*: 5, *e*: 3), *Amphipholis squamata* (*i*: < 1), *Amphiura securigera* (*i*: < 1)

Distribution: *Ampiura filiformis*: widespread, western Norway to the Mediterranean; common off all British coasts. *Acrocnida brachiata*: recorded from western coasts of Britain and Ireland, and from western edge of the Dogger Bank (Moyse and Tyler, 1990). *Amphiura chiajei*: from western Norway (Trondhjemfjord), southwards along European coasts to the Mediterranean, the west coast of North Africa, and the Azores (Moyse and Tyler, 1990; Budd, 2002a). *Amphipholis squamata*: cosmopolitan in temperate and warm temperate seas; common around Britain. *Amphiura securigera*: ranges northwards to Faroes and the Lofoten Isles; recorded sporadically off northern and western coasts of Britain (Moyse and Tyler, 1990).

Depth: *Ampiura filiformis*: sublittoral (Moyse and Tyler, 1990), 15–100 m (Hill and Wilson, 2001). *Acrocnida brachiata*: littoral and sublittoral (Moyse and Tyler, 1990). *Amphiura chiajei*: upper and lower circalittoral, bathyal; 10– > 100 m (Budd, 2002a). *Amphipholis squamata*: mid- and lower littoral, and sublittoral (Moyse and Tyler, 1990).

Substrate type: *Amphiura filiformis*: sandy mud, muddy sand (Hill and Wilson, 2001). *Acrocnida brachiata*: fine sand (Moyse and Tyler, 1990). *Amphiura chiajei*: muddy sand, mud (Budd, 2002a). *Amphipholis squamata*: mainly under stones and shell, and occasionally on sandy bottoms (Moyse and Tyler, 1990).

Coastal/offshore: *Amphiura filiformis*: offshore seabed, sealoch, enclosed coast/embayment (Hill and Wilson, 2001). *Amphiura chiajei*: open coast, offshore seabed, sealoch, enclosed coast/embayment (Budd, 2002a).

Densities: *Amphiura filiformis*: can be found in high densities in the north east Atlantic, generally in sediments consisting of 10 to 20% silt/clay. For example, in Galway Bay, western Ireland, populations studied over an 8 year period had a maximum of 904 ind. m^{-2} (O'Connor *et al.*, 1983). High densities of *A. filiformis* (> 3000 ind. m^{-2}) were recorded in some areas in the Kattegat (Josefson, 1995). The density of adult *A. filiformis* at a locality in the Öresund (27 m depth, muddy sand) has been stable for at least 20 years with an average of 575 ind. m^{-2}, and the maximum of 1050 ind. m^{-2} (Muus, 1981). Low density populations also occur along the north west European coastline (Hill and Wilson, 2001). *Acrocnida brachiata*: in Little Killary, west coast of Ireland, it colonises an extensive tract of sandy inshore ground (ca. 7 m depth), at densities of 150–200 ind. m^{-2} (Makra and Keegan, 1998). *Amphiura chiajei* is mostly found in low numbers throughout its range (Budd, 2002a). *A. chiajei* was a dominant member of the bottom community in Killary Harbour, west coast of Ireland. The highly dense population of about 700 ind. m^{-2}, occurred in sediments with a silt/clay content of 80–90% and organic carbon levels of 5–7% (Keegan and Mercer, 1986 cited in Budd, 2002a). In contrast, the average population density of *A. chiajei* off the Northumbrian coast (NE England) between 1961–1963 was reported to be 10–12 ind. m^{-2} (Buchanan, 1964), and only 2 ind. m^{-2} between 1971–1972 (Buchanan and Warwick, 1974). Intensive sampling on the west coast of Ireland has established high population densities of *Amphiura filiformis* (> 2,200 ind. m^{-2}) and *A. chiajei* (> 1,050 ind. m^{-2}) (Keegan and Könnecker, 1979).

Biomass: *Amphiura filiformis*: high total benthic biomass (up to 1000 g WW m^{-2}) were recorded in some areas in the Kattegat (Josefson, 1995). In the Skagerrak, west Sweden, disc growth and gonad production of *A. filiformis* accounted for ca 68.9% (1.8 g AFDW m^{-2} y^{-1}) of the total annual production in the population. About 13.3% (0.34 g AFDW m^{-2} y^{-1}) of the total production was allocated to regeneration of arms, probably lost through cropping by predators. Mean regenerated biomass in percent of total biomass for adult *A. filiformis* was between 12 and 30% (mean 22%). Annual P/B ratio was 0.46 y^{-1} (Sköld *et al.*, 1994). *Acrocnida brachiata*: in Douarnenez Bay (Brittany, France), subtidally, the annual production invested in regenerating tissue was 33 g DW m^{-2} (19 g AFDW m^{-2}) (Bourgoin and Guillou, 1994). *Amphiura chiajei*: the average annual biomass off the Northumberland coast between 1971–1972 was 70 mg AFDW m^{-2} (Buchanan and Warwick, 1974).

Natural mortality: *Amphiura filiformis*: mortality of newly settled larvae is extremely high with less than 5% contributing to the adult population in any given year (Muus, 1981). *A. filiformis* provides an important link between the benthic and pelagic environments; it is important in the diets of many fish and invertebrate predators including dab, haddock and Norwegian lobster *Nephrops norvegicus* (Duineveld and Van Noort, 1986; Baden *et al.*, 1990). These predators do not generally consume the entire brittle star but crop only the arms, which are later regenerated (Hill and Wilson, 2001). *A. chiajei* provides an important food source for fish, especially those belonging to Pleuronectidae (Budd, 2002a).

Life span: *Amphiura filiformis*: 10–20 years (Hill and Wilson, 2001), or up to 25 years (Muus, 1981). *A. chiajei*: 5–10 years (Budd, 2002a).

Reproduction: *Amphiura filiformis*: gonochoristic; reproductive frequency: annual protracted; fecundity: 10,000–100,000 (Hill and Wilson, 2001). *A. chiajei*: gonochoristic; reproductive frequency: annual episodic (Budd, 2002a).

Early development: *Amphiura filiformis*, *A. chiajei*: pelagic larva (ophiopluteus) (Hill and Wilson, 2001; Budd, 2002a). The larvae of *A. filiformis* can disperse over considerable distances due to their long planktonic phase (Hill and Wilson, 2001).

Feeding ecology: *Amphiura filiformis*: passive suspension feeder, surface deposit feeder; typically feeds on: plankton and detritus (Hill and Wilson, 2001). *A. filiformis* feed on suspended material in flowing water, but will change to deposit feeding in stagnant water or areas of very low water flow (Ockelmann and Muus, 1978). *A. chiajei*: surface deposit feeder; typically feeds on: organic detritus (Budd, 2002a).

Life style: burrowers, slow mobility.

Family: Antedonidae (Class: Crinoidea) (not present in the samples)

Key species: *Antedon bifida* (feather-star)

Distribution: *A. bifida*: widely distributed in north-west Europe from Shetland to Portugal; found around most of Britain and Ireland but is apparently absent from the southern part of the east coast of England (Hill, 2003c).

Depth: *A. bifida*: sublittoral down to 200 m (Moyse and Tyler, 1990), from ELWS to 450 m (Hill, 2003c).

Substrate type: *A. bifida*: bedrock, large to very large boulders, algae (Hill, 2001b); on hard substrata amongst colonial hydroids, bryozoans etc. (Moyse and Tyler, 1990).

Coastal/offshore: *A. bifida*: open coast, offshore seabed, strait/sound, enclosed coast/embayment; immediate sublittoral (Hill, 2003c).

Densities: Intensive sampling on the west coast of Ireland has established high population densities of *A. bifida* (> 1,200 ind. m^{-2}) (Keegan and Könnecker, 1979).

Reproduction: *A. bifida*: gonochoristic; reproductive frequency: annual episodic; spawning from May to July (Hill, 2003c).

Early development: *A. bifida*: eggs are brooded on the arms of the feather-star and pelagic larvae are then released into the water column. After a short pelagic phase, the larvae attach to the substratum and develop a short stalk (pentacrinoid larvae). The pentacrinoids eventually detach, having developed small, prehensile cirri on the undersurface of the disc (Hill, 2003c).

Feeding ecology: *A. bifida*: passive suspension feeder; typically feeds on: particulate matter such as detritus and plankton (Hill, 2003c)

Life style: free living; crawler (Hill, 2003c).

Family: Asteriidae (*e*: ?)

Key species: *Asterias rubens* (common starfish) (*e*: 79), *Leptasterias muelleri* (*e*: 7)

Distribution: *A. rubens*: abundant throughout the north-east Atlantic, from Arctic Norway, along Atlantic coasts to Senegal, and only found occasionally in the Mediterranean (Mortensen, 1927); abundant on all British coasts (Moyse and Tyler, 1990). *L. muelleri*: Iceland, west coast of Shetland, North Sea; not on southern coasts of Britain; distribution northwards to Spitzbergen, Greenland and North America (Moyse and Tyler, 1990).

Depth: *A. rubens*: midlittoral, infralittoral fringe and sublittoral to 400 (–650). *L. muelleri*: infralittoral fringe and sublittoral to about 800 m (Moyse and Tyler, 1990).

Substrate type: *A. rubens*: bedrock, gravel/shingle, coarse clean sand (Budd, 2001b).

Coastal/offshore: *A. rubens*: open coast, offshore seabed, strait/sound, enclosed coast/embayment (Budd, 2001b).

Densities: *A. rubens*: reported abundances vary between 2–31 ind. m^{-2} on fine sand and 324–809 ind. m^{-2} on algal carpets (Anger *et al.*, 1977). Feeding concentrations in Morecambe Bay, UK, attained 300–400 ind. m^{-2} (Dare, 1982). During a series of North Sea demersal fish surveys in 1978–1980, the largest numbers of *A. rubens* were trawled off the west coast of Denmark and in the southern North Sea (Dyer *et al.*, 1982).

Biomass: *A. rubens*: feeding concentrations in Morecambe Bay, UK, attained 12–16 kg WW m^{-2} (Dare, 1982). The biomass of *A. rubens* was estimated at different depths and for different sediment types in the Kiel Bight, averaging 11.7 g m^{-2}. The maximum biomass was found between 10 and 20 m depth (Nauen, 1978).

Natural mortality: *A. rubens* in the Kiel Bight: Z = 11.07 in summer and Z = 4.35 in winter (Nauen, 1978)

Life span: *A. rubens*: 5–10 years (Budd, 2001b).

Reproduction: *A. rubens*: gonochoristic; reproductive frequency: annual episodic; fecundity: > 1,000,000 (Budd, 2001b), up to 2.5 million eggs (Fish and Fish, 1996).

Early development: *A. rubens*: long lived pelagic larva (> 80 days) (Clark and Downey, 1992).

Feeding ecology: *A. rubens*: active carnivore, scavenger; typically feeds on: bivalves, polychaetes, small crustaceans, other echinoderms and carrion (Budd, 2001b).

Life style: free-living, mobile.

Family: Astropectinidae (*e*: 71)

Key species: *Astropecten irregularis* (*e*: 71)

Distribution: *A. irregularis*: from Norway to Morocco; common on all British coasts (Moyse and Tyler, 1990).

Depth: *A. irregularis*: sublittoral, 10–1000 m (Moyse and Tyler, 1990).

Substrate type: *A. irregularis*: partly buried in sandy substrata (Moyse and Tyler, 1990).

Densities: *A. irregularis* and *Asterias rubens* were the most frequently recorded starfish during a series of benthos surveys in the northern North Sea in the years 1980–1985. *A. irregularis* was the most common echinoderm (Basford *et al.*, 1989). Seawater temperature is probably an important factor regulating the abundance and distribution *of A. irregularis* in coastal waters (Freeman *et al.*, 2001). Population density of *A. irregularis* off the western and south-western coasts of the British Isles ranged from 5 to 592 ind. h^{-1} with higher densities typically associated with finer-grained sandy or muddy sediments (Freeman *et al.*, 1998).

Biomass: *A. irregularis*: the average annual biomass in Carmarthen Bay, S. Wales: B = 0.073 g AFDW m^{-2}; annual production: P = 0.0004 g AFDW m^{-2}; P/B = 0.005 (Warwick *et al.*, 1978).

Reproduction: *A. irregularis* from the coastal waters of North Wales spawns during late spring-early summer (Freeman *et al.*, 2001).

Early development: *A. irregularis* larvae are pelagic (Clark and Downey, 1992).

Feeding ecology: *A. irregularis*: a voracious carnivore, feeding primarily on molluscs, but also an opportunistic forager (Clark and Downey, 1992); a scavenger (Veale *et al.*, 2000).

Life style: free-living, slow mobility.

Family: <u>Echinidae</u> (*i*: 4, e: ≈ 25)

Key species: *Echinus* spp. (indet.) (*e*: 24), *Echinus esculentus* (*i*: < 1, *e*: 4), *Psammechinus miliaris* (green see urchin) (i: 3), *E. elegans* (*i*: < 1)

Distribution: *E. esculentus*: abundant in the N. E. Atlantic from Iceland, north to Finmark, Norway and south to Portugal. Absent from the Mediterranean. Common on most coasts of the British Isles but absent from most of east coast of England, the eastern English Channel and some parts of north Wales (Tyler-Walters, 2003a). *P. miliaris*: from Trondheim Fjord in northern Norway, inner Danish waters from the Skaw into the western Baltic, Iceland, British Isles, south to the Atlantic coast of Morocco and the Azores. Not in Greenland, the Mediterranean or Atlantic coasts of America. All British and Irish coasts. Evenly distributed in the southern North Sea but scarce in northern North Sea (Jackson, 2003b). *E. elegans*: uncommon; off north and west coasts of British Isles, east coast of Scotland; elsewhere southern Norway, southern Iceland to Biscay and the Azores (Moyse and Tyler, 1990).

Depth: *E. esculentus*: from infralittoral fringe (low tide), especially at 10–40 m and down to 1200 m. *P. miliaris*: intertidal, occasionally down to about 100 m. *E. elegans*: 50–2000 m (Moyse and Tyler, 1990).

Substrate type: *E. esculentus*: bedrock, large to very large boulders, small boulders, artificial (e.g. metal, wood, concrete), rockpools, under boulders, caves, crevices/fissures, overhangs (Tyler-Walters, 2003a). *P. miliaris*: bedrock, large to very large boulders, small boulders, cobbles, gravel/shingle, muddy gravel, muddy sand, mixed, algae, rockpools, under boulders, artificial (e.g. metal, wood, concrete) (Jackson, 2003b); under stones and rocks, and amongst *Zostera* (Moyse and Tyler, 1990).

Coastal/offshore: *E. esculentus*: open coast, strait/sound, sealoch, ria/voe, enclosed coast/embayment (Tyler-Walters, 2003a). *P. miliaris*: open coast, offshore seabed, strait/sound, sealoch, ria/voe (Jackson, 2003b).

Densities: *E. esculentus* was recorded at all stations in Sør-Trøndelag (Mid-Norway), and present in high densities (up to 15 ind. m^{-2}) at semi-exposed stations (Sjøtun *et al.*, 2000). *E. esculentus* occurred in the rocky sublittoral of the island of Helgoland (North Sea) in high population densities (1–7 ind. m^{-2}), while *P. miliaris* was less frequent (Krumbein and Pers, 1974). *E. acutus*: densities up to 247 ind. per 100 m^2 were reported by Dyer *et al.* (1982) in deep offshore waters in the North Sea. *P. miliaris*: average abundance off the north east coast of Anglesey, Liverpool Bay, was 3 and 6 ind. per 100 m^2, in April and October 1993, respectively (Kaiser *et al.*, 1998b).

Life span: *E. esculentus*: 5–10 years (Tyler-Walters, 2003a). Gage (1992) reports a specimen (based on growth bands) of at least 16 years of age. *P. miliaris*: 5–10 years (Jackson, 2003b), up to 12 years (Allain, 1978 cited in Jackson, 2003b).

Reproduction: *E. esculentus*: gonochoristic; reproductive frequency: annual episodic; fecundity: > 1,000,000. Maximum spawning occurs in spring although individuals may spawn over a protracted period. (Tyler-Walters, 2003a). *P. miliaris*: gonochoristic; reproductive frequency: annual protracted, fecundity: > 1,000,000 (Jackson, 2003b). Spawning occurs in spring and early summer (Mortensen, 1927; Kelly, 2000).

Early development: *E. esculentus*: planktonic development is complex and takes between 45 and 60 days in captivity (MacBride 1914 cited in Tyler-Walters, 2003a). Settlement is thought to occur in autumn and winter (Comely and Ansell, 1988).

Feeding ecology: *E. esculentus*: active omnivore, passive omnivore; recorded feeding on: worms, barnacles (e.g. *Balanus* spp.), hydroids, tunicates, bryozoans (e.g. *Membranipora* spp.), macroalgae (e.g. *Laminaria* spp.), bottom material and detritus. *P. miliaris*: active omnivore; typically feeds on: macroalgae, hydroids, bryozoans, boring sponges, barnacles, mussels, cockles and worms (review in Lawrence, 1975).

Life style: free living, small mobility.

Family: <u>Ophiotrichidae</u> (*i*: 2, *e*: 20)

Key species: *Ophiothrix fragilis* (*i*: 2, *e*: 20)

Distribution: *O. fragilis*: widely distributed in the eastern Atlantic from northern Norway to the Cape of Good Hope; very common on all British and Irish coasts, except for the east coast of Scotland. Rheophilic (Moyse and Tyler, 1990).

Depth: *O. fragilis*: in lower littoral and sublittorally (Moyse and Tyler, 1990), 0–85 m (Jackson, 1999b).

Substrate type: *O. fragilis*: bedrock, large to very large boulders, small boulders, cobbles, pebbles, gravel/shingle, maerl, muddy gravel, under boulders, crevices/fissures, other species (Jackson, 1999b). *O. fragilis* may be found in low densities on *Crepidula fornicata* (slipper limpet) beds (Bourgoin *et al.*, 1985 cited in Jackson, 1999b) or *Modiolus* shells (Magorrian *et al.*, 1995)

Coastal/offshore: *O. fragilis*: open coast, offshore seabed, strait/sound (Jackson, 1999b).

Densities: *O. fragilis* can be found in very high densities. Davoult (1989) observed high densities of 1,295 to 2,088 ind. m^{-2} in Dover Strait (French part). Basford *et al.* (1989) reported densities of *O. fragilis* in excess of 10,000 ind. per 1000 m^2 between 1980 and 1985 near the Fisher Banks off Denmark.

Biomass: *O. fragilis* in the Dover Strait: mean biomass: 210 g AFDW m^{-2}; production: 269 g AFDW m^{-2} y^{-1} (Davoult, 1989).

Natural mortality: Although not an important dietary component, *O. fragilis* may be found in the stomach contents of most common predators (Warner, 1971). *O. fragilis* avoids predation by moving away from sources of mechanical disturbance (Warner, 1971). The escape response of *O. fragilis* is slow in comparison to other brittle stars. Presumably, it avoids predation through sheltering in crevices etc. and cryptic colouration. Although not toxic, *O. fragilis* may be avoided by predators due to heavy calcification and possession of glassy spines (Sköld, 1998).

Life span: *O. fragilis*: 5–10 years (Jackson, 1999b).

Reproduction: *O. fragilis*: gonochoristic; reproductive frequency: annual episodic (Jackson, 1999b). Ball *et al.* (1995) found that *O. fragilis* had a long breeding season, extending from May to January, with peak activity in summer/autumn, a small percentage of the population can breed throughout most of the year in certain regions.

Early development: *O. fragilis* larvae appear in the water column about a week after gamete release and fertilisation of the eggs. The larvae metamorphose into juvenile brittlestars whilst still in the plankton. The pelagic phase lasts about 26 days (MacBride, 1907 cited in Jackson, 1999b).

Feeding ecology: *O. fragilis*: passive suspension feeder; typically feeds on phytoplankton (Jackson, 1999b).

Life style: free living, slow mobility.

Other information: *O. fragilis* is considered a keystone species in the coastal marine ecosystem of the eastern Channel and a dominant species of gravel communities (Lefebvre and Davoult, 1997).

Family: <u>Ophiuridae</u> (= Ophiolepidae) (*i*: 59, *e*: ?)

Key species: *Ophiura ophiura* (*i*: 4, *e*: 50), *O. albida* (*i*: 39, *e*: 34), *O. affinisi* (*i*: 25, *e*: 1)

Distribution: *O. ophiura*: distributed in the north-east Atlantic from northern Norway to Madeira, and the Mediterranean; common all round Britain. *O. albida*: distributed in the north-east Atlantic from Norway to the Azores, and in the Mediterranean; common all round Britain. *O. affinis*: distributed from northern Norway to the Bay of Biscay, and also recorded from the Mediterranean; all British coasts, but not in the southern North Sea (Moyse and Tyler, 1990).

Depth: *O. ophiura*, *O. albida*: mainly sublittoral (Moyse and Tyler, 1990).

Substrate type: *O. ophiura*, *O. albida*: on a variety of soft substrata. *O. affinis*: on muddy sand, fine shell, and gravel (Moyse and Tyler, 1990).

Densities: *O. ophiura* (=*O. texturata*) was the most common brittle star occurring in the northern North Sea in the years 1980–1985 (Basford *et al.*, 1989). *Ophiura* spp.: mean density in the southern North Sea in August 1989 was 118 ind. m^{-2} (Bergman and Hup, 1992). *O. affinis* and *O. albida* were reported to be abundant on the soft bottom at 30 m depth in

Oslofjord, Norway, where together they reached a density of 276 ind. m^{-2} (Ambrose, 1993).

Biomass: Annual production:biomass (*P*/*B*) ratios in the German Bight were estimated at 0.32 for *O. albida* and 0.43 for *O. ophiura* (Dahm, 1993).

Natural mortality: Ophiuroids formed 46% of the total consumption of the common dab in the North Sea (Greenstreet, 1996).

Feeding ecology: *Ophiura* spp. are omnivorous, feeding on organic detritus, microalgae and small sediment-dwelling organisms (Hughes, 1998b). Feder (1981) found the large *O. texturata* to be quite predatory in its feeding habits, eating a wide variety of small bivalves, polychaetes and crustaceans. Tyler (1977) recorded a similar diet in *O. texturata* from the Bristol Channel, whereas the smaller *O. albida* was found to rely more on microalgae and detritus.

Life style: free living, mobile.

Family: Solasteridae (*i*: < 1, *e*: 2)

Key species: *Crossaster papposus* (*e*: 2) (sunstar)

Distribution: *C. papposus*: distributed from the Arctic to the English Channel, also on both east and Pacific coasts of North America; common on all British coasts (Moyse and Tyler, 1990).

Depth: Infralittoral fringe to 50 (–1200) m (Moyse and Tyler, 1990).

Substrate type: *C. papposus*: found on sand, stones, mussel and oyster beds (Wilson, 2002).

Feeding ecology: *C. papposus*: is considered to be the dominant predator in some habitats. *C. papposus* plays an important role in determining community structure in the Mingan Islands, northern Gulf of St. Lawrence (Himmelman and Dutil, 1991).

Life style: free living, mobile.

Family: Spatangidae (*i*: 66)

Key species: *Echinocardium cordatum* (*i*: 39), *E. flavescens* (*i*: 33), *Brissopsis lyrifera* (*i*: 5), *Spatangus purpureus* (*i*: 2, *e*: 13)

Distribution: *E. cordatum*: cosmopolitan with the exception of polar seas: Norway to South Africa, Mediterranean, Australasia and Japan; all coasts of Britain and Ireland. *E. flavescens*: distributed elsewhere from Finnmark and Iceland south to the Azores and the Mediterranean; all British coasts; less common than *E. cordatum*. *B. lyrifera*: distributed from Norway and Iceland to South Africa and the Mediterranean, also present on the east coast of North America but not Greenland; recorded off the west, north and east coasts of the British Isles, but not off the south coast. *S. purpureus*: distributed elsewhere from North Cape, Norway, to North Africa, the Azores, and the Mediterranean; locally common around coasts of British Isles (Moyse and Tyler, 1990).

Depth: *E. cordatum*: mainly intertidal (lower midlittoral and infralittoral fringe) but also sublittoral to 230 m. *E. flavescens*: sublittoral down to 300 m, rarely found intertidally. *B. lyrifera*: sublittorally 5–500 m. *S. purpureus*: infralittoral down to about 900 m (Moyse and Tyler, 1990).

Substrate type: *E. cordatum* occurs buried about 80 (to 150) mm deep in sand. *B. lyrifera* lives buried in mud. *S. purpureus* occurs shallowly buried in coarse sand or gravel, rarely mud (Moyse and Tyler, 1990).

Coastal/offshore: *E. cordatum*: open coast, offshore seabed, strait/sound, enclosed coast/embayment (Hill, 2000b). *B. lyrifera*: offshore seabed, open coast, sealoch (Budd, 2002b).

Densities: *E. cordatum*: mean density in the southern North Sea in August 1989, small: 97 ind. m^{-2}, large: 23 ind. m^{-2} (Bergman and Hup, 1992). *E. flavescens* was the most common echinoid during the benthos surveys in the northern North Sea in the years 1980–1985 with densities up to 600 ind. per 1000 m^2 in shallower water off Denmark (Basford *et al.*, 1989). *B. lyrifera* is a gregarious species. Tunberg (1991 cited in Budd, 2002b) found densities of *B lyrifer*a to be up to 30 ind. m^{-2} at various locations along the Swedish coast. However, in the North Sea densities of up to 60 ind. m^{-2} have been reported (Ursin, 1960).

Biomass: *E. cordatum*: the average annual biomass in Carmarthen Bay, S. Wales: B = 5.138 g AFDW m^{-2}; annual production: P = –0.012 g AFDW m^{-2}; P/B = –0.02 (Warwick *et al.*, 1978). *B. lyrifera*: the average annual biomass off the Northumberland coast (NE England) between 1971–1972 was 366 mg AFDW m^{-2} and the species was considered to be the only significant large producer of biomass in the area with a total production of 108 mg AFDW m^{-2} y^{-1} (Buchanan and Warwick, 1974).

Life span: *E. cordatum*: 10–20 years. *B. lyrifera*: short lived (Buchanan, 1967)

Reproduction: *E. cordatum*: gonochoristic; reproductive frequency: annual episodic; fecundity: > 1,000,000 (Hill, 2000b). *B. lyrifera*: gonochoristic; reproductive frequency: semelparous; fecundity: > 1,000,000 (Budd, 2002b).

Early development: *E. cordatum*: planktonic larvae (Fish and Fish, 1996). *B. lyrifera*: planktonic larvae (Budd, 2002b).

Feeding ecology: *E. cordatum*: surface deposit feeder; typically feeds on detritus (Hill, 2000b). *B. lyrifera*: sub-surface deposit feeder; typically feeds on: organic detritus, foraminifers and other small organisms within sediment (Budd, 2002b).

Life style: free living, burrowers.

Other information: *B. lyrifera* typically co-occurs with the brittle star, *Amphiura chiajei*, on muddy, soft bottom areas of the North Sea, the Skagerrak and the Kattegat (Hollertz *et al.*, 1998). *B. lyrifera* is an important active bioturbator which can alter the physical and chemical environment of the sediment, and consequently influence the associated meiofauna (Budd, 2002b).

Phylum: Echiura

Family: Echiuridae (*i*: 9, *e*: < 1)

Key species: *Echiurus echiurus* (*i*: 9, *e*: < 1), *Maxmuelleria lankesteri* (not present in the samples)

Distribution: *E. echiurus*: holarctic, extending to Kattegat and North Sea (Knight-Jones and Ryland, 1990). *M. lankesteri*: previously thought to be rare and localized in the Irish Sea, west Scotland, Kattegat, Skagerrak (Knight-Jones and Ryland, 1990), now it is known to be common in the Irish Sea, Clyde Sea, and in many of the Scottish sea lochs; there are so far no records from the North Sea (Hughes *et al.*, 1996b).

Depth: *M. lankesteri*: 10–80 m (Hughes, 1998a).

Substrate type: *M. lankesteri*: fine muds and muddy sands (Hughes, 1998a).

Densities: *E. echiura*: the populations in the German Bight (southern North Sea) were found to fluctuate widely: from being apparently absent (between 1973–1975) to 250 ind. m^{-2} (in 1976) and entire disappearance (in 1978) (Rachor and Bartel, 1981).

Early development: *M. lankesteri*: no information is available about the early development, but the planktonic stage is likely to be brief or absent (Hughes, 1998a).

Life style: burrowers (Hughes *et al.*, 1996a).

Phylum: Mollusca

Family: Arcticidae (*e*: 7)

Key species: *Arctica islandica* (ocean quahog, Icelandic cyprine) (*e*: 7)

Distribution: *A. islandica*: ranges from Arctic waters to the Bay of Biscay; off all British coasts (Hayward, 1990).

Depth: *A. islandica*: found at extreme low water, but predominately in the sub-littoral (Pizzolla, 2002).

Substrate type: *A. islandica*: in sand and muddy sand (Hayward, 1990).

Coastal/offshore: *A. islandica*: offshore, to the edge of the Continental Shelf (Hayward, 1990).

Densities: *A. islandica*: De Wilde *et al.* (1986) recorded a density of 12 ind. m^{-2} in the Fladen Ground area (northern North Sea).

Biomass: *A. islandica*: The recorded biomass in the Fladen Ground was 7.8 g AFDW, which made up 67% of the total macrofaunal biomass in the area (De Wilde *et al.*, 1986).

Natural mortality: *A. islandica* was the most common mollusc species recorded in cod stomachs in the central North Sea (Adlerstein and Welleman, 2000).

Life span: *A. islandica*: extremely long-lived (over 100 years) (Witbaard, 1997; Witbaard *et al.*, 1997).

Early development: *A. islandica*: Trochophore larvae swim continuously, while veliger larvae alternate between periods of active upward swimming and periods of passive sinking

(Mann and Wolf, 1983). Time to settlement ranges from 4 to 8 weeks and is temperature-dependent (Lutz *et al.*, 1982).

Feeding ecology: *A. islandica*: suspension feeder (Witbaard, 1997).

Life style: infaunal; limited mobility (Witbaard, 1997).

Family: <u>Buccinidae</u> (*i*: 4, *e*: ?)

Key species: *Colus gracilis* (*i*: 2, *e*: 39), *Neptunea antiqua* (red whelk) (*i*: < 1, *e*: 39), *Buccinum undatum* (common whelk) (*i*: 1, *e*: 37), *C. jeffreysianus* (*e*: 14)

Distribution: *C. gracilis*: distributed from Norway to Portugal; recorded all round British Isles, rare in southern North Sea and Channel. *N. antiqua*: widely distributed from Biscay to Arctic; locally common around much of British Isles. *B. undatum*: distributed from Iceland and northern Norway to the Bay of Biscay; common and often abundant around British Isles, except Scilly Isles (Hayward *et al.*, 1990). Sometimes present in brackish waters (Ager, 2003b). *C. jeffreysianus*: distributed from Mediterranean to Norway and Iceland; not common around British Isles, though more often encountered off south-west coasts (Hayward *et al.*, 1990).

Depth: *C. gracilis*: 30–80 m; occasionally intertidal in north of range. *N. antiqua*: sublittoral, 15–1200. *B. undatum*: occasionally at LWST but usually sublittoral down to 1200 m. *C. jeffreysianus*: 30–2000 m (Hayward *et al.*, 1990).

Substrate type: *C. gracilis*: on sandy and muddy substrata. *N. antiqua*: mainly on soft substrata (Hayward *et al.*, 1990). *B. undatum*: on hard and soft substrata. *C. jeffreysianus*: on soft substrata (Hayward *et al.*, 1990).

Densities: *B. undatum*: Gros and Santarelli (1986) observed local densities in the Channel Isles region (Western Channel) of 0.4 ind. m^{-2}. Density estimates for the French coast of the English Channel ranged in the period from February 1983 to March 1984 from 0.2 ind. m^{-2} in summer months to 0.5–1 ind. m^{-2} in the remaining months (Santarelli Chaurand, 1988).

Natural mortality: *B. undatum* is preyed on by starfish *Asterias rubens* (Ramsay and Kaiser, 1998).

Life span: *B. undatum*: the maximum age observed in waters around Iceland was 13 years (Gunnarsson and Einarsson, 1995).

Reproduction: *B. undatum*: annual reproductive cycle with a single major egg-laying period in the autumn (Valentinsson, 2002). No seasonality was detected in the reproductive cycles of *C. jeffreysianus* (Tyler *et al.*, 1985).

Feeding ecology: *B. undatum* is known to be a predator feeding on bivalve molluscs, such as *Cardium edule*, *Mytilus edulis*, *Modiolus modiolus*, *Astarte montagui*, *Arctica islandica*, and *Venus striatula* (Nielsen, 1974). Thompson (2002) argues that feeding on *M. edulis* may be opportunistic and that *B. undatum* is primarily a scavenger. *B. undatum* were observed to feed on damaged bivalves, echinoderms, crustaceans, whelks and polychaetes in areas of intense beam trawling, such as the southern North Sea (Evans *et al.*, 1996; Ramsay *et al.*, 1998).

Life style: free living, mobile.

Family: Cardiidae (*i*: 16, *e*: ≈ 10)

Key species: *Parvicardium minimum* (*i*: 7), *Acanthocardia echinata* (*i*: 5, *e*: 9), *Cerastoderma ovale* (=*P. ovale*) (*i*: 1, *e*: < 1), *A. tuberculata* (*i*: < 1), *C. edule* (common cockle) (*i*: < 1),

Distribution: *P. minimum*: from Iceland to the Mediterranean and north-west Africa; present off western coasts of Britain and Ireland. *A. echinata*: from Norway to the Mediterranean; off all British coasts. *C. ovale*: from Iceland to Mediterranean and Canary Isles; off all British coasts. *A. tuberculata*: south to the Mediterranean and north-west Africa; southern British coasts only. *C. edule*: distributed from north-east Norway to West Africa; common on all British coasts (Hayward, 1990).

Depth: *P. minimum*: to about 160 m depth. *C. ovale*: to about 100 m depth. *A. tuberculata*: from the lower shore into the shallow sublittoral. *C. edule*: from mid-tidal level to just below ELWS (Hayward, 1990).

Substrate type: *P. minimum*: in mud, sand, and fine gravel. *A. echinata*: in fine sand and gravel. *C. ovale*: in sand and gravel. *A. tuberculata*: on muddy sand and gravel. *C. edule*: in sandy mud, sand, fine gravel (Hayward, 1990), or sea grass (Tyler-Walters, 2003b).

Coastal/offshore: *P. minimum*, *A. echinata*, *C. ovale*: offshore (Hayward, 1990). C. *edule*: enclosed coast/embayment, open coast, strait/sound, sealoch, ria/voe, estuary (Tyler-Walters, 2003b).

Densities: *C. edule*: high densities (1300 ind. m^{-2}) were recorded in the western Wadden Sea in the beginning of June 1993 (Van der Veer *et al.*, 1998).

Biomass: *C. edule*: average biomass on an intertidal mudflat in Southampton Water in two successive winters (1972 and 1973): B = 17–66 g AFDW m^{-2}; production: P = 20–71 g m^{-2} y^{-1} (Hibbert, 1976). Average biomass (including shell organics) on tidal flats in the Oosterschelde, SW Netherlands, in August varied from 140 g AFDW m^{-2} in 1980 to 21 g AFDW m^{-2} in 1989 (Coosen *et al.*, 1994).

Natural mortality: *C. edule* are preyed on by shore crab *Carcinus maenas,* shrimps, flatfish and oystercatcher *Haematopus ostralegus* (review in Tyler-Walters, 2003b). *Crangon crangon* was a dominant predator of *C. edule* in marine shallow waters of western Sweden, while *C. edule* were the dominant prey of the flounder *Platichthys flessus* (Möller and Rosenberg, 1983). *C. edule* is important food for eider *Somateria mollissima* in the Wadden Sea (Leopold, 2002). Natural mortality of *C. edule* in the western Wadden Sea in June–July 1993 was estimated at 0.056 d^{-1}, and the main predators were *Crangon crangon* and *Carcinus maenas* (Van der Veer *et al.*, 1998).

Life span: *C. edule*: 5–10 years (Tyler-Walters, 2003b).

Reproduction: *C. edule*: gonochoristic; reproductive frequency: annual protracted; fecundity: 1,000–10,000 (Tyler-Walters, 2003b). *C. edule* spawns mainly in the spring or autumn and may more easily colonise areas during this period (Ferns *et al.*, 2000).

Early development: *C. edule*: eggs develop into a trochophore stage within the egg membrane and then into a typical bivalve veliger. The veliger metamorphoses into a juvenile cockle. Settlement and recruitment is sporadic and varies with geographic location, year, season, reproductive condition of the adults and climatic variation (review in Tyler-Walters, 2003b).

Feeding ecology: *C. edule*: active suspension feeder; typically feeds on: phytoplankton, zooplankton and organic particulate matter (Tyler-Walters, 2003b).

Life style: infaunal, slow mobility.

Family: <u>Mactridae</u> (*i*: 31, *e*: ?)

Key species: *Spisula elliptica* (*i*: 18, *e*: 7), *S. subtruncata* (*i*: 10, *e*: 4), *Mactra stultorum* (*i*: 5, *e*: < 1), *S. solida* (*i*: 1, *e*: 2)

Distribution: *S. elliptica*: distributed northwards to the Barents Sea; off all British coasts. *S. subtruncata*: distributed from Norway to the Mediterranean and Canary Isles; widespread and common off most British coasts. *M. stultorum*: distributed from Norway to the Mediterranean and West Africa; widespread, and often abundant, off most British coasts. *S. solida*: distributed from south Iceland and Norway to Spain and Morocco (Hayward, 1990).

Depth: *S. elliptica*: to about 100 m. *S. subtruncata*, *M. stultorum*: from the lower shore into the shallow sublittoral. *S. solida*: from the lower shore down (Hayward, 1990).

Substrate type: *S. elliptica*: in mixed soft substrata. *S. subtruncata*: borrowing in muddy or silty sand. *M. stultorum*: in clean sand. *S. solida*: burrows in sand (Hayward, 1990).

Coastal/offshore: *S. elliptica*, *S. subtruncata*, *M. stultorum*: offshore (Hayward, 1990).

Densities: Average abundance of *S. elliptica* off the north east coast of Anglesey, Liverpool Bay, was 1 and 0.5 ind. per 100 m^2, in April and October 1993, respectively (Kaiser *et al.*, 1998b). *S. subtruncata*: the mean density in the southern North Sea in August 1989 was 1 ind. m^{-2} (Bergman and Hup, 1992). The annual mean density of *S. subtruncata* in the Southern Bight of the North Sea was 42 ind. m^{-2} (Amara *et al.*, 2001).

Biomass: *S. subtruncata*: annual mean biomass in the Southern Bight 6463.5 mg AFDW m^{-2} (Amara *et al.*, 2001). *S. solida*: the biomass at ‘Røde Klit Sand’ (Danish part of the North Sea) varied between 0 and 2,046 g WW m^{-2}. The mean biomass was 265 g WW m^{-2}. Only densities, where the biomass is greater than or equal 200 g m^{-2} are considered as fishable (Kristensen, 1996).

Natural mortality: *S. subtruncata* in the Dutch Wadden Sea is preyed upon by common eiders *Somateria mollissima* (Piersma and Camphuysen, 2001).

Feeding ecology: *S. subtruncata*: suspension feeder (Kiørboe and Møhlenberg, 1981).

Life style: infaunal.

Family: Myacidae (*i*: 9)

Key species: *Mya truncata* (*i*: 5), *M. arenaria* (*i*: 2)

Distribution: *Mya truncata*: in the north-east Atlantic extending south to Biscay (Hayward, 1990). Common around the coast of Britain, and recorded in several locations around the east and south coasts of Ireland (Ballerstedt, 2002). *Mya arenaria*: circumboreal, not reaching the Mediterranean; off all British coasts (Hayward, 1990).

Depth: *Mya truncata*: from the lower shore to about 70 m. *Mya arenaria*: on the lower shore to about 20 m (Hayward, 1990); but has been recorded down to 192 m depth (Strasser, 1999).

Substrate type: *Mya truncata*: in mixed sandy substrata. *Mya arenaria*: in coarse or fine sand, often mixed with mud or gravel (Hayward, 1990; Tyler-Walters, 2003c).

Coastal/offshore: *Mya arenaria*: strait/sound, sealoch, ria/voe, estuary, enclosed coast/embayment (Tyler-Walters, 2003c).

Densities: *M. arenaria*: densities vary between years and location, e.g. Clay (1966 cited in Tyler-Walters, 2003c) reported adult densities between 5 and 300 ind. m^{-2} in the U. K. and Strasser *et al.* (1999) reported abundances between 0 and 243 ind. m^{-2} (with a mean of 11.8 ind. m^{-2}) in the Wadden Sea. *M. arenaria* populations demonstrate pronounced patchiness, e.g. in the Dutch Wadden Sea (Strasser *et al.*, 1999).

Biomass: *M. arenaria*: Winther and Gray (1985) estimated production in the eutrophic inner Oslofjord at 42.52 g DW m^{-2} y^{-1}. The P/B ratio was 1.59.

Natural mortality: *M. arenaria* juvenile stages are preyed upon by crabs (e.g. *Carcinus maenas*), shrimp *Crangon crangon*, shorebirds, nereids, nemerteans and flatfish (*Pleuronectes platessa*, *Platichtys flesus*). Adults are preyed on by crabs, oystercatchers (*Haematopus ostralegus*) and curlew (*Numenius arquata*) (Emerson *et al.*, 1990; Strasser, 1999).

Life span: *M. arenaria*: normally 10–20 years (Tyler-Walters, 2003c), maximum recorded age 28 years (Strasser, 1999).

Reproduction: *M. arenaria*: gonochoristic; reproductive frequency: annual protracted; fecundity: 100,000–1,000,000, or > 1,000,000. Spawning occurs once or twice annually, and can occur between March and November depending on locality (Tyler-Walters, 2003c).

Early development: *M. arenaria*: pelagic larva; larval life lasts about 2–3 weeks. Recruitment is influenced by larval and post-settlement mortality. The high larval and juvenile mortality decreases with age and size (Tyler-Walters, 2003c). Brousseau (1978) estimated that 0.1% of egg production survived to successful settlement.

Feeding ecology: *M. arenaria*: active suspension feeder; typically feeds on: phytoplankton, small zooplankton, benthic diatoms, suspended particulates and dissolved organic matter (Tyler-Walters, 2003c).

Life style: infaunal.

Family: Mytilidae (*i*: 8, *e*: ≈ 3)

Key species: *Modiolula phaseolina* (*e*: 2), *Modiolus modiolus* (horse mussel) (*i*: 3, *e*: 1), *Modiolus barbatus* (*i*: < 1, *e*: 1), *Modiolarca tumida* (*e*: < 1), *Mytilus galloprovincialis* (*e*: < 1), *Musculus discors* (*i*: 1, *e*: < 1), *Mytilus edulis* (common mussel) (*i*: 3)

Distribution: *Modiolula phaseolina*: distributed from northern Norway to the Mediterranean and north-west Africa; reported from most British coasts. *Modiolus modiolus*: off all British shores, south to the Bay of Biscay. *Modiolus barbatus*: southern and western, north to Yorkshire on the east coast and the Clyde in the west, ranging south to the Mediterranean and north-west Africa. *Modiolarca tumida*: widespread and common, off all British coasts; present in the Mediterranean. *Mytilus galloprovincialis*: along the coasts of France and south to the Mediterranean; around south-west England, South Wales, and southern and western Ireland. *Musculus discors*: distribution circumboreal, in the north-east Atlantic ranging south to the Mediterranean and Madeira; widespread and common off all British coasts. *Mytilus edulis*: ranges from Arctic waters south to the Mediterranean; widespread and common on all British coasts (Hayward, 1990).

Depth: *Modiolula phaseolina*: from lower shore downwards. *Modiolus modiolus*: from lower shore to about 150 m. *Modiolus barbatus*: from lower shore to about 100 m. *Modiolarca tumida*: on the lower shore and in the shallow sublittoral. *Mytilus galloprovincialis*: intertidal. *Musculus discors*: from mid-tidal zone into shallow sublittoral. *Mytilus edulis*: from upper shore and into the shallow sublittoral (Hayward, 1990).

Substrate type: *Modiolus modiolus*, *Modiolus barbatus*: on coarse grounds. *Modiolarca tumida*: among algal holdfasts, attached to undersides of shells and stones, or embedded in the tests of large tunicates (Hayward, 1990). *Musculus discors*: on rocky shores (Hayward, 1990); on the holdfasts of seaweeds (Tyler-Walters, 2001b). *Mytilus edulis*: attached to their substratum using byssus threads (Hayward, 1990).

Coastal/offshore: *Modiolus modiolus*: open coast, offshore seabed, strait/sound, sealoch, ria/voe, enclosed coast/embayment (Tyler-Walters, 2001c); offshore it may form immense aggregations (Hayward, 1990). *Musculus discors*: open coast, strait/sound, sealoch, ria/voe, enclosed coast/embayment (Tyler-Walters, 2001b). *Mytilus edulis*: open coast, strait/sound, sealoch, ria/voe, estuary, enclosed coast/embayment (Tyler-Walters, 2002a).

Densities: *Modiolus modiolus*: reported densities of horse mussel beds were relatively low (compared to common mussel beds) and variable. Holt *et al.* (1998) observed densities of 20–40 large ind. m^{-2} north of the Isle of Man. Comely (1978) observed 1–2 ind. m^{-2} in the intertidal and 37 ind. m^{-2} 100 m from the west coast of Scotland. *Musculus discors* occasionally forms dense aggregations, especially in strong tidal streams, covering rock surfaces (Tyler-Walters, 2001b). *Mytilus edulis* forms dense beds of one or more (up to 5 or 6) layers, with individuals bound together by byssus threads (Tyler-Walters, 2002a).

Egerrup and Laursen (1992) observed a mean density of 3682 ind. m^{-2} on an intertidal *Mytilus edulis* bed in the Danish Wadden Sea (Hobo Deep).

Biomass: *Mytilus edulis*: mean biomass on intertidal mudflat in Southampton Water in two successive winters (1972 and 1973) was 4–5 g AFDW m^{-2} (Hibbert, 1976). Egerrup and Laursen (1992) estimated the mean annual biomass of mussels on the intertidal mussel bed in Hobo Deep (the Danish Wadden Sea) at 740 g AFDW m^{-2}. The *P*/*B* ratio was 0.19. Mussel patches of a biomass of about 1300 g AFDW m^{-2} were observed in Koenigshafen, a sheltered bay in the Wadden Sea (Nehls *et al.*, 1997). The biomass was found to be constant over several years.

Natural mortality: *Modiolus modiolus* are preyed upon by crabs and starfish. These predators play an important role in the population structure of horse mussel beds (review in Tyler-Walters, 2001c). *Mytilus edulis*: mortality is size dependant, e.g. Dare (1976) reported annual mortalities of 74% in 25 mm mussels and 98% in 50 mm mussels in Morecambe Bay, England. The main factors contributing to mortality are temperature, desiccation, storms and wave action, siltation and biodeposits, intra- and interspecific competition, and predation (Tyler-Walters, 2002a). Overcrowding in dense beds can result in mortality as underlying mussels are starved or suffocated by the accumulation of silt and faeces, especially in rapidly growing populations (Richardson and Seed, 1990 cited in Tyler-Walters, 2002a). The vulnerability of mussels to predation decreases as they grow. *Mytilus* spp. may be preyed upon by neogastropods (e.g. *Nucella lapillus*), starfish (*Asterias rubens*), the sea urchin *Strongylocentrotus droebachiensis*, crabs (*Carcinus maenas* and *Cancer pagurus*), fish (plaice *Pleuronectes platessa*, flounder *Platichthys flesus* and dab *Limanda limanda*), and birds such as oystercatcher, eider, knot, turnstone, gulls and crows (review in Tyler-Walters, 2002a). Kristensen (1995) estimated that 1/4 of the mussel biomass eliminated from the Danish Wadden Sea in 1991–1993 was removed by fishing, whereas 3/4 was consumed by birds. Birds preying on *Mytilus edulis* in the Koenigshafen, Wadden Sea, annually removed 30% of the standing stock (Nehls *et al.*, 1997). Hilgerloh (1997) found that predation by birds on mussel beds in the tidal flats of the East Frisian island Spiekeroog (Lower Saxony, Germany) was responsible for 7 and 15% of the total removal in 1991 and 1994, respectively. The most important predators of *Mytilus edulis* in Hobo Deep (the Danish Wadden Sea) were common eider *Somateria mollissima* and oystercatcher *Haematopus ostralegus*. (Egerrup and Laursen, 1992).

Life span: *Modiolus modiolus*: individuals over 25 years old are frequent in British populations, with occasional records of individuals of up to 35 years old. However, maximum ages are thought likely to be in excess of 50 years (Anwar *et al.*, 1990). *Musculus discors*: 2–5 years (Tyler-Walters, 2001b). *Mytilus edulis*: longevity is dependant on locality and habitat, and may range from 2–3 years on the lower shore, due to intense predation (Seed, 1969), to 18–24 years in high shore populations (Thiesen, 1973).

Reproduction: *Modiolus modiolus*: gonochoristic; fecundity: > 1,000,000 (Tyler-Walters, 2001c). The spawning season is variable or unclear and varies with depth, geographic location, and probably with temperature (review in Tyler-Walters, 2001c). *Musculus discors*: protandrous hermaphrodite; reproductive frequency: annual episodic (Tyler-Walters, 2001b). Eggs are laid throughout summer. Large eggs are laid in mucus strings within the adult nest (Thorson, 1935; Ockelmann, 1958, both cited in Tyler-Walters, 2001b). *Mytilus edulis*: gonochoristic; reproductive frequency: annual protracted with a peak of spawning in spring and summer (Tyler-Walters, 2002a); fecundity: from 7–8 million in small to 40 million in large individuals (Thompson, 1979).

Early development: *Musculus discors*: embryos are found in the mucus strings. Development is direct, there is no pelagic phase, the juveniles leave the egg string as free living organisms (Thorson, 1935; Ockelmann, 1958, both cited in Tyler-Walters, 2001b). *Mytilus edulis*: growth and metamorphosis in the plankton between spring and early summer, at about 10°C, usually takes 1 month (Tyler-Walters, 2002a).

Feeding ecology: *Modiolus modiolus*, *Musculus discors*, *Mytilus edulis*: active suspension feeders; typically feed on: bacteria, phytoplankton, detritus, and dissolved organic matter (DOM) (Tyler-Walters, 2001c, 2001b, 2002a).

Life style: *Modiolus modiolus*: temporary attachment (Tyler-Walters, 2001c). *Musculus discors*, *Mytilus edulis*: sessile (permanent attachment) (Tyler-Walters, 2001b; 2002a).

Other information: Clumps or beds of *Modiolus modiolus* increase considerably habitat complexity. They provide a habitat for a rich assemblage of species representing most of the major groups of organisms (review in Tyler-Walters, 2001c). Beds of *Mytilus* spp. provide substratum for epiflora and epifauna, and refuges for a diverse community of organisms. Accumulation of fine sediments within beds can support diverse assemblages of infauna (Tyler-Walters, 2002a)

Family: <u>Ostreidae</u> (not present in the samples)

Key species: *Ostrea edulis* (European flat oyster), *Crassostrea gigas* (Pacific oyster, Portuguese oyster)

Distribution: *O. edulis*: occurs naturally from Norway south to the Mediterranean; widely distributed around the British Isles (Hayward, 1990). *C. gigas* introduced initially to south-east and south-west coasts of Britain for mariculture. ‘Escapees’ have established populations in various regions (Hughes, 2002).

Depth: *O. edulis*: from the lower shore to about 80 m (Hayward, 1990). *C. gigas*: on the lower shore and shallow sublittoral to a depth of around 80 m (Hughes, 2002).

Substrate type: *O. edulis*: typically on hard bottoms; boulders, cobbles, pebbles, gravel/shingle, artificial (metal, wood, concrete), muddy gravel, muddy sand, mud (Jackson, 2003a).

Coastal/offshore: *O. edulis*: open coast, sealoch, ria/voe, estuary (Jackson, 2003a).

Densities: *C. gigas* growing on natural mussel beds near the island of Sylt (North Sea) reached densities of 8 ind. m^{-2} on exposed mussel beds at low tidal level, not covered by algae (Reise, 1998).

Natural mortality: *O. edulis*: native oysters are preyed on by a variety of species including starfish and two gastropods, sting winkle *Ocenebra erinacea* and common whelk *Buccinum undatum* (Jackson, 2003a). There has been significant mortalities in *O. edulis* caused by the ascetosporan parasite *Bonamia ostreae* at a number of European sites over the past twenty years (Culloty *et al.*, 2001).

Life span: *O. edulis*: typically 5–10 years. Majority of individuals in populations are 2–6 years old. However, they may reach in excess of 15 years old (Jackson, 2003a).

Reproduction: *O. edulis*: protandrous hermaphrodite; reproductive frequency: annual protracted with peaks during full moon periods; fecundity: 10,000–1,000,000 (up to 2,000,000 in large individuals) (Jackson, 2003a).

Early development: *O. edulis*: larviparous (incubatory) development takes place in the gills and mantle cavity of the female; after 7–10 days from fertilization, the veliger stage is reached, which is a planktonic stage. After a metamorphosis the veliger changes into a juvenile oyster, which attaches to a suitable rock with its byssus threads and cements itself to the substratum (Jackson, 2003a).

Feeding ecology: *O. edulis*: active suspension feeder; typically feeds on suspended organic particles (Jackson, 2003a).

Life style: sessile (permanent attachment).

Family: <u>Pectinidae</u> (*i*: 2, *e*: ?)

Key species: *Pecten maximus* (great scallop, king scallop) (not present in the samples), *Aequipecten opercularis* (queen scallop) (*e*: 16), *Pseudamussium septemradiatum* (*e*: 8)

Distribution: *Pecten maximus*: distributed from Norway to the Atlantic coast of Spain; widespread off all British coasts. *A. opercularis*: from Norway to the Mediterranean and Canary Islands; widespread and common off all British coasts. *Pseudamussium septemradiatum*: from Norway to the Mediterranean and north-west Africa (Hayward, 1990).

Depth: *Pecten maximus*, *A. opercularis*: to about 100 m. *Pseudamussium septemradiatum*: to about 200 m (Hayward, 1990).

Substrate type: *Pecten maximus, A. opercularis*: on sand and fine gravel (Hayward, 1990).

Coastal/offshore: *Pecten maximus*: offshore. *A. opercularis*: offshore, occasionally between tidemarks. *Pseudamussium septemradiatum*: offshore (Hayward, 1990).

Densities: *A. opercularis*: occurs in dense aggregations (Hayward, 1990).

Reproduction: *P. maximus*, *A. opercularis*: the main spawning period in the Irish Sea was during summer, with 1–3 peaks (Wanninayake and Brand, 1994). *A. opercularis*: off the north-west Spain, a spawning period from spring until the end of summer was observed with several partial spawnings. The spawning period was followed by a resting period in autumn and a period of recovery in winter (Roman *et al.*, 2002).

Early development: *Pecten maximus*, *A. opercularis*: veliger larvae live in the plankton (*P. maximus* larvae for 3–11 weeks depending on temperature) before settling out. Spat of both species was observed to produce a long, fine byssus drifting thread, which can slow down their descent (Beaumont and Barnes, 1992).

Feeding ecology: *A. opercularis*: selective suspension feeder; feeds mainly on sedimenting phytoplankton (Thouzeau, 1996).

Life style: *Pecten maximus*, *A. opercularis*: juvenile stages are attached with byssus threads, while the adult stages are free living and capable of swimming (Hayward, 1990).

Family: Scrobiculariidae (*i*: 56)

Key species: *Abra prismatica* (*i*: 41), *A. nitida* (*i*: 16), *A. alba* (*i*: 13)

Distribution: *A. prismatica*, *A. nitida*, *A. alba*: distributed from Norway to the Mediterranean and north-west Africa (*A. alba* to west Africa) (Hayward, 1990).

Depth: *A. prismatica*: from the lower shore to about 60 m. *A. nitida*: to the edge of the Continental Shelf. *A. alba*: shallow waters to about 60 m, occasionally on the lower shore (Hayward, 1990).

Substrate type: *A. prismatica*: in mixed sandy bottoms. *A. nitida*: burrowing in mixed soft substrata (Hayward, 1990). *A. alba*: soft substrata such as muddy gravel, sandy mud, muddy sand and mud (Hayward, 1990; Budd, 2003).

Coastal/offshore: *A. nitida*: offshore waters (Hayward, 1990). *A. alba*: open coast, offshore seabed, strait/sound, sealoch, enclosed coast/embayment (Budd, 2003).

Densities: *A. nitida*: the average annual population density off the coast of Northumberland (NE England) between 1971–1972 was 16 ind. m^{-2} (Buchanan and Warwick, 1974). *A. alba*: adult densities may exceed 1000 ind. m^{-2} in favourable conditions. Abundance varies and depends largely on recruitment success (Budd, 2003). High densities of newly settled spat have been recorded, e.g. 16,000–22,000 ind. m^{-2} in the western part of the Limfjord, Denmark (Jensen, 1988 cited in Budd, 2003). Average densities of adult *A. alba* in Kiel Bay in the late 1970s varied over a period of 1–3 years from 70 to 659 ind. m^{-2} depending on locality. Densities varied widely with season (maximum in winter) and interannually (Rainer, 1985). The annual mean density of *A. alba* in the Southern Bight of the North Sea was 311 ind. m^{-2} (Amara *et al.*, 2001).

Biomass: *A. nitida*: the average annual biomass off the Northumberland coast between 1971–1972 was 106 mg AFDW m^{-2}; the total production in the area was 118 mg AFDW m^{-2} y^{-1} (Buchanan and Warwick, 1974). *A. alba*: the mean biomass in Kiel Bay in 1968 was estimated by Arntz (1971a cited in Rainer, 1985) to be 19.5 g WW m^{-2} (ca. 0.55 g C m^{-2}). The mean annual biomass in Kiel Bay in the late 1970s ranged from 84 to 900 mg C m^{-2}; production estimates ranged from 110 to 3,000 mg C m^{-2} y^{-1}; P:B ratios varied between sites and between years from 1.4 to 3.4, with a long-term average P:B = 2.2 (Rainer, 1985). The long-term estimate of *A. alba* biomass in Kiel Bay between 1968 and 1978 was found to be around 13.6 g WW m^{-2} (ca. 0.38 g C m^{-2}) (Arntz, 1980 cited in Rainer, 1985). At a location off the French coast, B = 0.1–2 g AFDW m^{-2} and P:B = 1.7–2.9 (Dauvin, 1986). In the Bristol Channel, England, B = 0.3 g AFDW m^{-2} and P:B = 1.4 (Warwick and George, 1980). Annual mean biomass in the Southern Bight: 10.0 g AFDW m^{-2} (Amara *et al.*, 2001).

Natural mortality: *A. alba* was reported to be important prey for plaice, dab and flounder in Kiel Bay (review in Rainer, 1985) and for plaice and larger dab in Øresund (Degel and Gislason, 1988). This bivalve also dominated in the diet of plaice off eastern Anglesey (Basimi and Grove, 1985). Rainer (1985) considered *A. alba* to be important food for juvenile fish and for intermediate-level predators that are themselves prey for larger fish.

Life span: *A. prismatica*: one year in the Bay of Morlaix (western English Channel) (Dauvin, 1986). *A. alba*: between >1 and 2.5 years in Kiel Bay (Rainer, 1985). Maximum life span in individuals from the Bay of Morlaix, France was estimated at 1 or 2 years depending on whether settlement took place in autumn or summer. They could spawn once or twice during their life span, respectively (Dauvin and Gentil, 1989).

Reproduction: *A. nitida* in southern Skagerrak showed some degree of spawning activity throughout the whole year, but the number of spawning individuals was highest in the autumn months (Brown, 1982). *A. alba*: gonochoristic; reproductive frequency: annual episodic; fecundity: 10,000–100,000 (15,000–17,000 in average-sized individuals); external fertilization. Two distinct spawning periods in summer and autumn have been observed in the Irish Sea (Budd, 2003).

Early development: *A. prismatica*: recruitment in the Bay of Morlaix occurs in spring. The population shows interannual variations in recruitment (Dauvin, 1986). *A. alba*: the eggs develop into free-swimming trochophore and then veliger larvae. Larvae are subject to very high mortality (Budd, 2003). The planktonic stage lasts about a month (Dauvin and Gentil, 1989). Young post-larvae secret a long drifting thread that enables them to be carried along on the current before they settle out (Sigurdsson *et al.*, 1976). Peak recruitment usually occurs in summer (Dauvin and Gentil, 1989).

Feeding ecology: *A. nitida*: deposit feeder (Ekelund *et al.*, 1987). *A. alba*: active suspension feeder, surface deposit feeder; can switch between these two feeding methods, depending upon the conditions of the environment (Dame, 1996); typically feeds on: phytoplankton and detritus (Rosenberg, 1993; Budd, 2003).

Life style: infaunal.

Family: <u>Solenidae</u> (*i*: 43)

Key species: *Phaxas pellucidus* (*i*: 32), *Ensis* spp. (razor shell) (*i*: 13)

Distribution: *P. pellucidas*: distributed from Norway to north-west Africa; widespread, and often abundant, around Britain. *E. ensis*, *E. silica* and *E. arcuatus*: from Norway south to the

Mediterranean and north-west Africa (*E. arcuatus*: to Spain); off all British coasts (Hayward, 1990).

Depth: *P. pellucidas*: to about 100 m. *E. ensis*, *E. silica* and *E. arcuatus*: from the lower shore into the shallow sublittoral (Hayward, 1990), to a depth of 60 m (Hill, 2000c).

Substrate type: *P. pellucidas*: in mixed fine substrata. *E. ensis*: fine sand. *E. silica*: sand. *E. arcuatus*: in sand and gravel (Hayward, 1990).

Coastal/offshore: *P. pellucidas*: offshore. *Ensis* spp.: open coast, offshore seabed, strait/sound, enclosed coast/embayment (Hill, 2000c).

Densities: *Ensis* spp.: abundance can vary greatly (Hill, 2000c). Average abundance of *Ensis* spp. off the north east coast of Anglesey, Liverpool Bay, was 1.5 and 0.5 ind. per 100 m^2, in April and October 1993, respectively (Kaiser *et al.*, 1998b).

Natural mortality: *Ensis* spp.: occasional mass mortalities have been reported attributable to adverse environmental conditions (e.g. storms) (review in Hill, 2000c).

Life span: *Ensis* spp.: 10–20 years (Hill, 2000c).

Reproduction: *Ensis* spp.: gonochoristic; reproductive frequency: annual episodic (Hill, 2000c). Spawning occurs during the spring and summer (review in Hill, 2000c).

Early development: *Ensis* spp.: Planktonic stage (veliger larvae) lasts about a year (Fish and Fish, 1996). The success of larval settlement is variable from year to year (Hill, 2000c).

Feeding ecology: *Ensis* spp.: active suspension feeders; typically feed on suspended organic detritus (Hill, 2000c).

Life style: infaunal, slow mobility.

Family: <u>Tellinidae</u> (*i*: 32)

Key species: *Fabulina fabula* (*i*: 25), *Moerella pygmaea* (*i*: 8)

Distribution: *F. fabula*: distributed from Norway to the Mediterranean and north-west Africa; off all British coasts. *M. pygmaea*: from northern Norway to the Mediterranean and West Africa; reported from south-west and west coasts of Britain (Hayward, 1990).

Depth: *F. fabula*: from the lower shore into the shallow sublittoral (Hayward, 1990), to 55 m (Rayment, 2001b). *M. pygmaea*: from the lower shore into shelf waters (Hayward, 1990).

Substrate type: *F. fabula*: in mixed sandy deposits such as fine clean sand and muddy sand (Hayward, 1990; Rayment, 2001b). *M. pygmaea*: in sand and shell-gravel (Hayward, 1990).

Coastal/offshore: *F. fabula*: open coast, offshore seabed, enclosed coast/embayment (Rayment, 2001b).

Densities: *F. fabula* can be found in high densities (Rayment, 2001b). It is one of the most abundant species on the Dogger Bank (Johnston *et al.*, 2000). Salzwedel (1979) reported densities of *F. fabula* from the German Bight ranging from ca. 500 ind. m^{-2} in February to ca. 2000 ind. m^{-2} in September. The mean annual abundance was approximately 1000 ind. m^{-2}. Warwick *et al.* (1978) reported densities of 80 ind. m^{-2} in Carmarthen Bay, Bristol Channel. Bergman and Hup (1992) reported mean densities of 20 and 130 ind. m^{-2} for small and large *F. fabula*, respectively (studied as *Tellina fabula*).

Biomass: The mean biomass of *F. fabula* in Carmarthen Bay was 340 mg m^{-2} (Warwick *et al.*, 1978).

Natural mortality: *F. fabula*: Salzwedel (1979) reported annual mortalities for *F. fabula* in the German Bight of 82–96%. These high mortalities were attributed to predation and erosion of substratum. Salzwedel (1979) reported that *F. fabula* is preyed upon by the boring gastropod *Lunatia intermedia*, and Aberkali and Trueman (1985 also cited in Rayment, 2001b) reported predation by the starfish *Astropecten irregularis*.

Life span: 2–5 years (Rayment, 2001b).

Reproduction: *F. fabula*: gonochoristic; reproductive frequency: annual protracted (Rayment, 2001b). *F. fabula* from the German Bight spawned from March to September, but the main spawning period was in July/August. Individuals that spawned early in the spring, spawned again in the autumn (Salzwedel, 1979).

Early development: *F. fabula*: planktonic larvae. The larval phase lasts at least a month (Salzwedel, 1979). Development after settlement is highly dependent on environmental conditions (Rayment, 2001b).

Feeding ecology: *F. fabula*: active suspension feeder, surface deposit feeder; typically feeds on phytoplankton and detritus (Rayment, 2001b).

Life style: burrower.

Superclass: Tunicata (Phylum: Chordata)

Family: Ascidiidae (*i*: 29, *e*: ≈ 30)

Key species: *Ascidiella scabra* (sea squirt) (*e*: 25)

Distribution: *A. scabra*: Norway to the Mediterranean; all British coasts (Knight-Jones and Ryland, 1990).

Depth: *A. scabra*: lower shore to about 300 m (Knight-Jones and Ryland, 1990).

Substrate type: *A. scabra*: on algae, stones and shells (Knight-Jones and Ryland, 1990).

Coastal/offshore: A. scabra: open coast, offshore seabed, strait/sound, sealoch, ria/voe, estuary, enclosed coast/embayment (Hiscock, 2003).

Densities: *A. scabra* occurs in moderate densities (Hiscock, 2003).

Life span: *A. scabra*: 2–5 years (Hiscock, 2003).

Reproduction: *A. scabra*: reproductive frequency: annual protracted; high fecundity (Hiscock, 2003).

Early development: *A. scabra*: larval settling time: 2–10 days (Hiscock, 2003).

Feeding ecology: *A. scabra*: active suspension feeder (Robbins, 1983); typically feeds on suspended particles including phytoplankton (Hiscock, 2003).

Life style: *A. scabra*: sessile (permanent attachment) (Hiscock, 2003).

Other information: *A. scabra* is a fast colonizing species and may be a fouling organism (Schmidt, 1983). It may compete with the scallops *Chlamys opercularis* and *Pecten maximus* for space or for food (Brand *et al.*, 1980).

Phylum: Porifera

Family: Suberitidae (*e*: ?)

Key species: *Suberites ficus* (*e*: 16), *Suberites ficus* ssp. *pagurorum* (*e*: 22)

Distribution: *S. ficus*: common on all British coasts (Dyrynda and Dyrynda, 1990).

Depth: *S. ficus*: occasionally in the low littoral, more commonly in the sublittoral (Dyrynda and Dyrynda, 1990).

Substrate type: *S. ficus*: epilithic, occurs on rock and other hard substrata such as wreckage, also on stones and shells (Dyrynda and Dyrynda, 1990; Avant, 2002d). Reported to prefer being exposed to tidal currents (Avant, 2002d).

Feeding ecology: active suspension feeders. Reiswig (1975) found that bacteria alone could satisfy the entire food requirement for these sponges.

Life style: sessile.

Other information: *S. ficus* is often found attached to shells inhabited by hermit crabs (*Pagurus* spp.) (Sole-Cava and Thorpe, 1986) or associated with queen scallops *Chlamys opercularis* (Armstrong *et al.*, 1999).

APPENDIX 7. Summary of the monetary value of benthic invertebrates and habitats within the North Sea.

Monetary value of exploited benthic invertebrates and habitats in selected areas.

Species	Method of harvesting	Area	Ranked importance	Value in million £	Reference
Nephrops norvegicus	Fishery	UK (west and east, average for 1996–2000)	3	62	DEFRA, 2001
	Fishery	UK-North Sea (estimate)	3	26	DEFRA, 2001
	Fishery	Denmark (average for 1990–1999)	3	17	ICES, 2002c
Crangon crangon	Fishery	Wadden Sea	3	approx. 23	Del Norte-Campos and Temming, 1998
	Fishery	Denmark (average for 1990–1999)	3	3	Anon, 2000
Cerastoderma edule	Suction dredging, hand raking	Netherlands	3	6	Kamermans and Smaal, 2002
	Hand raking	UK	3	3	DEFRA, 2001
	Shell ranching	UK	3	0.3	DEFRA, 2001
Mytilus edulis	Seed fishery	Netherlands	3	34	Kamermans and Smaal, 2002
	Seed fishery	UK	3	3.6–7.4	Burton *et al*., 2001
Ostrea edulis	Harvested/mariculture	UK	3	1.1	Burton *et al*., 2001
Scallops (mainly *Pecten maximus*)	Fishery	UK	3	29.5	DEFRA, 2001
	Seed fishery	UK	3	0.9	Burton *et al*., 2001
Arenicola marina	Bait digging	North Sea	2	?	Fowler, 1999
Nereis virens	Bait digging	UK	2	≤ 5	Fowler, 1999
Rhodophyceae (maerl)		Brittany (France)	2	?	Blunden *et al*., 1975; Guiry and Blunden, 1991
Homarus gammarus	Fishery/mariculture	UK/Norway	2	13.4	Burton *et al*., 2001
Pandalus borealis	Fishery	UK	2	5.5	ICES, 2003d
	Fishery	Denmark (average 1990-1999)	2	11	Anon, 2000
Nephtyidae	Bait digging	UK	1	?	Fowler, 1999
	Aquaculture	UK	1	0.7	Fowler, 1999
Cancer pagurus	Fishery	North Sea	1	?	QSR, 2000
Munida rugosa	Fishery	North Sea	1	?	Hughes, 1998
Echinus esculentus	Fishery and aquaculture	UK,	1		Kelly *et al*., 1998
Modiolus modiolus	Fished for bait	Scotland/Norway	1	?	Comely 1978; Fowler, 1999
Periwinkles	Hand picking	UK	1	1.7	DEFRA, 2001
Aequipecten opercularis	Fishery	UK	1	2.2	DEFRA, 2001
Other shellfish	Fishery/mariculture	UK	1	8.5	DEFRA, 2001
Laminaria hyperborea	Harvesting	Norway	1	?	Dauvin *et al*., 1997 cited in Birkett *et al*., 1998

Catches and value of landings of invertebrates by Danish vessels within the North Sea (Anon., 2000a).

Danish nominal catches from the North Sea by species

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	average
Nephrops norvegicus	756	880	582	691	1133	1182	1317	1309	1440	1963	1125.3
Pandalus borealis	2086	750	1881	1985	1362	4699	4085	3315	3272	1678	2511.3
Crangon crangon	652	855	2502	1521	1742	2066	2207	3250	2509	2908	2021.2
Other shrimps	0	0	0	0	0	0	0	0	0	0	0
Other crab species	129	151	119	116	328	112	77	85	101	93	131.1
Mytilus edulis	1759	5539	5041	3498	4398	8931	2213	263	3774	4195	3961.1
Other molluscs	3024	331	2923	2197	2748	3139	6	2614	2003	267	1925.2

Value of landings by Danish vessels in Danish ports by species (in £ million)

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	average
Nephrops norvegicus	22.0	18.9	13.0	10.4	12.3	13.4	15.9	18.8	23.0	29.8	17.7
Pandalus borealis	7.0	53.4	7.0	5.1	3.8	7.8	8.4	6.3	6.3	3.6	10.9
Crangon crangon	1.6	2.4	3.3	2.3	3.4	4.0	3.6	3.5	3.4	6.7	3.4
Other shrimps	0.3	0.3	0.3	0.2	0.4	0.2	0.2	0.2	0.2	0.2	0.3
Other crab species	0.3	0.3	0.3	0.3	0.4	0.3	0.4	0.5	0.4	0.4	0.4
Mytilus edulis	4.0	7.2	7.6	7.2	5.7	6.8	4.8	5.3	7.0	7.6	6.3
Other molluscs	0.3	0.0	0.3	0.3	0.2	0.3	0.0	0.3	0.3	0.0	0.2

Landings of invertebrates in the UK and abroad by UK and foreign vessels for the period 1996-2000 (DEFRA, 2001). Value of the landings are shown in £ million.

Species	Quantity ('000 tonnes)						Value (£ million)					
	1996	1997	1998	1999	2000	Mean	1996	1997	1998	1999	2000	Mean
Cockles	24.2	19.5	12.1	14.2	20.3	18.1	3.3	3.6	4.2	2.5	3	3.32
Crabs	20.3	22.5	27.2	23	25.7	23.7	22.2	24.3	32.3	27	28.1	26.7
Mussels	12.3	9.6	12.7	8.4	7.5	10.1	4.6	3.1	3.5	2.1	1.4	2.94
Nephrops	29	31.1	28.6	31.1	28.3	29.6	57.2	63.5	57	74.3	60.8	62.5
Periwinkles	2.4	2.9	2	1.2	1.1	1.9	2	2.7	1.9	1.2	1.1	1.7
Queens	2.3	5.6	8.1	5.9	5.3	5.4	1.2	2	2.9	2.6	2.3	2.2
Scallops	17.3	18.7	20.6	19.4	20.1	19.2	27.4	27.9	31	29.6	31.3	29.4
Lobsters	1.3	1.5	1.6	1.8	1.2	1.5	11.9	13.1	14.5	14.9	12.5	13.4
Shrimps	3	1	2.4	2	1.7	2	3.7	1.	2.8	3	2.1	5.5
Other shellfish	18.7	12.3	7.7	8	14.8	12.3	12.4	8.2	7.7	5.4	8.7	8.5

The mariculture production of shellfish in the North Sea in piece (p) or tonnes (t) (QSR, 2000).

Country	Oysters	Scallops (p)	Mussel (t)
Netherlands (1996)	17,000,000 p		
Denmark (1996)			59,602
France	48,000 t		41,000
Germany(1966)	75 t		38,028
Netherlands			95,000
Norway (1996)	530,000 p	90,000	180
UK (1996)	14,000,000 p	3,000	7,700
Sweden (1996)			1,800

APPENDIX 8. Dominant infauna of the North Sea.

Families found in more than 50% of stations are shown. Data are from Craeymeersch *et al.* (1997).

Family	Phylum	% presence	Mean abundance (no. ind. m^{-2})	Mean abundance in stations where recorded (no. ind. m^{-2})
Spionidae	Annelida	98.3	130.0	132.3
Nephtyidae	Annelida	90.9	29.4	32.3
Nemertea indet.	Nemertea	87.0	26.6	30.5
Goniadidae	Annelida	81.8	23.1	28.2
Orbiniidae	Annelida	81.0	39.4	48.7
Sigalionidae	Annelida	79.7	38.3	48.1
Phyllodocidae	Annelida	73.6	12.0	16.3
Oweniidae	Annelida	71.4	135.8	190.1
Amphiuridae	Echinodermata	68.0	114.1	167.9
Haustoriidae	Arthropoda	66.7	59.9	89.8
Spatangidae	Echinodermata	66.2	13.4	20.2
Anthozoa indet.	Cnidaria	63.6	16.3	25.6
Capitellidae	Annelida	63.2	52.5	83.1
Paraonidae	Annelida	62.3	47.2	75.7
Cirratuloidea	Annelida	61.9	13.9	22.5
Montacutidae	Mollusca	61.5	59.1	96.2
Phoronidae	Phoronida	61.5	29.8	48.5
Veneridae	Mollusca	60.6	20.1	33.2
Opheliidae	Annelida	59.3	30.7	51.8
Ophiolepidae	Echinodermata	58.9	19.8	33.5
Naticidae	Mollusca	58.0	7.2	12.5
Ampeliscidae	Arthropoda	57.1	11.7	20.5
Scrobiculariidae	Mollusca	56.3	11.4	20.3
Oedicerotidae	Arthropoda	53.7	6.8	12.6
Phoxocephalidae	Arthropoda	52.8	17.8	33.7
Glyceridae	Annelida	51.9	20.9	40.2
Leuconidae	Arthropoda	51.1	26.6	52.1

Families found in greater mean abundance than 10 ind.$^{-1}$ m^{-2}

Family	Phylum	% presence	Mean abundance (no. ind. m^{-2})	Mean abundance in stations where recorded (no. ind. m^{-2})
Oweniidae	Annelida	71.4	135.8	190.1
Spionidae	Annelida	98.3	130.0	132.3
Amphiuridae	Echinodermata	68.0	114.1	167.9
Haustoriidae	Arthropoda	66.7	59.9	89.8
Montacutidae	Mollusca	61.5	59.1	96.2
Capitellidae	Annelida	63.2	52.5	83.1
Thyasiridae	Mollusca	31.2	47.6	152.6
Paraonidae	Annelida	62.3	47.2	75.7
Orbiniidae	Annelida	81.0	39.4	48.7
Magelonidae	Annelida	45.0	39.1	86.9
Sigalionidae	Annelida	79.7	38.3	48.1
Opheliidae	Annelida	59.3	30.7	51.8
Phoronidae	Phoronida	61.5	29.8	48.5
Nephtyidae	Annelida	90.9	29.4	32.3
Ophiuroidea indet.	Echinodermata	18.6	27.8	149.3
Leuconidae	Arthropoda	51.1	26.6	52.1
Nemertea indet.	Nemertea	87.0	26.6	30.5
Syllidae	Annelida	35.9	26.1	72.6
Goniadidae	Annelida	81.8	23.1	28.2
Glyceridae	Annelida	51.9	20.9	40.2
Ampharetidae	Annelida	43.3	20.7	47.8
Veneridae	Mollusca	60.6	20.1	33.2
Ophiolepidae	Echinodermata	58.9	19.8	33.5
Phoxocephalidae	Arthropoda	52.8	17.8	33.7
Tellinidae	Mollusca	32.0	17.4	54.4
Anthozoa indet.	Cnidaria	63.6	16.3	25.6
Cirratuloidea	Annelida	61.9	13.9	22.5
Spatangidae	Echinodermata	66.2	13.4	20.2
Nuculidae	Mollusca	39.0	12.7	32.5
Cirratulidae	Annelida	42.0	12.4	29.6
Terebellidae	Annelida	45.9	12.3	26.9
Phyllodocidae	Annelida	73.6	12.0	16.3
Pectinariidae	Annelida	45.0	11.9	26.4
Diastylidae	Arthropoda	37.2	11.7	31.6
Ampeliscidae	Arthropoda	57.1	11.7	20.5
Scrobiculariidae	Mollusca	56.3	11.4	20.3
Maldanidae	Annelida	33.8	11.0	32.5
Lumbrineridae	Annelida	35.5	10.8	30.5
Pisionidae	Annelida	12.1	10.7	88.4

Families found in greater mean abundance than 40 ind.$^{-1}$ m^{-2} in those stations where they were recorded.

Family	Phylum	% presence	Mean abundance (no. ind. m^{-2})	Mean abundance in stations where recorded (no. ind. m^{-2})
Oweniidae	Annelida	71.4	135.8	190.1
Amphiuridae	Echinodermata	68.0	114.1	167.9
Thyasiridae	Mollusca	31.2	47.6	152.6
Ophiuroidea indet.	Echinodermata	18.6	27.8	149.3
Protodrilidae	Annelida	0.9	1.2	139.6
Spionidae	Annelida	98.3	130.0	132.3
Siphonodentaliidae	Mollusca	2.2	2.2	100.0
Montacutidae	Mollusca	61.5	59.1	96.2
Haustoriidae	Arthropoda	66.7	59.9	89.8
Dorvilleidae	Annelida	8.7	7.8	89.6
Pisionidae	Annelida	12.1	10.7	88.4
Magelonidae	Annelida	45.0	39.1	86.9
Dexaminidae	Arthropoda	1.7	1.5	84.4
Capitellidae	Annelida	63.2	52.5	83.1
Paraonidae	Annelida	62.3	47.2	75.7
Syllidae	Annelida	35.9	26.1	72.6
Tellinidae	Mollusca	32.0	17.4	54.4
Anomiidae	Mollusca	1.3	0.7	54.1
Amphinomidae	Annelida	16.5	8.6	52.3
Leuconidae	Arthropoda	51.1	26.6	52.1
Opheliidae	Annelida	59.3	30.7	51.8
Orbiniidae	Annelida	81.0	39.4	48.7
Phoronidae	Phoronida	61.5	29.8	48.5
Sigalionidae	Annelida	79.7	38.3	48.1
Ampharetidae	Annelida	43.3	20.7	47.8
Donacidae	Mollusca	2.2	1.0	47.6
Glyceridae	Annelida	51.9	20.9	40.2

APPENDIX 9. Dominant epifauna of the North Sea.

The most frequently recorded species of epibenthos in the North Sea (found in more than 20% of stations). Data from Anon. (2001).

Species	Family	Phylum	% presence
Pagurus bernhardus	Paguridae	Arthropoda	87.0
Asterias rubens	Asteriidae	Echinodermata	78.5
Astropecten irregularis	Astropectinidae	Echinodermata	71.1
Liocarcinus holsatus	Portunidae	Arthropoda	53.3
Ophiura ophiura	Ophiuridae	Echinodermata	50.4
Hydractinia echinata	Hydractiniidae	Cnidaria	47.8
Crangon allmanni	Crangonidae	Arthropoda	46.3
Colus gracilis	Buccinidae	Mollusca	38.5
Neptunea antiqua	Buccinidae	Mollusca	38.5
Anapagurus laevis	Paguridae	Arthropoda	38.1
Hydrallmania falcata	Sertulariidae	Cnidaria	38.1
Buccinum undatum	Buccinidae	Mollusca	37.4
Hyas coarctatus	Majidae	Arthropoda	34.8
Ophiura albida	Ophiuridae	Echinodermata	34.4
Pagurus pubescens	Paguridae	Arthropoda	34.1
Flustra foliacea	Flustridae	Bryozoa	32.2
Pandalus montagui	Pandalidae	Arthropoda	30.7
Aphrodita aculeata	Aphroditidae	Annelida	29.3
Hormathia digitata	Hormathiidae	Cnidaria	29.3
Alcyonium digitatum	Alcyoniidae	Cnidaria	27.8
Luidia sarsi	Luidiidae	Echinodermata	26.7
Epizoanthus incrustatus (=E. papillosus)	Epizoanthidae	Cnidaria	26.3
Hyalinoecia tubicola	Onuphidae	Annelida	25.9
Ascidiella scabra	Ascidiidae	Chordata	24.8
Alcyonidium diaphanum	Alcyonidiidae	Bryozoa	24.4
Echinus spp.	Echinidae	Echinodermata	24.4
Spirontocaris lilljeborgi	Hippolytidae	Arthropoda	24.1
Hydroides norvegica	Serpulidae	Annelida	23.7
Corystes cassivelaunus	Corystidae	Arthropoda	23.7
Pagurus prideaux	Paguridae	Arthropoda	23.7
Liocarcinus depurator	Portunidae	Arthropoda	23.3
Psammechinus miliaris	Parechinidae	Echinodermata	23.3
Suberites pagurorum	Suberitidae	Porifera	22.2

APPENDIX 10. Classification of feeding guilds of infauna by Swift (1993).

A classification system of infaunal bioturbatory activity ranging from 0=no bioturbatory impacts to 4= large bioturbatory impacts (Swift, 1993).

	Slow movement within sediment with a non-permanent burrow formation	2
	Freely mobile within sediment in a permanent. excavated burrow system	3
Feeding		
	Carnivore or a filter feeder	0
	Sub-surface sediment ingestion; egestion at the same level	1
	detritus or surface sediment ingestion; egestion below the surface	2
	Detritus or surface sediment ingestion; egestion below the surface	3
	Sub-surface sediment ingestion; egestion at the surface	4
Burrowing		
	No burrowing activity	0
	Construction of simple surface hole or pit or covering the body in sediment as camouflage	1
	Burrowing by displacement of particles without net particle transport	2
	Burrowing with selective particle transport to surface	3
	Burrowing extensively horizontally and/or vertically with net transport to surface	4

Classification on feeding guilds after Swift (1993) on the basis of infaunal activity.

Phylum	Species	Mobility	Feeding	Burrowing	Total
Arthropoda	*Callianassa subterranea*	3	4	4	11
	Jaxea nocturna	3	4	4	11
	Upogebia deltaura	3	4	4	11
	Goneplax rhomboides	3	4	4	11
	Corystes cassivelaunus	1	0	1	2
Echiura	*Maxmuelleria lankesteri*	3	3	4	10
Polychaeta	*Notomastus latericeus*	3	1	2	6
	Nephtydae	2	0	2	4
	Glycera tridactyla	3	0	2	5
	Lagis koreni	2	4	3	9
	Opheliidae	2	1	2	5
	Orbinidae	3	1	2	6
	Polynoidae	2	0	2	4
	Aphrodita aculeata.	2	0	2	4
	Nereidae	2	0	2	4
	Chaetopterus variopedatus	0	0	0	0
	Owenia fusiformis	0	0	0	0
	Scalibregma inflatum	0	0	0	0
	Amphicteis gunneri	0	0	0	0
Sipuncula	*Golfingia vulgaris*	1	3	1	4
Echinodermata	*Echinocardium cordatum*	2	1	2	5
	Amphiura filiformis	0	0	1	1
	Ophiura ophiura	1	0	1	2
	Astropecten irregularis	1	0	0	1
	Asterias rubens	1	0	0	1
	Trachythyone elongata	0	0	1	1
	Leptosynapta inhaerens	2	3	3	8
Mollusca	*Philine aperta*	1	0	1	2
	Abra abra	0	3	1	4
	Cardidae	0	0	1	2
	Veneridae	0	0	1	1
	Phaxas pellucidus	0	0	1	1
	Ensis siliqua	0	0	1	1
	Mya arenaria	0	0	1	1
	Arctica islandica				
Cnidaria	*Virgiularia mirabilis*	0	0	0	0
	Peachia cylindrica	0	0	1	1
Priapulida	*Priapulus caudatus*	0	0	1	1

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