The European anchovy

(*Engraulis encrasicolus*) increase in the North Sea

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"In liebevoller Verehrung"…

To my teachers,

past and present.

Contents

CHAPTER 1

Introduction: A background review for the anchovy increase in the North Sea

Small pelagic fish populations, i.e. planktivorous schooling fish, mainly of the order Clupeiformes, are of global importance both socio-economically and ecologically (Pikitch et al. 2012a, Pikitch et al. 2012b).

In the North Sea, herring and sprat are important species in terms of number and fishery (Dickey-Collas et al. in press). European anchovy (*Engraulis encrasicolus*) is usually found further South in Europe: in the Bay of Biscay, Mediterranean and Black Seas (Barange et al. 2009) but also in small numbers on the southern coast of the North Sea (Boddeke & Vingerhoed 1996). In the mid-1990s, anchovy in the North Sea showed an increase in abundance and distribution as far North as Scotland (Beare et al. 2004).

The reasons for this increase were unknown, but changes in this population may reflect or indicate changes in other components of the North Sea ecosystem. Indeed, many concurrent changes were happening in the North Sea. Among these, changes in the plankton and general warming due to climate change appeared likely to influence this planktivorous fish previously found further South in Europe.

This thesis therefore addresses the ecology of anchovy in the North Sea, including possible causes and mechanisms for the anchovy increase. First by establishing basic trophic and life cycle characteristics of anchovy, then by focusing on the impact of environmental variables like food availability and temperature on young anchovy and lastly by generalising to possible spatial range expansion processes.

This introductory chapter gives an overview of the main background to the thesis and outlines the questions, hypotheses and approaches we use. The importance of small pelagic fish in global ecosystems is presented, as well as further details on the North Sea anchovy and its population increase. I then give an overview of important processes regulating population dynamics, relating these to changes observed in the North Sea. The importance of space and scale in ecology is noted and we briefly explain the implications for the concept of regime shifts in the oceans.

Small pelagic fish in a global perspective

The economic importance of small pelagic fish results from the magnitude of the catches of these fish across several major oceans, rather than from a high value of the fish *per se*. Indeed, the catches make up over 50% of the world's wild-caught catches despite coming from only 3.7% of all recorded fish species (Cury et al. 2000). Ecologically, small pelagic fish play a crucial role because they can constitute such a large biomass in pelagic systems that they have the capacity to exert strong bottom up or top down control. Bottom up control is the type of ecological control where resource availability controls consumer/predator

populations – e.g. the small pelagics supporting large populations of carnivorous fish, seabirds and marine mammals. However, these small pelagics may also exert top-down control, where resource populations are controlled by a predator, e.g. they might be limiting the populations of the plankton species they feed on (e.g. mesocosm experiments by Mowitt et al. 2006 and suggested in e.g. the Baltic by Casini et al. 2006).

The extent to which bottom up and top down control plays a role in ecological systems and in marine systems specifically has been heavily debated. Generally systems were thought of as being controlled either in a bottom up/resource-limited or a top down/predation-controlled way, but then the example of small pelagics opened a way to a more diversified way of considering the ecological control mechanisms. Small pelagics were singled out as so-called "wasp-waist" control species (Rice 1995, Cury et al. 2000, Bakun 2006), controlling the higher trophic levels by bottom up control and the lower trophic levels by top down control. This makes them a pivotal component of the system, possibly in the North Sea as well (Fauchald et al. 2011), although recent analyses suggest the wasp-waist idea in general may be an oversimplification (Fréon et al. 2009, Madigan et al. 2012).

An interesting feature of small pelagic fish populations is that they naturally undergo large-scale abundance fluctuations associated with range changes on a regular basis (Lluch-Belda et al. 1989, Schwartzlose et al. 1999, Lehodey P. et al. 2006). Sometimes, species pairs in a same system alternate in their dominance by biomass, e.g. anchovy and sardine in the Benguela, Humboldt, California and Japan systems (reviewed by Schwartzlose et al. 1999 or sardine and herring in the English Channel Alheit & Hagen 1997). Nowadays and historically however, fluctuations in species abundance do not always correspond to species alternations (Soutar & Isaacs 1974).

Climate was long considered to be the main driver behind these abundance fluctuations, although the possible impact of other factors such as fishing has not been excluded (fishing has been invoked as possible cause for large-scale declines of fish populations e.g. Hutchings & Myers 1994, Jackson et al 2001, Roberts 2007). Support for the climate theory comes from the close correspondence between population abundance and climate conditions e.g. in the North Pacific for instance, sardine dominates under warm conditions, while in cold phases, anchovy prevails (Lluch-Belda et al. 1989). Moreover, there is a correspondence of phase timings across different ocean basins, with pelagic stocks fluctuating in phase with each other (e.g. Northwest and Southeast Pacific sardine) which resulted in the suggestion that long distance climatic linkages may be involved. There are however some exceptions such as e.g. the Californian sardine stock which is out of phase with the others (Schwartzlose et al. 1999). Yet since climate cannot be controlled for in large-scale marine systems, progress is largely made by the comparative rather than experimental method, which makes advances slow as there

are many case studies to bring under one consistent framework. It should be noted that even if the climate hypothesis is correct and climate were the ultimate cause of fluctuations, the proximate mechanisms remain unknown. Mechanisms proposed include that the species alternations are trophodynamically mediated (van der Lingen et al. 2006) with one species benefitting from slight changes in plankton availability, or related to the species having different optimal temperatures for growth (Takasuka et al. 2007) or differential abilities to evade biological controls (loophole concept, Bakun & Broad 2003) but consensus has not yet emerged. A recent synthesis (MacCall 2009) tries to bridge between climate behaviour and other factors to provide such a framework.

Many questions remain unanswered regarding the causes and mechanisms of the strong fluctuations of small pelagics. We use European anchovy in the North Sea as a case study to investigate the possible mechanisms behind its increase in the North Sea. It is a data-poor species in the North Sea but widely distributed and studied elsewhere and it is relevant in this area because of the potential competitive interaction with other species already under exploitation pressure, e.g. herring.

European anchovy in the North Sea

The European anchovy (*Engraulis encrasicolus*) is distributed from western Africa to Norway and in Europe its main populations are found in the Mediterranean and Black Sea (FAO, 2008) and formerly in the Bay of Biscay. The Bay of Biscay anchovy biomass and catches decreased dramatically around 2000 (Borja et al. 2008) and the shared French-Spanish fishery was closed down in 2005 by a European Commission emergency measure (Commission Regulation EC No 1037/2005). It was reopened in January 2010 (ICES, WGANSA report 2010) and spawning stock biomass has recovered (ICES, WGHANSA 2012).

In the North Sea, anchovy has traditionally been present in the southern areas, such as on the Dutch coast. The Wadden Sea and Zuiderzee (before the latter was dammed in 1932) supported a fishery of over 5000 tons in the late 1930s (Meijer 1983) catches continued in the Wadden Sea at variable levels until the early 1960s (Boddeke & Vingerhoed 1996) and in the Oosterschelde, anchovy has been a steady target of a (now dwindling) coastal fishery (Petitgas et al. 2012). In northern areas of the North Sea on the other hand, records of anchovy catches are found more rarely. Recently (mid-1990s), anchovy started to appear regularly and in rapidly increasing abundances in the Irish Sea and northwestern North Sea (Armstrong et al. 1999, Beare et al. 2004). The International Bottom Trawl Survey (IBTS), a major source of information on this species, indicates that the observed increase (displayed in figure 1) occurred throughout most of the North Sea area in first quarters of the year (Petitgas et al 2012). Anchovy have also been recorded or fished in the Skagerrat, Kattegat and Baltic Sea area since its recent increase

(Enghoff et al. 2007, Schaber et al. 2010, Alheit et al. 2012) and archaeological records from northern Denmark show that it was likely present there a few thousand years ago (Enghoff et al. 2007).

Similarities can be found between the recent 1990s increase and a sudden increase recorded in the 1940s in the sense that the increase was unexpected and strong (catches over 100 000 tons in 1948 and 1949) and spurred speculations about a possible fishery at the time (Aurich 1950). Anchovy also spawned and completed its whole life cycle in the North Sea (Aurich 1953), which appears to be the case during the recent increase as well (Alheit et al. 2007, Alheit et al. 2012). Catches increased to sufficient levels in 2007 for pelagic fishing boats to switch to targeting this species (Cheung et al. 2012). As in the 1950s, now too a potential causal link to climate has been made (Alheit et al. 2007), now more concrete in the form of the Atlantic Multidecadal Oscillation, AMO, but what are the mechanisms involved? Current and historic abundance and distribution of anchovy in the North Sea brings up many unanswered questions; until recently, it was even unclear whether the current observation of anchovy in the North Sea was a range expansion of a local population, a northward movement of a whole stock, or a newly seeded population (but see chapter 4). In order to study such mechanisms, the use of general concepts and a population dynamics framework are essential.
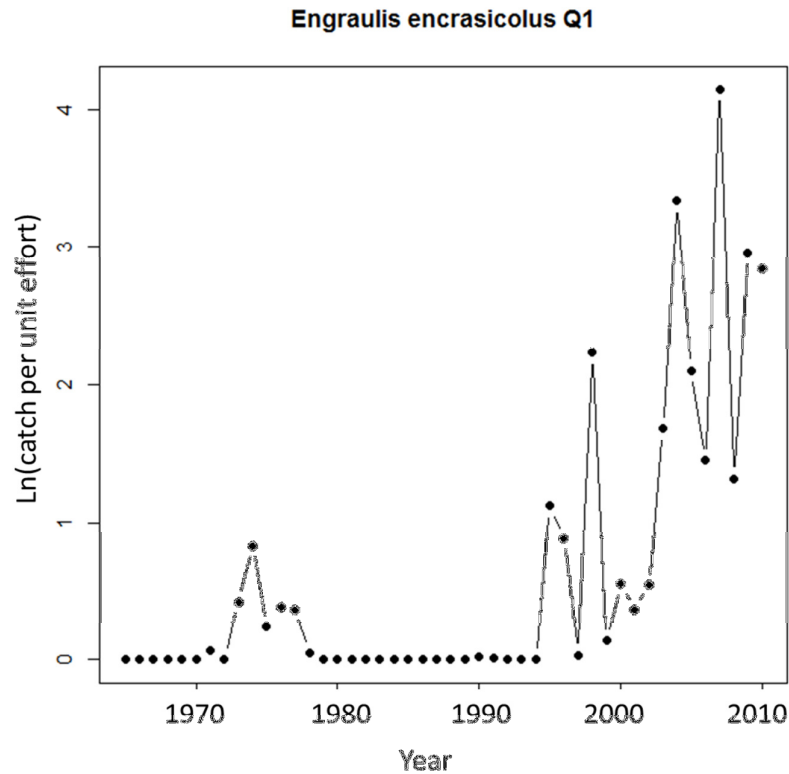
Engraulis encrasicolus Q1

Figure 1: Anchovy catch per unit effort in the North Sea IBTS survey in quarter 1 between 1965-2011.

Population dynamics and ecological interactions

Changes in a species' abundance (or density, if a specific area is considered) can be thought of in the population dynamics framework (for a detailed introduction, see e.g. Case, 2000). In the classic equation of population dynamics, numbers of individuals are represented by births, B, immigration, I, deaths, D, and emigration, E, such that abundance (or density) = B-D+I-E. Emigration and Immigration are usually ignored for simplicity by making the assumption of a 'closed population', i.e. that has limited exchange of individuals with other populations. The birth and death terms, which essentially represent reproduction and survival in ecology, are influenced by abiotic and biotic resource availability,

competition and predation processes, although the distinction can become blurred between these types of effects (see e.g. intraguild predation, or definitions of competition).

 Abiotic effects on populations result from physical changes in the environment either because a pre-requisite for survival (e.g. oxygen levels, temperature, wind/currents for dispersal) or because a non-living resource (e.g. sunlight, physical space) changes.

Biotic effects on populations are mediated through changes in abiotic resource availability and species interactions, including predation or competition, which in turn affect resource availability. Predation can be defined as an organism deriving an energetic gain from the consumption of another organism. The presence of predators has both lethal and non-lethal effects on prey populations (Preisser et al. 2005) and can be important in structuring communities (top down control). Competition can be defined as organisms impacting the growth of another either by exploitative competition (the use of a common, limiting resource) or interference competition (e.g. space occupancy). Disease and parasitism also fall under species interactions and are often ignored in studies of fish population dynamics although the prevalence of viral haemorrhagic septicaemia virus in e.g. herring was recently reported to be much higher than previously thought (Johansen et al. 2013) and recent study showed that the negative impact of crustacean parasites (such as sea lice) on salmon recruitment may be substantial (Krkošek et al. 2013).

Populations usually grow well when there is high overlap with resources and low overlap with predators/competitors in both space and time. A well-known hypothesis integrating/addressing the correspondence between fish and their food is the "match/mismatch" hypothesis (Cushing 1990). This hypothesis was developed in search for a reliable stock-recruitment relationship and it postulated that the overlap between first feeding fish larvae and their food critically influences their survival and development, thus determining recruitment. Later the concept developed to include resource match/mismatches of other life stages too.

Question 1: what factors in the North Sea allowed for the anchovy increase in the North Sea?

When major changes in population abundances are seen, one can induce/expect that any of the above biotic or abiotic factors or matches in time/space has changed. Generally, when life cycle closure occurs, the hypotheses can be categorized into two large categories: food availability and habitat availability effects. In this project we choose to first focus on food availability and the trophic interactions surrounding anchovy since there was a conspicuous change in plankton community of the North Sea not very long before the anchovy increase (Beaugrand et al 2002). Thus hypothesis

H1: anchovy abundance in the North Sea has changed due to changes in food availability.

Food availability may change due to changes in food source itself or because of changes in trophic competitive interactions. Before this research project was started very little was known on North Sea anchovy diet; a crucial issue was therefore to define anchovy food, because this knowledge determines our ability to study resource effects and the potential/likely competitors' effects on anchovy. Anchovy are zooplanktivores in the Bay of Biscay (Plounevez & Champalbert 1999), in the Mediterranean (Tudela & Palomera 1995) and in the Benguela (van der Lingen et al. 2006). For lack of more detailed information specific to anchovy in the North Sea, we expected anchovy food in the North Sea to also be zooplankton but since this was a crucial assumption influencing several mechanism pathways for the increase, it had to be verified. We therefore carried out diet analysis on existing anchovy samples from different areas of the North Sea. Potential competitors of a zooplanktivorous anchovy were likely to be other small pelagic planktivores such as herring, sprat, Norway pout or sandeel. A diet comparison was therefore undertaken to determine the diet overlap between anchovy and two of its potential competitors for which this was possible due to prior joint sampling of herring and sprat with anchovy in the German Bight area of the North Sea. Although predators can have strong impacts by predatory release of their prey populations (noted in other systems, e.g. Pace et al. 1999, Jackson et al. 2001, Frank 2005, Myers et al. 2007), potentially affecting both competitors' and anchovy populations, we did not explicitly include predators in the approach included in this thesis. Below, we give an overview of the main changes and ecological background of the North Sea system.

The changing North Sea system

The North Sea is a complex and dynamic system; many changes, both physical and biological, occurred in the North Sea before and during the anchovy increase. Despite these perpetual changes, occasionally "sudden", "extreme" or "large-scale" phenomena receive much attention (e.g. the "gadoid outburst", the "great salinity anomaly", the "regime shifts") when many authors agree on certain time periods being critical in one or several aspects of North Sea dynamics.

The North Sea is a marginal sea; its hydrology is determined by freshwater runoff from precipitation and rivers, as well as by oceanic inputs from the North Atlantic. Oceanic waters enter mainly in the North but also in the South through the English Channel (Winther & Johannessen 2006). Periodically, large-scale inflows of oceanic water occur. Their origin is hypothesized to be from the Eastern

Shelf Current and through the Rockall Trough, though the exact mechanism as well as possible connection to the North-Atlantic Oscillation (NAO) is not clearly established (see Holliday & Reid 2001). Such strong inflows occurred several times throughout the last century but the late 1980s and late 1990s inflow events received more attention due to the co-occurrence of other major (faunal) changes around the same time in both the plankton and in fish (Corten & van de Kamp 1996, Reid et al. 2003, Beaugrand 2004).

One such major hydrological event that received much attention was the "Great Salinity Anomaly" (GSA) of the mid-1970s. This term was coined for a period of unusually low salinity and temperature observed at various locations of the North Atlantic and proposed to have propagated by advection throughout the area (Dickson et al. 1988), including into the North Sea in the late 1970s (and ultimately spanning about 14 years!). Another "GSA"-event has been described for the late 1980s (Belkin et al. 1998) and the exceptional character of these GSA events may be eroding as these temperature-salinity anomalies are starting to be considered as more or less regular phenomena (as cited by Belkin et al 1998).

Additional physical forcing is provided by climatic variability (including cycles like the NAO/AMO) and by climate change. Climatic influences are expected to affect organisms in a variety of ways (Hughes 2000, Stenseth et al. 2002) and already several such changes have been empirically observed in the North Sea. Distribution and abundance of organisms are affected (Perry et al. 2005, ter Hofstede et al. 2010, Engelhard et al. 2011), with many species adjusting to warmer conditions by apparently expanding their range northwards, and phenology changes observed in the North Sea are suggested to have been caused by climate change (e.g. Edwards & Richardson 2004 for plankton).

The North Sea plankton has changed in biomass (Reid et al. 1998a, McQuatters-Gollop et al. 2007b, Kirby et al. 2008), species composition (Beaugrand & Reid 2003, McQuatters-Gollop et al. 2007a) and phenology (Reid et al. 1998a, Edwards & Richardson 2004) over the past decades. These changes have been documented as centred around two critical periods due to the co-occurrence of many changes in different components of the system. The zooplankton assemblage changed from a cold-boreal to a warm-boreal assemblage in the late 1980s (Beaugrand & Reid, 2003), biomass decreased (Pitois & Fox 2006) and phenology changed to zooplankton peaking earlier in the year (Edwards & Richardson 2004). In the late 1990s, autumn plankton changed from being dominated by small plankton to being dominated by larger species, possibly affecting herring recruitment (Payne et al. 2009).

Of the potential competitors to anchovy, herring is probably the most important by biomass and this species suffered a series of 6 years of low recruitment from 2002 (Payne et al. 2009) suggesting that its hypothesized competitive pressure on anchovy would have been lowered and food availability increased. Norway pout,

another small pelagic planktivore also suffered lowered recruitment during a similar time period (ICES 2006).

The predators of anchovy in the North Sea are likely similar to those consuming other small palegic species; therefore saithe, mackerel and horse mackerel (Engelhard et al. in press) come to mind, as these predators consume sprat and herring for instance. Cod is also a known piscivore (Floeter & Temming 2005) but its importance may be low due to its lowered population size. North Sea cod stock has strongly declined and stock size is below reference points set by ICES (ICES advice, 2012; Horwood et al. 2006) due to fishing and/or climate (O'Brien et al. 2000).

Further in the past, fish stock dynamics in the North Sea were quite different: another exceptional "event" perceived by marine scientists was the so-called "gadoid outburst" of the 1960s (Cushing 1980, 1984), a period of about 20 years during which many gadoid species (cod, haddock, whiting, saithe and Norway pout) all produced exceptionally high year classes. Around the same time or just before, herring stocks underwent a strong decline which led to a complete closure of the fishery (but recovered well thereafter). It was suggested that the gadoid outburst was due to a "window of opportunity" for the gadoids (i.e. favourable feeding conditions, based on changes in phenology of *Calanus finmarchicus*) but ultimately, the causes remained unknown more than a decade after it ended (Hislop 1996)

It should be noted that many of the insights around the special events (great salinity anomaly, regime shifts, gadoid outburst) rest on correlational studies that do not (and can not) go beyond invoking hypothetical explanations for the mechanisms causing events. There are, for instance, many correlations that have been made surrounding the North Sea "regime shift" of the late 1980s. These, however, do not always stand the test of time: e.g. the hypothesized relationship between the copepod *Calanus finmarchicus* and the North Atlantic Oscillation which breaks down in 1996 or that between the Gulf Stream Index and copepod abundance which also breaks down in 1996 (see Reid et al. 1998b). It is questionable whether the approach of correlating various biological variables with various hydrological and climatic features (see Reid et al. 1998b for a summary), including various (sometimes arbitrary) time lags, provides more insights than it increases the risk of finding spurious patterns. Thus, it is important to focus research on processes in addition to patterns, e.g. by mechanistic modelling, so as to gain an understanding of the system's drivers and mechanisms of change. In this way, it can perhaps be avoided that the understanding of the 1980s regime shift will approach the situation of the gadoid outburst – where, despite its receiving great attention, more than 30 years after its onset in the 1960s we were not much closer to understanding (Hislop 1996). The Great Salinity Anomalies seem to show

too that perhaps the studies that pointed it out as exceptional perhaps only looked at too short a scale in both space and time.

A conclusion from these observed changes is that there has always been variation in physical and biological components of the North Sea system through time. It can't be excluded that certain variation events are larger in impact than others, but empirically documenting a change in many components does not in itself explain the mechanisms causing the changes, although it may help to formulate ideas about potential mechanisms. The North Sea is a complex ecosystem (many species, many trophic levels, many hydrological processes) and in addition it is affected anthropogenically in many ways. To gain more understanding of its dynamics, moving beyond a mainly empirical approach to include conceptual or mechanistic modelling might be necessary.

Life cycle and spatial processes

The variety of possible impacting factors on the population outlined above means that a wealth of hypotheses can be put forward as to the various pathways leading to increased anchovy populations in the North Sea. This includes the question whether it results from a local population increase or reflects distributional changes of other more southern populations, i.e. is only an "apparent" North Sea increase.

Q2: where did the observed North Sea anchovy increase originate?

H2: the North Sea anchovy increase is a result of the local anchovy population increase in the North Sea

The approach to addressing the question was to compare between this hypothesis and alternative hypotheses stating that the population originated from movement of Bay of Biscay anchovy to the North Sea either by adults or young fish. So getting people from different fields of expertise together to attempt to form a coherent picture about the anchovy increase was a good idea to weigh up indications for different pathways and happened under the auspices of ICES through the working group on anchovy and sardine in North Sea. The question whether the North Sea anchovy increase was a result of a local increase or immigration by young or adult stages from nearest neighbouring population, from the Bay of Biscay, was successfully addressed.
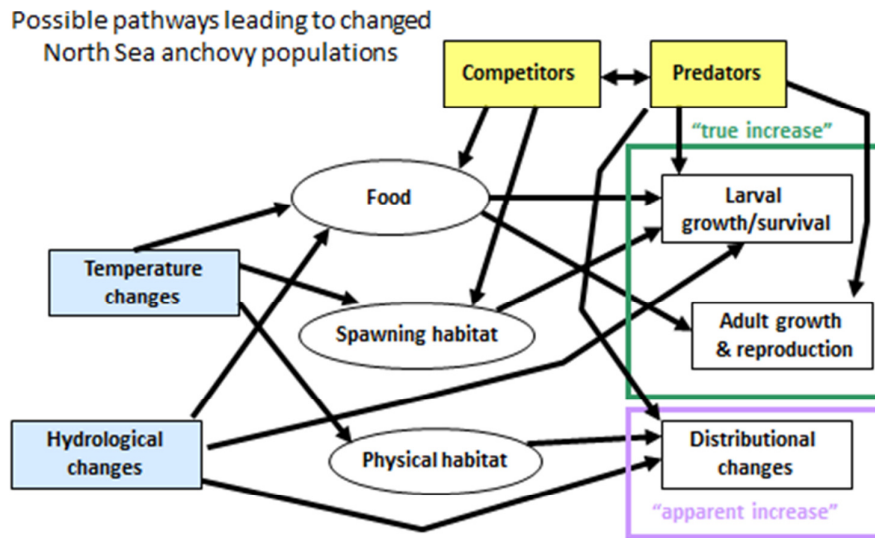
Figure 2: Possible pathways leading to anchovy population changes in the North Sea

Indeed, combining physical oceanography, genetics, larval transport models and empirical survey information yielded a relatively clear answer to the question. Larval transport work showed that young anchovies are unlikely to be able to reach the North Sea (Petitgas et al 2012). A genetic study showed that the North Sea population is distinct from the Bay of Biscay (Petitgas et al 2012, Zarraonaindia et al. 2012). And environmental data indicated that warming is likely to have increased thermal windows for this species, as number of days per year above specific spawning thresholds have been increasing while colder winters have been decreasing during the same period (Petitgas et al 2012 chapter 4).

This provides a potential opportunity for other parts of the North Sea anchovy population to complete their life cycle apart from those that spawn in the very South of the North Sea and gives a new sense of importance to temperature as a major influencing factor. The critical processes are likely to be related to reproduction and overwinter survival (as focused on by Petitgas et al 2012 with regard to temperature windows). Of course growth and survival of population both at young and adult stages are important in productivity of the population and its life cycle closure too.

Life cycle based on ch 4
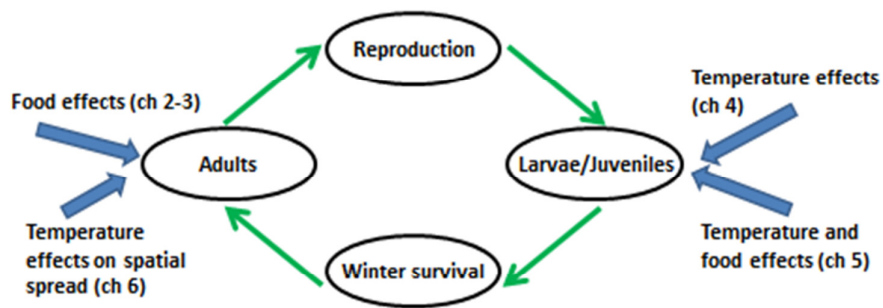
Figure 3: Overview of what chapters address which part of the North Sea anchovy life cycle.

The question of whether trophic versus spatial processes are more important in determining fish population dynamics is not new. The member-vagrant hypothesis (Sinclair & Iles 1989) postulates that energetic processes (emphasized in the match/mismatch hypothesis, Cushing 1990) are much less important than spatial processes or vagrancy (movement) of members of the population. These would be a major reason for certain populations not achieving life cycle closure. Life cycle closure requires that each life stage survives and makes it to the next and spawning.

Climate change is likely to affect habitat availability and connectivity between habitats required by different life history stages of fish, and both are important for life cycle closure (Petitgas et al. 2010). Climate can affect fish populations at different life stages and levels of organisation from organismal to population to ecosystem level (Rijnsdorp et al. 2009) and thus life cycle closure can be disrupted or positively affected at many different points in the life cycle, so:

Q3: which part of the anchovy life cycle is likely to have changed in the North Sea population?

Generally speaking, early life stages are expected to be most likely to be affected by climate change (Rijnsdorp et al. 2009) and this has also been suggested in North Sea anchovy (Petitgas et al 2012). As a consequence, we hypothesize that:

H3: influence of temperature or food during <u>early life</u> allowed for anchovy to increase.

We use a two way approach to this issue, first we model the energetics of anchovy in its first 6 months of life using the dynamic energy budget approach. Then we use spatio-temporal statistical modelling to identify which environmental variables encountered as young fish best co-vary with anchovy survey catches after the following winter.

Organisms must respond to their environment based on their state, influencing their capacity to use environmental resources, absorb shocks and withstand environmental stress. Dynamic energy budgets (DEB, Kooijman 2010) can be used to model an organism's rate of energy assimilation and utilisation for body maintenance, growth and reproduction as a function of the state of the organism. Linking such a model to environmental data such as we did from a 3D ecosystem model can give insights into the growth potential of a particular fish at a particular point in time and space reflecting habitat suitability (e.g. Teal et al. 2012).

As a second step, we relate environmental information to anchovy survey catches in order to find out which of temperature or food conditions encountered as young fish better co-vary with empirical survey data. The generalised additive modelling methods used (Hastie & Tibshirani 1990, Wood 2006) allow for a maximum amount of spatio-temporal information to be taken into account.

In practice, when studying the relationship between anchovy and its plankton food or environment, an issue that must be kept in mind is that an environmental influence and its true (rather than observed) effect are not always located in the same place. Impact and effect are, however, more easily identifiable when there is spatial correspondence between them. When studying ecological processes, means over time and space are often used. While the use of time-series analysis has increased in fisheries science, spatial studies are still much less common (but see Ciannelli et al. 2007a, Ciannelli et al. 2007b). Yet the crucial importance of space to understanding population dynamics was shown by a study of two competitor species, herring and sprat, in which dynamics were expected to result in competitive exclusion but by integrating space, coexistence became possible - the observed dynamics are in fact a product of extinction and recolonisation dynamics (Tilman 1994). Thus, it must be remembered that local population dynamics are a result of the balance between local (births & deaths) and regional (immigration & emigration) processes. It follows from the latter that the spatial location of the focal

dynamics within a realistic (i.e. non-uniform) environment affects dynamic outcomes.

When studying interactions between species in a spatial way, two keywords in spatial ecology must be taken into account: heterogeneity and scale. These are also interlinked since observed heterogeneity is highly dependent on the scale at which the observations are made. In fact, the term heterogeneity itself has also been divided into so-called "measured" and "functional" heterogeneity (see Dutilleul & Legendre 1993 for discussion). Measured heterogeneity is a result of the observer's point of view via the sampling technique (it thus includes the consideration of scale). Functional heterogeneity on the other hand is the (ecologically more relevant) heterogeneity viewed from the organism's perspective; it is heterogeneity in biotic and abiotic influences perceived and reacted to by the organism. The relative importance of top-down, bottom-up, and other ecological forces is likely to vary in space (see Gripenberg & Roslin 2007). This insight has in fisheries science been translated in to the concept of a "loophole", short for a "loophole in the fields of biological controls on reproductive success" (Bakun & Broad 2003). For instance, predation pressure is one such control mechanism on reproductive success that may be lower (than normally expected) under certain environmental conditions or in certain spatial areas. This allows those prey species which gain access to those loophole areas or opportunities to increase their reproductive success.

Empirical studies are often carried out on highly aggregated data (in both space and time), but the process inferred from results may have been different if spatial information had been taken into account. Mean-field models, simply assuming uniform distributions, produce the same results as more realistic models when the systems represented are simple, but when there is biotic heterogeneity, outcomes between the types of model can differ (Levin & Pacala 1997). To circumvent the problems of using datasets with aggregated data, in the spatio-temporal modelling study we carry out we added mechanistic modelling to gain extra insights into ongoing processes. We represented the ecophysiology of young anchovy to understand the impact of temperature and food on the potential growth of the species (chapter 5).

Moreover, there can be a mismatch between the spatial scale of the impact and the scale of the impact's effect; depending on the resolution of the data being used, one may or may not be able to observe the impact or effect at the right scale and this might lead to errors in the inferred process. The statistical methods employed should take this into account, but there is strong dependency on sampling having occurred at the appropriate resolution to capture the impact.

The question of how the mobility of organisms affects the spatial spread of a regime shift is of particular relevance when considering that small pelagics are the first actively mobile level in marine trophic web (as pointed out by Bakun 2006).

They are thus the first element that can pass environmental information between spatial areas, probably making them important agents in spreading or limiting local regime shifts.

Regime shifts and mechanisms involved in hysteresis

So-called regimes in the oceans were first described in upwelling systems as having different abundance 'regimes' such that different pelagic species dominate the system at different periods in time (Lluch-Belda et al. 1989). From this essentially descriptive definition, the concept of different states of structure and functioning being possible in one same system has been expanded on and become a key concept (albeit unclear in its definition at times) in a large and growing field of theory with ample empirical support from marine systems (e.g. Hare & Mantua 2000, in the Pacific; Alheit et al. 2005, in the North and Baltic Seas). In freshwater biology, the phenomenon of alternating states of different properties within one system is well studied. Many lakes alternate between clear and turbid states under similar conditions (Scheffer et al. 1993, Scheffer 2004). In the marine realm however, the application of this concept is comparatively recent and the terminology remains a little confused from being influenced by the ideas of abundance regimes (purely descriptive of fish biomass trends), alternative stable states or equilibria (influenced by the ideas of stability and attractors) and climatic cycles (where large scale climatic changes simply propagate up the food web). At present when regime shifts are discussed, usually a more or less rapid shift to another more or less stable state is meant. Definitions which include some information on mechanisms usually describe a system in which a response variable (the 'state' of the system) responds in a non-linear way to a slowly changing forcing variable/stressor, and may include hysteresis (Scheffer & Carpenter 2003). Hysteresis describes the phenomenon whereby the pathway back to an original state is different from the path away from it; in such a case, the forcing variable might have to be brought back much beyond its original state to restore the response variable to initial levels.

In theoretical studies, it has now also been possible to create depensation, a lowering of population growth rate at low abundances, from individual properties (de Roos & Persson 2002). Indeed, rather than assuming depensation *a priori* in the model, processes were modelled at an individual level with growth depending on amount of ingested food and mortality decreasing with body size. Under these conditions, depensation of the population is an emergent phenomenon. Empirical evidence of depensation in fish populations however remains elusive: a comprehensive study of 128 fish stocks found evidence of depensation in only three of these (Myers et al. 1995). Nevertheless, there are many reasons why depensation seems likely to occur, so the concept continues to be used. Intraguild

predation (Polis & Holt 1992), the school trap (Bakun & Cury 1999) and the predatory pit (Bakun 2006), detailed/described in the following three paragraphs, are empirically derived mechanisms providing depensation effects that are adapted to the case of small pelagics.

Traditionally, the field of population dynamics has focused on competition and predation separately, but these two processes become blurred when intraguild predation is taken into account (see Polis & Holt 1992). Species or organisms that feed on similar resources, and are thereby potential competitors, are considered as belonging to the same trophic guild. If a species preys on another species but both also feed on a common resource, the first species gets a double advantage by undertaking this intraguild predation: a direct energetic gain and a reduction in number of potential competitors. This phenomenon is widespread, especially when considering different ontogenetic phases, and common in small pelagic fish (Irigoien & de Roos 2011). In pelagic fish populations, adults of one species may for example consume their intraguild predator's recruits, thereby decreasing competition for itself with these young predators as well as reducing predation pressure later. The dynamics of intraguild predation systems are inherently less stable and in addition to causing competitive exclusion, may result in alternative stable states (Holt & Polis 1997). So if anchovy is involved in intraguild predation in the North Sea, a change in the relative abundance of one of the involved species might hasten a more extreme change in population abundances.

Schooling is a fundamental behavioural trait of many pelagic fish that may provide improved protection from predators and hydrodynamic advantages, outweighing the negative effects that individuals may experience by schooling, such as reduced food availability due to intensive feeding around them. But if the subordination of individual needs to the schooling needs goes too far, a species may suffer from the schooling instinct, falling into the school trap (Bakun & Cury 1999). Pure schools of only conspecifics are formed when a species' abundance is high, but when abundance is low, fish may school with others regardless of species membership indicating some sort of 'schooling imperative' (Bakun & Cury 1999, Cury et al. 2000): anchovy and sardine of similar sizes have been found together in mixed schools in several systems (e.g. Radovitch 1979, Cury et al. 2000), and for anchovy off South Africa and for *Sardinella* stocks off Senegal, school composition is related to the relative abundance of the species (Cury et al. 2000, Fréon 1984). This schooling with other species can pose problems if it is obligatory and each of the species has different interests (e.g. spatially or temporally) in how to maximize e.g. feeding or survival. Then the schooling 'instinct' might actually cause population decline instead of increasing survival.

Another concept that bridges processes often considered separately is the predatory pit idea suggested by Bakun (2006), which includes functional and numerical responses of predators. A relationship between a predator and a prey

(with an implicit alternative prey species) is described, postulating two threshold levels of prey abundance that change the dynamics of the system. At low prey populations, there is little predation and the prey population can grow but above the first threshold of intermediate prey abundances, the predator takes interest in the prey populations (functional response) and begins intense predatory exploitation ("carnage") thereby strongly reducing the prey population's growth rate. If, however, growth continues enough and the prey populations can reach the threshold of high prey population abundances that results in satiation of the predatory population, predation pressure on the overall prey population is lowered and this results once again in high prey population growth ("explosion phase"). The phase (in time or in prey abundances) between the two thresholds is called the predatory pit – here the prey abundance is kept in check by intensive predation pressure. Whatever allows the prey species to overcome that pit (i.e. those intermediate abundance levels) can allow for sudden rapid population growth phases as seen in many pelagic populations around the world. Because the predation pressure onset is dependent on the predator's functional response, the other prey populations are important in this process. Actually population growth is the most crucial. If the population can grow rapidly enough, it can overcome the predatory pit. Anchovy has a high growth rate and it has been suggested that by virtue of changing ocean production patterns, anchovy can overcome the pit in phases of high zooplankton food production because it can assimilate such high production rapidly. While in the opposite temperature phase, it may not be as fast growing and therefore cannot make it out of the pit. So year to year background variation in background primary production alone could cause species alternations without any adverse interactions between them (Bakun 2006). Note that these three mechanisms, the predatory pit, the school trap and intraguild predation all result in reduced population growth of the considered fish at low abundances. This depensation can give rise to non-linear responses in ecosystems.

Q4: could depensation be in any way related to the North Sea anchovy increase?

H4: depensation leads to more accentuated dynamics in a spatial spread of a local population

In the last chapter different assumptions in a model of anchovy population are compared for their effect on the spread of a local population from the southernmost portion of the system. We make a spatial model of a local anchovy population and test how different outcomes would look if we assume logistic population growth or population growth that includes depensation.

Few have addressed the implications of space in the theory of regime shifts (but see (van Nes & Scheffer 2005, van de Leemput et al. in review). Indeed, including space results in the possibility for regime shifts that occur locally to spread through space or be contained, depending on the characteristics of the system. Spatial heterogeneity has been found to be a stabilizing mechanism that prevents global regime shifts from happening easily; outcomes also differ depending on the mobility of organisms, and the pattern of spatial heterogeneity (van Nes & Scheffer 2005). The next questions include what proportion of a system must have switched to the alternative state for a global shift to occur, and also how organisms' properties, such as mobility, affect the spread or localization of local regime shifts within the system as a whole.

Thesis outline

There are many uncertainties surrounding the causes, mechanisms and consequences of anchovy increases in the North Sea. The issues addressed in this introduction can be summarised in three points which will be treated in this thesis:

1. Anchovy increases in the North Sea are concurrent with many other changes. Major changes in abundance and composition of zooplankton occurred a few years prior to the increases leading to the hypothesis of increased food availability having caused anchovy increases, either via plankton dynamics *per se* or changed trophic competitive interactions. (H1). This will be verified by carrying out diet analyses for anchovy (chapter 2), and determining the degree of dietary overlap, potential competition with other pelagic planktivores sprat and herring (chapter 3).

2. The hypothesis that anchovy might have spread from a local population in the North Sea (H2) rather than by movement of adults or young stages from the neighbouring Bay of Biscay population is addressed using a combination of methods involving physical oceanographic models, empirical survey analysis and genetic studies (chapter 4).

3. The importance of space in studying ecological processes is noted; the importance of food availability and temperature on early life stages will be tested for and compared relative to one another in allowing for the anchovy increase (H3). General additive modelling will be used to relate the variation in anchovy populations with that of its food, and mechanisms involved will be studied using the dynamic energy budget of anchovy (chapter 5).

4. Since the North Sea appears to have undergone a regime shift in the late 1980s, it is possible that anchovy increases reflect this regime shift. Simulating the dispersal of a fish population in a spatially explicit system with hysteresis, the pattern and process of such a regime shift spreading is examined (chapter 6).

Finally the thesis contents are synthesized and discussed in a broader context (chapter 7).

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CHAPTER 2

**Anchovy *Engraulis encrasicolus* diet
in the North and Baltic Seas**

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AD, Temming A, Dickey-Collas M (2011)

ABSTRACT

The diet of anchovy (*Engraulis encrasicolus*) in the North and Baltic Seas was studied using stomach analysis from four sampling events in different areas. Zooplanktivory was confirmed; the most frequent prey items (in over 40% of stomachs) were copepods, malacostracan larvae and fish larvae. In the Baltic Sea, *Paracalanus* spp. and *Pseudocalanus* spp. were important in relative terms; in the German Bight, *Temora* spp. dominated the stomach contents. Relative abundances of prey items varied with area more than absolute abundance or presence absence of items. Moreover, the level of resolution of prey categories influenced which prey categories were considered to be most important in driving variability in stomach content. Anchovy diet is broad across the seasons, years and areas sampled, suggesting that it is not a specialist feeder in the North Sea. The similarity of diet between anchovy and other clupeids, as well as anchovy consumption of larval fish, makes the new increased anchovy population a potential intraguild predator of commercial species like herring.

INTRODUCTION

The recent increase in abundance of European anchovy (*Engraulis encrasicolus* L.) in the North Sea has attracted attention from scientists interested in variability in ecosystems and climate-induced changes in the North Sea (Beare et al., 2004b; Graham and Harrod, 2009; Hannesson, 2007). An increase in abundance has occurred around the British Isles (Armstrong et al., 1999; Beare et al., 2004a) in recent years and parallels can be draw with previous sporadic increases, followed by decline, in the North Sea over the last 100 years (Aurich, 1950; Boddeke and Vingerhoed, 1996; Cunningham, 1890). It is unclear what causes these increases; a range expansion or shift of a southern population, a growth of an existing small local population or a newly seeded population. It is also unknown how the pelagic ecosystem will respond to the change but it seems likely that some interaction will occur with other small pelagic planktivores (e.g. sprat *Sprattus sprattus*, herring *Clupea harengus*, sandeel *Ammodytes* spp., and Norway pout *Trisopterus esmarkii*) through shared habitat or shared prey or predators. In the Baltic Sea for instance, several authors propose that competition for prey occurs between sprat and herring due to dietary overlap (e.g. Möllmann et al., 2004).

We assume that in the North Sea, anchovy are zooplanktivores just as in the Bay of Biscay (Plounevez and Champalbert, 1999), the Mediterranean (Tudela and Palomera, 1995) and the Benguela system (van der Lingen et al., 2006), but there are no studies to support this assumption. Our study focuses on the diet of adult anchovy in the North and Baltic Seas as this knowledge is a first step required to investigate the trophic interactions of anchovy with other small pelagic fish. These interactions are probably complex and include competition for prey and predation on eggs and larvae of small pelagic fish, including of their own species. North Sea herring diet varies by season and location but is characterised by copepods (*Calanus*, *Temora* and *Pseudocalanus* species) and juvenile sandeels (*Ammodytes* spp.) with other plankton components like fish eggs, amphipods, chaetognaths (*Sagitta* spp.) and larvaceans (*Oikopleura* spp.) also found (Bainbridge and Forsyth, 1972; Daan et al., 1985; Hardy, 1924; Last, 1989). Sprat (Casini et al., 2004; Ellis and Nash, 1997; Möllmann et al., 2004; Tičina et al., 2000) and Norway pout (Albert, 1995; Bromley et al., 1997) rely mainly on the copepods and less on the larger planktonic items.

Recently much attention has been given to the ecological changes that took place since the 1980s in the North Sea and that have been collectively termed regime shift (Beaugrand, 2004). Specifically, the changes in phytoplankton and zooplankton are well studied (Reid et al., 2003; Reid et al., 1998). The suggestion that the North Sea pelagic system has become bottom-up regulated (Kenny et al., 2009) in recent years emphasises the importance of understanding plankton dynamics and the repercussions these may have in the higher trophic levels, where commercial or recreational benefits to humans are more easily recognised.

By using archives of preserved stomachs of anchovy, this study describes the diet of North Sea and Baltic Sea anchovy and the variability in stomach contents between sampling events. As the distribution of zooplankton is not homogenous (Young et al., 2009); it is expected that the fish sampled close in time and space, i.e. during the same cruise, should have more similar stomach contents than those from more distant locations (spatially or temporally), i.e. from different cruises. Overall, we expect anchovy to have a generalist's diet that varies with area, season and anchovy length class. The study's objective will be to describe what species and what size of prey are consumed by anchovy across the North Sea. The second objective relates to the analysis of prey composition data and the influence of how the prey items are aggregated on the perceived results.

MATERIALS & METHODS

Stomach analysis

In this study, we used stomach content analysis to gain information on anchovy diet. A criticism of this method has been that it may misrepresent rare or rapidly digested items (see (Hyslop, 1980), such as gelatinous zooplankton (a known "survival food" for anchovy in some areas; (Mianzan et al., 2001) or microzooplankton. Other methods can give a more integrated picture of diet over time and space (fatty acid analysis, stable isotope analysis), or a very detailed taxonomic picture with less precision on relative abundances (DNA analysis) and the same issue of giving only a snapshot information on diet. Stomach analysis has been in use for a long time and while the other methods offer advantages like reduced work load and processing time per sample, stomach analysis can provide, depending on observer skill and degree of digestion of prey items, highly detailed information on prey numbers, size, maturity stage (in addition to prey identity), making it highly suited to the investigation of small scale variability in diet or selectivity studies when the background available prey field is known.

Stomachs of anchovy were collected in 2003-4 and 2008-9 by the Global Ocean Ecosystem Dynamics (GLOBEC) Germany project and the International Bottom Trawl Survey (IBTS) respectively (Table 1, Figure 1). During GLOBEC cruises, stomachs were preserved after extraction from the fish's body; during the IBTS cruises, fish were preserved whole after carefully cutting open the abdominal cavity. In both cases, 4% buffered formaldehyde was used as preservation agent. Generally, three non-empty stomachs were analysed per station; this was considered sufficient since stomach contents from one same station tend to be more similar than contents from different stations (Bogstad et al., 1995) and we wanted to increase effective sample size by using more stations (Pennington et al., 2002). The 78 stomachs analysed belonged to adult anchovy of a size range of 8-19 cm total length. Stomach contents were identified to the lowest taxonomic level and developmental stage possible and counted using a binocular microscope. *Paracalanus* spp. and *Pseudocalanus* spp. were always recorded as "parapseudocalanus", and decapods and euphausids were grouped as "malacostracans" due to uncertainty in identification. Unquantifiable remains of recognizable prey items were not included in the analysis. Eight empty stomachs were not included in the following analysis.

Table 1: Overview of the stomachs analysed

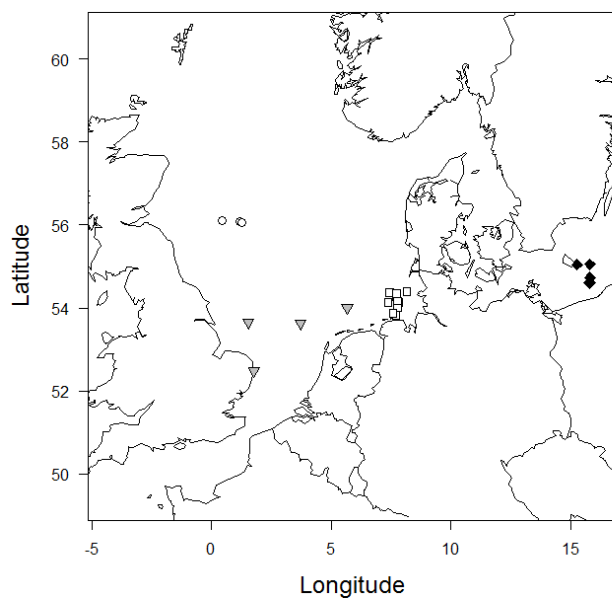| Area	Stomachs analysed	Non-empty stomachs	Year	Time period
Baltic Sea	22	15	2003	late Nov. - early Dec.
German Bight	35	34	2004	mid May - mid Aug.
Northern North Sea	9	9	2008 & 2009	early - mid Feb.
North Sea	12	12	2008	late Jan. - mid Feb.

Figure 1: Map showing stomach collection sites in the Baltic Sea (black diamonds), German Bight (empty squares), northern North Sea (empty circles) and North Sea (grey triangles).

Table 2: List of prey items making up different taxonomic categorisation schemes and size category attributed to the most detailed taxonomic scheme. Approach of empirically or derived weight estimates described in the methods.

6 categories	8 categories	Pooled, 12 categories	14 categories	Detailed, 24 categories	Size Category	Dry weight used (µg)	Source
Copepods	*Acartia* spp.	*Acartia* spp.	*Acartia* spp.	*Acartia* spp.	S	14	Empirical
Fish larvae	*Centropages* spp.	*Calanus* spp.	*Calanus* spp.	Barnacles	M	38	Empirical
Malacostracans	Copepods	*Centropages* spp.	*Centropages* spp.	*Calanus* spp.	L	75	Empirical
Other	Fish larvae	Chaetognaths	Chaetognaths	*Candicia* spp.	S	19	Derived
Parapseudocalanus	Malacostracans	Cladocerans	Cladocerans	*Centropages* spp.	M	38	Empirical
Temora spp.	Other	Copepods	Copepods	Cephalopods	XL	300	Derived
	Parapseudocalanus	Fish larvae	Fish larvae	Chaetognaths	L	92	Empirical
	Temora spp.	Malacostracans	Gastropods	Cladocerans	M	32	Empirical
		Oikopleura spp.	Hydroid	Copepods	S	18	Derived
		Other	Malacostracans	*Corycaeus* spp.	S	18	Derived
		Parapseudocalanus	*Oikopleura* spp.	Eggs	M	42	Empirical, fish eggs
		Temora spp.	Other	Fish larvae	XL	150	Empirical
			Parapseudocalanus	Gastropods	L	80	Derived
			Temora spp.	Hydroids	M	30	Derived

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Isopods	L	85	Derived
Malacostracans	XL	110	Empirical, Euphausid larvae
Oikopleura spp.	S	15	Empirical
Oithona spp.	S	15	Derived
Other	U	0	-
Parapseudocalanus	S	17	Empirical, *Pseudocalanus* spp.
Polychaetes	L	90	Derived
Temora spp.	S	19	Empirical
Unidentified crustacean	U	0	-
Unidentified items	U	0	-

Grouping by taxonomic level and data summarisation

Raw data on food items recorded as described above were aggregated into prey categories as often done in stomach analysis studies (e.g. Möllmann et al., 2003; Segers et al., 2007) to decrease the importance of rare items. Larger copepod stages (IV-adult) were prevalent, with copepodite stages I-III of all species making up less than 2% of all stomach content items, therefore these were not considered separately as this would have created many zero-dominated categories. The creation of prey categories in diet studies is limited by practicalities related to the degree of digestion and identifiability interacting with observer skill or experience that are seldom fully acknowledged. Yet it seems likely that these constraints would influence the biological interpretation of the results of a diet analysis. Therefore we chose to impose further constraints to our dataset to explore the result of these choices on the results. Five different categorisation schemes with 6 – 24 categories (Table 2) were used to understand the effect of the categorisation on the results of the analysis. The categorisation schemes differed by grouping different copepod species into "copepods" or less abundant items into "other". The most detailed categorisation scheme of 24 categories was used to calculate the cumulative abundance of prey items. The top categories that included over 95% of all items by numbers (Figure 2) were included explicitly (grey bars on Figure 3), all other categories from the detailed scheme were pooled into the generic category "other" (white bars on Figure 3) resulting in 12 categories, the pooled categorisation scheme, that were used in further analyses.

Raw stomach content data were summarized in three different ways: presence absence of each prey category, absolute abundance per category, and proportions by numbers of items in each category per fish stomach. These measures emphasize different aspects of the data. Presence-absence reflects species composition only, thus overemphasizing the importance of very rare items present and underrepresenting abundant or relatively abundant items in the diet. However they do show the breadth of prey items consumed. The abundance of various prey items gives absolute stomach contents of the fish, and are useful for comparing the variation in amount of total items consumed, or of a specific prey item of interest but are of reduced value when considering the diversity of prey items in the diet. Proportions data give information on relative diet composition, i.e. the general diet composition adjusted for total abundances, without overemphasis of very rare items.
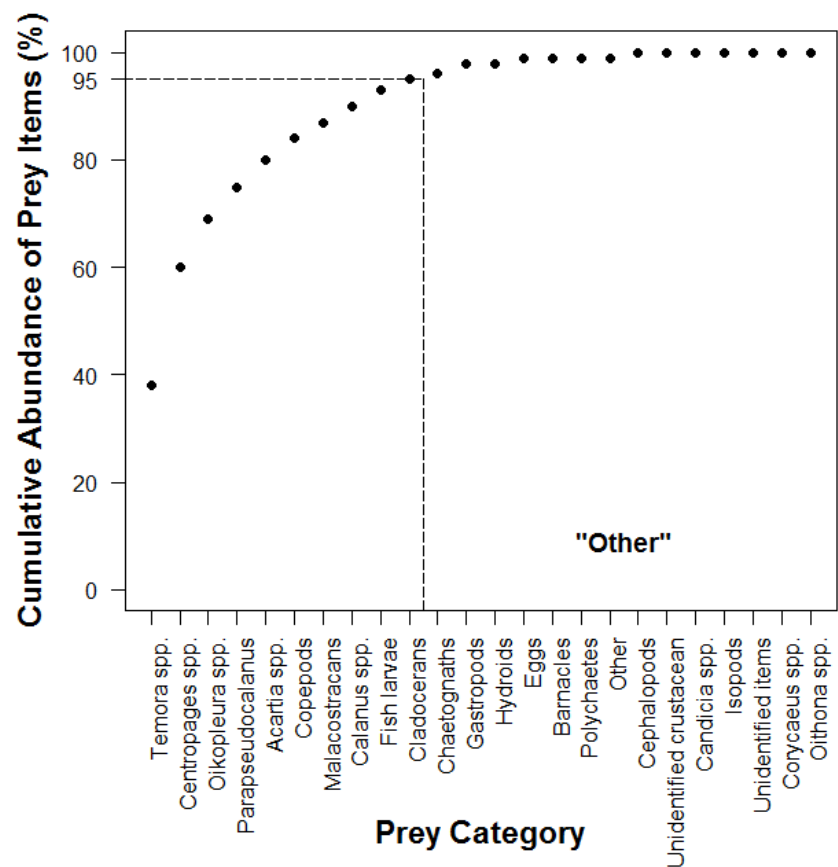
Figure 2: Cumulative abundance of (detailed) prey categories for all areas. Categories to the left of the vertical dashed line make up 95% of all stomach contents by abundance. Categories to the right of the vertical dashed line were grouped as "other".
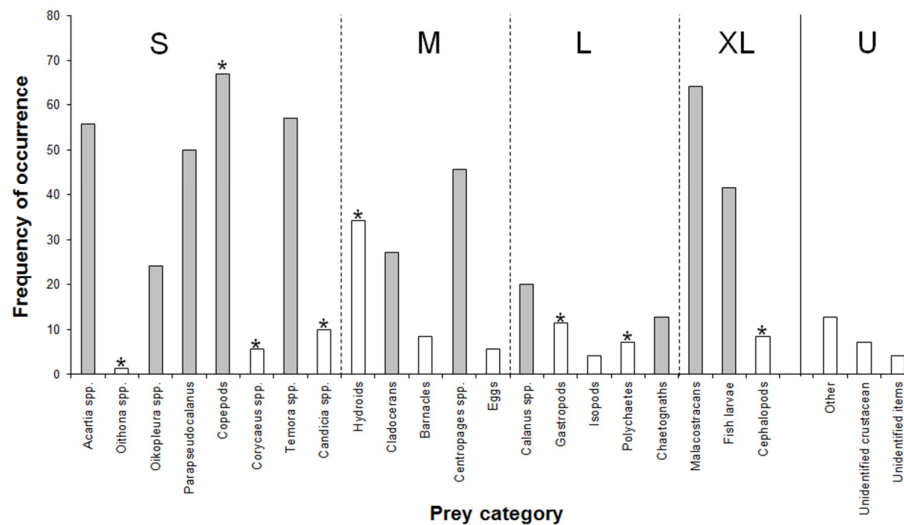
Figure 3: Frequency of occurrence of taxonomic prey categories. Filled bars represent those largest categories that comprise of over 95% by abundance (when ranked) of all items found in stomachs. Empty bars were pooled as "other" for the PCA. Apart from the three right-most categories (of unknown size, U), categories are ordered by dry weight on the x-axis and their size category is displayed above. Estimates of dry weight derived empirically were used where available (Snijder, unpublished data) and otherwise derived from volumes, see methods (indicated by *).

Frequency of occurrence

The frequency of occurrence (i.e. the proportion of all stomachs in which the prey item was found) for the detailed taxonomic categorisation scheme was calculated from the pool of all fish sampled to understand the prevalence of different prey categories in the diet.

Principal components analysis

For the analysis of diet similarities between areas, principal components analysis (PCA) was used. PCA is an exploratory multivariate statistical method that creates artificial variables (the principal components, or PCs) successively in such a way that each of these explain the maximum variability of the multivariate

dataset. PCA thus summarizes in a few dimensions (the first few PCs) most of the variance of the data set and can be used for clearer visualization of the overall differences between samples (Legendre and Legendre, 1998). The total variance explained by the first few PCs (we chose to use the first three in this study), hereafter referred to as "cumulative variance" gives an indication of how much variation is explained by these artificial PCs. This exploratory method, PCA, is useful in interpreting the multivariate data as each PC that explains a given part of the dataset's variation is correlated to the original variables to different degrees, as given by the PCs' loadings, allowing for interpretation of which biological variables are responsible for most of the variation between samples. The PCA results were used to visualise differences in prey composition (taxonomic and size) between four areas (Table 1, Figure 1) and four length class groups (small: <12cm; medium: 12-14cm; large: 15-16cm; extra large: 17-19cm).

Taxonomy-based diet

Principal components analyses were carried out on the pooled taxonomic categories using singular value decomposition in R (R Development Core Team, 2008) on presence-absence, abundance and proportions per stomach data. The proportions data were arcsine transformed ($x'=asin[\sqrt{x}]$) prior to carrying out the PCA, to further normalise their distribution. Data were always centred, which shifts the variables to be zero centred; and scaling, to variables having unit variance, was done only on the abundance data before the analysis was carried out, to decrease the effect of high abundance values in the dataset. PCA results were used to explore whether diets differed by area in terms of taxonomic composition. Area differences in the most important prey items' proportions were compared using a Kruskal-Wallis test. The impact of anchovy length on the observed diet was explored using Pearson's product moment correlation between the each stomach's principal components (PC1-PC3 from the proportions PCA) and anchovy length class; as well as between prey item proportions and anchovy length class.

Size-based diet

The taxonomic categories of the detailed categorisation scheme were attributed to semi-quantitative size categories (see Table 2), according to their estimated mean dry weights (given in Table 2). These were based on measurements from

Irish Sea species where available (R. Snijder[1], unpublished data), and otherwise on our own estimates (indicated by an asterisk in Figure 3) based on estimated volume relative to the items of measured dry weight. The resulting categories are: small (S, dry weight<20µg), medium (M, dry weight between 20-50µg), large (L, dry weight between 50-100µg) and extra-large (XL, dry weight>100µg) and PCA was carried out on the arc-sine transformed proportions of items of these categories per stomach. Items of unknown size/dry weight (i.e. all unidentified items, U) were not included in this PCA. The results of the PCA were used to explore whether diets differed between areas in terms of prey item size. The dry weight estimates were used to calculate estimated dry weight of each stomach's content based on the abundances in each prey category. Estimated dry weight per stomach and measured wet weight per stomach were tested for differences between areas using a Kruskal-Wallis test. The impact of anchovy length on the observed diet was explored using Pearson's product moment correlation between each stomach's principal components and anchovy length class.

RESULTS

Eight stomachs were empty and deleted before the analysis: seven came from the Baltic Sea and one from the German Bight (Figure 1). This left 70 stomachs to be used in the analysis from 22 stations. The mean dry weight per stomach was estimated at ca.6 mg. Estimated dry weight per stomach differed significantly between areas (Kruskall-Wallis test, $H=36.4$; $d.f.=3$, $p<0.001$); the average German Bight stomach contained about 11mg while the northern North Sea and North Sea areas contained ca 0.4mg, and the Baltic ca. 0.7mg. It should be noted that samples were collected in different areas in different seasons (Table 1). Measured wet weights also differed significantly by area (Kruskall-Wallis test, $H=39.4$; $d.f.=3$, $p<0.001$); the overall mean was 0.18g with the German Bight having a mean of 0.28g per stomach; Baltic Sea 0.15g; northern North Sea 0.05g; North Sea 0.01g. Based on the median coefficients for the length-weight relationship $Weight=a \cdot Length^b$, ($a=0.0027$, $b=3.3200$ on total length; FishBase (Froese & Pauly, accessed 10 Nov. 2009), the weight of a medium-sized anchovy (15cm) would be ca. 22g. Thus the mean estimated wet weight per stomach constitutes 0.8% of body weight.

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Taxonomy-based analysis

Frequency of occurrence

Using the detailed categorisation scheme, the most common prey categories (occurring in ≥50% of stomachs) were malacostracans (mostly larvae), the copepods *Acartia* spp., *Temora* spp., "parapseudocalanus" and other copepods (Figure 3). When separating these data by area, the frequency of occurrence shows that in the Baltic Sea (number of stomachs, n=15), "parapseudocalanus" is the most prevalent, along with copepods, malacostracans and *Acartia* spp. (all found in more than 50% of stomachs). In the German Bight (n=34), many categories are found at high frequencies, e.g. *Temora* spp., malacostracans, *Centropages* spp., copepods, *Acartia* spp., "parapseudocalanus", fish larvae, hydroids are found in more than 60% of all stomachs. In the northern North Sea (n=9), an unidentified species and fish larvae were most frequently found items, followed by *Acartia* spp. and malacostracans. Compared to other areas, the frequencies in northern North Sea samples were low (the most frequently found prey item was present in 56% of stomachs while other areas' maximal frequencies reached or exceeded 80%). Several stomachs contained low numbers of prey items and this area had the lowest mean number of prey items per stomach (8 items). The North Sea stomachs (n=12) most frequently contained items of the category "copepods" (83% of all stomachs), followed by *Temora* spp. at 50%, then *Acartia* spp. and *Candicia* spp.

Abundance and proportions

The mean proportions of different prey items differed between areas (Figure 4), with the Baltic Sea having a high proportion of "parapseudocalanus" (41%) and malacostracans (32%), while in the German Bight the highest mean proportion of items was *Temora* spp. (47%). The northern North Sea had a high proportion (40%) of "other" items due to the high variability of items found in those stomach and the relative rarity of these across all stomachs considered across areas. The North Sea had a high proportion of other copepods (30%). The mean abundance per stomach in the different areas differed greatly as well with the mean stomach from the German Bight having 324 items, an order of magnitude higher than the mean abundance per stomach in other areas (23 items in the Baltic Sea, 8 in the northern North Sea, ca 16 in the North Sea).
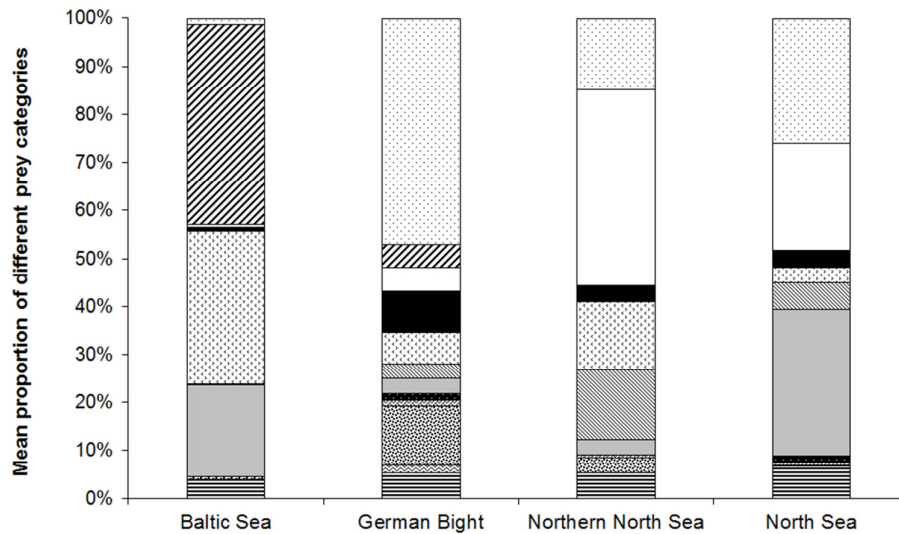
Figure 4: Mean proportion per stomach of different prey categories of the pooled scheme and mean abundance [±95% confidence interval] per stomach in the Baltic Sea (n=15), German Bight (n=34), northern North Sea (n=9) and North Sea (n=12). Patterning (from bottom up): horizontal stripes: *Acartia spp.*; waves: *Calanus spp.*; large black dots: *Centropages spp.*; tiles: cheatognaths; white dots on black: cladocerans; grey: copepods; diagonal stripes: fish larvae; arrowheads: malacostracans; black: *Oikopleura spp.*; white: other; thick diagonal stripes: parapseudocalanus; black dots on white: *Temora spp.*

The interpretation with regard to area/sampling occasion differences that could be gained from PCA results on the pooled categories varied depending on whether abundance, proportions or presence absence data were used. Area differences were not visible on the biplots from abundance data. With presence-absence data, stomachs group together slightly. However it is with proportions data that there appear to be area differences in diet, with stomachs from the Baltic Sea grouping apart from the other areas (see below and Figure 5a).

The cumulative variance explained by the first three principal components varied in the expected way with the categorisation schemes and type of data used (Table 3). Categorisation schemes with fewer categories with which to explain the

variation in the data had the highest cumulative variance explained by the first three principal components. Using abundance data, the first three components had highest explanatory power, followed by proportions data; presence absence data had the lowest total variance explained by PC1, PC2 and PC3.

The prey categories with the highest loading on the first three principal components also varied according to categorization scheme and data type (Table 3). With abundance data, the prey category with highest loading on PC1 is different in each categorisation scheme. With presence absence data, the more highly resolved schemes show cladocerans as determining PC1 but other items seem important as well. Only in the proportions data is there some consistency in the prey categories that are most important in determining the first three principal components: malacostracans and *Temora* spp. appear as highest loading for one of these principal components across all categorisation schemes (Table 3).

These three ways of summarizing the raw stomach contents data provide information on different aspects of the data; since how the relative abundance of prey items varied between samples was the most interesting to us, the emphasis was placed on analyzing the proportions data.

Using the pooled categorisation scheme on (transformed) proportions data, stomachs from the same area had similar PC1 and PC2 scores, with especially the stomachs from the Baltic Sea grouping together (Fig. 5a). These differences, shown two-dimensionally on the PC1 and PC2 axes of the biplot, are driven mostly by the categories *Temora* spp. (highest loading on PC1: -0.89), malacostracans(-0.82 on PC2) and "parapseudocalanus" (0.76 on PC3). The variability in proportions of these categories between samples/stomachs constitutes much of the total variability in the total dataset. The (non arcsine transformed) proportions of these important taxonomic categories were then tested for area differences by using the non-parametric Kruskal-Wallis test. *Temora* spp. (H=27.1; d.f.=3; p<0.001), malacostracans (H=9.2; d.f.=3; p=0.03), "parapseudocalanus" (H=34.0; d.f.=3; p<0.001) and "other" (H=27.2; d.f.=3; p<0.001) all showed a significant effect of area. The German Bight and northern North Sea had high proportions of *Temora* spp., and the proportion of "parapseudocalanus" and malacostracans per stomach were higher in the Baltic Sea than in other areas.

The correlation between each of PC1, PC2 and PC3 (from the PCA on proportions data) with length class showed that only PC1 was significantly correlated to anchovy length class (cor=0.34, d.f.=68, p=0.002). When testing for correlation between predator size and proportion of different prey items directly,

using Pearson's product moment correlations (Bonferroni adjusted alpha= 0.0042), only one item showed a significant relationship (*Calanus*: cor= 0.81, d.f.= 7, p=0.004).
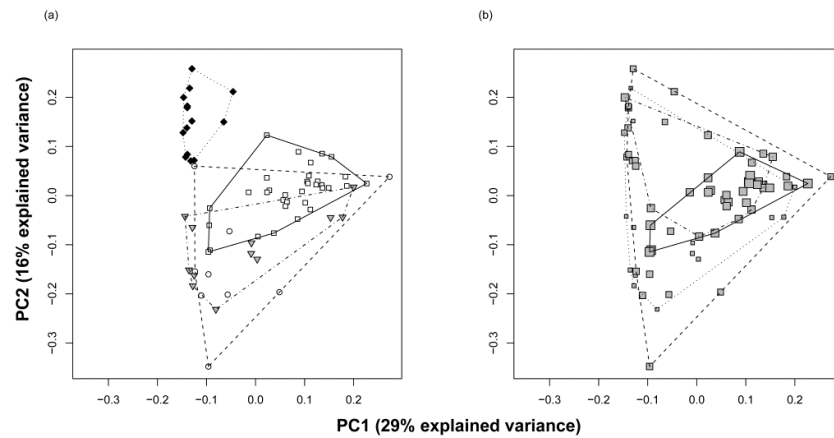

Figure 5: Results of a PCA on proportions stomach content items of certain taxonomic groups based on pooled categories. (a) The different symbols represent the area of origin of each stomach: the German Bight (white squares, solid line), the Baltic Sea (black diamonds, dotted line), the northern North Sea (white circles, dashed line) and the North Sea (grey upside down triangles, dotted-dashed line). (b) The size of the symbols represents length class of the anchovy that provided the stomach, and four groups for fish length are displayed: small (<12cm, dotted line), medium (12-14cm dashed line), large (15-16cm, dot-dashed line), extra large (17-19cm, solid line).

Table 3: Variance explained by the first three principal components and prey categories with highest principal component loadings when using different ways of summarizing raw stomach content data: presence-absence, abundance, proportions for five ways of grouping raw data into categories.

Number of categories		Variance explained			Categories with highest absolute loading		
		Abundance	Proportions	Presence-Absence	Abundance	Proportions	Presence-Absence
24, detailed	PC1	0.38	0.29	0.27	*Calanus* spp.	*Temora* spp.	Cladocerans
	PC2	0.11	0.15	0.09	Cephalopods	Malacostracans	*Temora* spp.
	PC3	0.08	0.13	0.09	Eggs	Parapseudocalanus	*Acartia* spp.
	Total PC1-3	**0.57**	**0.57**	**0.45**			
14	PC1	0.53	0.3	0.3	Cladocerans	*Temora* spp.	Cladocerans
	PC2	0.11	0.16	0.11	chaetognaths	Malacostracans	Other
	PC3	0.08	0.13	0.1	Copepods	parapseudocalanus	*Acartia* spp.
	Total PC1-3	**0.72**	**0.59**	**0.51**			

12, pooled	PC1	0.57	0.29	0.31	Other	*Temora* spp.	Cladocerans
	PC2	0.1	0.16	0.12	Chaetognaths	Malacostracans	Other
	PC3	0.08	0.16	0.1	*Oikopleura spp.*	Parapseudocalanus	Malacostracans
	Total PC1-3	**0.76**	**0.62**	**0.53**			
8	PC1	0.55	0.32	0.34	*Acartia* spp.	*Temora* spp.	*Centropages* spp.
	PC2	0.12	0.2	0.14	Other	Other	Parapseudocalanus
	PC3	0.11	0.17	0.13	Other	Malacostracans	Malacostracans
	Total PC1-3	**0.79**	**0.69**	**0.61**			
6	PC1	0.53	0.33	0.35	Malacostracans	*Temora* spp.	Fish larvae
	PC2	0.16	0.23	0.19	Other	Malacostracans	Parapseudocalanus
	PC3	0.12	0.21	0.16	Fish larvae	Other	*Temora* spp.
	Total PC1-3	**0.82**	**0.77**	**0.7**			

Size-based analysis

Frequency of occurrence

Using the size categories described above, the most frequent items were generally found in the small and extra-large categories (Figure 3), with only *Centropages* spp. having a high frequency amongst the medium or large items. The main differences in the proportions of items of different size categories were that the Baltic and northern North Sea areas had higher proportion of XL items (29-32%) while the German Bight had more (12%) L items than other areas (<4%, Figure 6). The proportion of small items was similar (67-75%) in all areas except the northern North Sea (34% of S items), where items of unknown size constituted a higher proportion of the total (23% compared to 10% in the North Sea and <1% in the Baltic and German Bight).
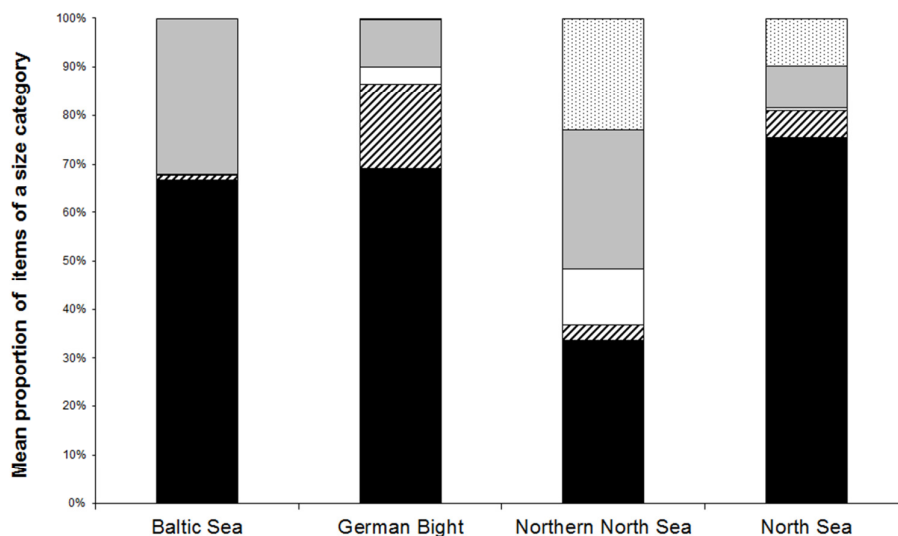

Figure 6: Mean proportion of items of each size category (black=S, small; striped=M, medium; white=L, large; grey=XL, extra large; dotted=U, unknown).

Principal components analysis

The mean proportions of different sized items differed somewhat between areas (Figure 6) with the "small" items being most important in all areas (as this included the common copepods). The Baltic Sea and northern North Sea have a high proportion of very large items (mostly malacostracans in the Baltic, cephalopods and fish larvae in the northern North Sea). The highest factor loading on PC1 was from the small category, on PC2 (and PC3) the medium category. The cumulative variance explained by the first three PCs is high but this is an expected result as there are only four variables (i.e. the size categories S, M, L and XL) to explain the variance with. Differences by area on the PC1-PC2 biplot are weak (Figure 7). Of the first three PCs, only PC3 was positively correlated with predator length (cor=0.29, d.f.= 68, p= 0.008).
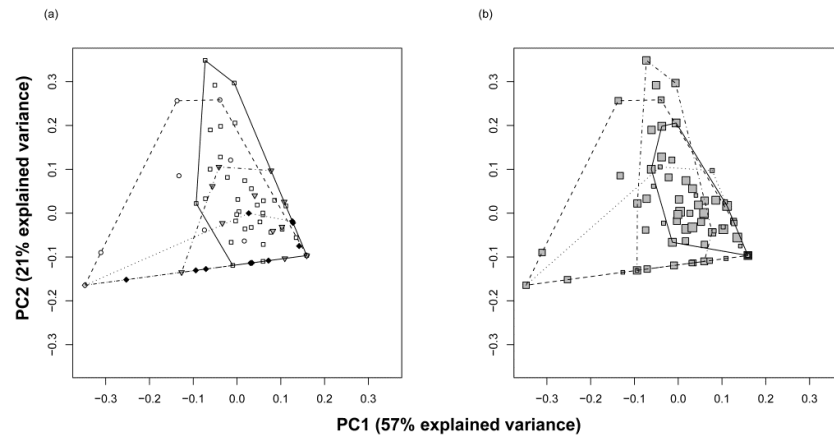

Figure 7: Results of a principal components analysis on proportions of stomach content items of different sizes per stomach. (a) The different symbols represent the area of origin of each stomach: the German Bight (white squares, solid line), the Baltic Sea (black diamonds, dotted line), the northern North Sea (white circles, dashed line) and the North Sea (grey upside down triangles, dotted-dashed line). (b) The size of the symbols represents length class of the anchovy that provided the stomach, and four groups for fish length are displayed: small (<12cm, dotted line), medium (12-14cm dashed line), large (15-16cm, dot-dashed line), extra large (17-19cm, solid line).

DISCUSSION

The analysis of stomach contents confirmed that anchovy is a zooplanktivore in the North and Baltic Seas. The main prey items found in the stomachs were malacostracans and copepods, but other items varied in both taxonomy (fish, chaetognaths, larvaceans, gastropods, cephalopods) and size (from <mm, e.g. barnacle cypris, to >cm scale: fish larvae) indicating that anchovy is unlikely to be a specialist. The most frequently found items were of small and extra large size, which would be expected from filter-feeding on small prey and selectively predating larger prey items as described for anchovy in other systems (James and Findlay, 1989; Plounevez and Champalbert, 2000). However, this does not mean that medium-sized items are not consumed by anchovy, in fact, *Centropages* makes up the second highest proportion of stomach contents in the German Bight area. There was some variability in prey composition between sampling events, most clearly observed when analysing proportions of prey categories. The most prominent area differences in diet were the high proportion of "parapseudocalanus" and malacostracans in the Baltic Sea, and high proportions of *Temora* spp. in the German Bight and northern North Sea stomachs. The mean wet weight of stomach contents also varied by area, it was much higher in the German Bight sampling event. This may be due to the sampling time in the summer, when more prey are available (Greve et al., 2004) and higher temperatures also make for higher metabolic requirements (Clarke and Johnston, 1999). The observed diets in the different areas from this study, as well as a more recent study on Kiel Bight anchovy diet (Schaber et al., 2010), show that North and Baltic Sea anchovy have a varied diet with higher proportions of non-copepod items than in studies of adult anchovy from other Seas where 93.6% of prey items are copepods (van der Lingen et al., 2009).

Subjective choices made before the statistical analysis of stomach contents influenced the results and the ensuing interpretation. The type of summary data as well as the categorisation scheme affected the degree to which area separation was apparent, and the prey categories considered to drive these differences. Whilst the patterns of differences in e.g. cumulative variance explained by PC1-3 can be expected from the properties of the data and its analysis (Krebs, 1999), what is more problematic is that the biological interpretation of these results changes in a less transparent manner. The prey categories considered most important in driving the variability in the data vary across categorisation scheme for abundance and presence-absence data. This shows that the decisions made with regard to

categorisation scheme may have unexpected consequences for the biological interpretation of the results. Only proportions data show similarities across the different categorisation schemes (malacostracans and *Temora* spp. being important), thus proportions data may be more robust to subjective grouping choices than abundance and presence-absence data.

Since PCA results based on taxonomic categories depended on the aggregation into groups, the PCA results of size data would probably also depend on how the items are grouped together. It may thus be useful to always carry out a sensitivity analysis of the own grouping choices as was done here for the taxonomic categorisations. We were unable to do this for the size-choices as the information on size was not at a sufficient resolution to carry out detailed size-analysis with different size groupings, semi-quantitative (or quantitative, as not measured). Much information can be determined from the same set of data: by using many different categorisation schemes and seeing which ones come out as representing most of the variability, it can be determined which ways of categorising do and do not allow for area/sampling occurrence separation. This may give an indication of what may be important in the process of choosing prey. The appropriate level of detail in any particular property of the stomach contents (taxonomic level, size, swimming speed, defences) is that which is the closest to the criteria used by the fish in feeding behaviour. This method is useful in the cases where little is known *a priori* about which of the prey properties determine the diet but the characteristics can be attributed to the prey items. Studies using a different approach have used attributed characteristics of prey and functional links between these and fish preferences to successfully predict fish diet (e.g. Sibbing and Nagelkerke, 2000).

An important influencing factor in small pelagic fish diet studies is usually length class of the predator (see e.g. Casini et al., 2004) for Baltic herring and sprat). This study was limited to adults and due to the small number of samples could not address this issue adequately. In European anchovy, prey item composition has been shown to be relatively similar across length classes with only few items (the copepods *Microsetella rosea*, *Centropages typicus* and *Candicia armata)* showing a strong relation to anchovy size (Plounevez and Champalbert, 2000). And while mean food size increases in anchovy of 3-12 mm, there seems to be no relation between prey length and predator length in adult sizes (van der Lingen et al., 2009). Our results suggest that the importance of some items may change with length class but most likely the interaction between area and season and length of predator is more influential, which we did not control for in this

study. It seems that length class is important but not sufficient to explain the variation in diet. PC3 of the size-based PCA were significantly correlated with anchovy length, suggesting that with the prey size categories used here, predator length does not seem to be very influential in explaining the variation of prey item sizes – a lot of variation is already explained by the other two PCs. In the taxonomic analysis size may be more influential as PC1, which explains the most variation in the dataset, is correlated with predator length. However, principal components can represent a multitude of effects beyond this generic relation. Thus the exact relationship between size and diet remains unclear as further exploration through correlations between length class and individual prey item proportions did not show significant relationships, except for *Calanus'* positive relation with predator length. *Calanus* was present mainly in the German Bight stomachs, which were generally from larger (14-19cm) anchovy. Therefore, for more information on length effects a more directed sampling and analysis will have to be carried out.

Selectivity for particular prey items could not be determined from this study (e.g. Rowlands et al., 2008). Though zooplankton samples were available from the same cruise as the anchovy samples in one area (the German Bight), zooplankton was sampled distantly in time and/or space from anchovy (days-weeks, several tenths of degrees latitude/longitude). It was expected that the plankton samples would not have been representative of the plankton environment encountered by the sampled anchovy, due to the large variability in plankton communities (Young et al., 2009). At higher scales however, e.g. area-scale in this study, the plankton composition is expected to be similar but as zooplankton information was available only for one of the four sampling cruises, studying area differences on a more general level (e.g. using the mean zooplankton composition by area/cruise) was not possible. Knowledge of the background zooplankton is important because several explanations for stomach content difference by area can be found. Regardless, the observed differences in diet by area corroborate the expectation that stomachs sampled close in time and space should be more similar than distantly sampled ones. Additionally, the variability in items found in anchovies' stomachs reflects a flexibility in consumable items that may indicate that anchovy is not dependent on a particular type of prey in its North/Baltic Seas range, although studies of condition and survival would be needed to confirm this expectation.

The observed differences between the diets in the different areas could for instance be due to the areas having differing zooplankton composition consistently every year, or the areas may have similar zooplankton composition within a year

but be changing through time; in the latter case, an artificial area difference would have been created due to sampling in different years. Moreover, diet changing by season, as observed in herring and sprat (Möllmann et al., 2004) may be another confounding factor. While the background zooplankton in the North Sea is known to be show changing trends through time (e.g. Pitois and Fox, 2006), we expect that the area differences are likely to play more of a role in the sampled period spanning only a few years. Generally, the zooplankton composition by biomass in the northern North Sea and southern North Sea are similar with the exception of *Calanus finmarchicus*, more common in the North (Pitois and Fox, 2006). This is reflected in the similar taxonomic composition of the anchovy diets from the NNS and NS areas. Those samples were collected in winter, when *Paracalanus/Pseudocalanus/Microcalanus*, *Acartia* spp., *Oithona similis*, *Evadne nordmanni* and *Temora longicornis* are the most abundant items (Clark et al., 2003) but the stomach contents are composed mainly of *Temora*, malacostracans, fish, copepod and other items. It could be that anchovy consume more *Temora* as these are larger items, and this applies also to malacostracan and fish larvae. Anchovy consumed high proportions of *Temora* and *Centropages* in the German Bight area, which has overall similar background zooplankton as the previously described areas, but due the sampling time being in summer in the German Bight, many copepod groups are likely to be at their peak seasonal abundance (Greve et al., 2004) possibly explaining why the mean number of items per stomach is so high in that area. The variety of items consumed at that time may also simply be a result of the availability of many different zooplankton groups. In the Baltic, the winter zooplankton community would be composed mostly of *Acartia* spp., *Pseudocalanus elongatus*, *Temora longicornis* and *Centropages hamatus* (Casini et al., 2004) and the observed diet is composed mostly of "parapseudocalanus", malacostracans and copepods. Thus it seems that there are differences between the available and consumed zooplankton, with *Acartia* appearing to be less consumed than the other copepods.

The North Sea anchovy population increased fairly recently (Armstrong et al., 1999; Beare et al., 2004a) though the causes and consequences of the increase are not yet understood, factors favouring it are likely to be either habitat changes or changed trophic interactions. While little is known about anchovy habitat in the North Sea (but see e.g. Alheit, 2007; ICES, 2007), this study adds to knowledge on the trophic interactions surrounding anchovy and establishes anchovy as a zooplanktivore in the North Sea trophic web likely to interact with other

planktivorous fish. Anchovy feeds off a changing food source (e.g. Beaugrand and Reid, 2003) and is a potential competitor and predator of other planktivorous fish, themselves undergoing changes likely due to climate (e.g. Payne et al., 2009) or fisheries. The interactions with other fish are important from a fisheries management perspective: some species, e.g. herring, are major commercial species in the North Sea (Dickey-Collas et al., 2010). The main items found in these anchovy stomachs correspond to the same genera and taxonomic groups consumed by herring (Last, 1989; Möllmann et al., 2004) and sprat (Möllmann et al., 2004; Tičina et al., 2000) suggesting diet overlap between these species. For instance, anchovy stomach contents from the Baltic Sea contained a high proportion of "parapseudocalanus", an important prey item for both sprat and herring in the Baltic Sea in the spring (Möllmann et al., 2004) and winter (Casini et al., 2004), when the Baltic Sea anchovy samples were collected. To establish the potential for trophic competition, a single study analysing the diets of e.g. herring and anchovy from the same sampling events would be desirable as this would approach the situation where both species have the same plankton available as prey. Other studies have suggested competition is present between Baltic sprat and herring based on their overlapping diet (Möllmann et al., 2004) and cause for reduction in growth, therefore an additional predator on a similar food source may be detrimental for existing planktivorous fish populations.

Moreover, fish larvae were frequently found in individual anchovies' stomachs. Though initial identification suggested the fish larvae were sandeel, it seems likely that they are sprat larvae, due to the location of sampling (the German Bight) and their size (ca 2cm) at the sampling time in August (J. Alheit, pers. com.). Herring (Hardy, 1924; Last, 1989; Segers et al., 2007) and sprat also consume fish larvae and eggs (Möllmann et al., 2004). Intraguild predation, i.e. consumers of a common resource preying on each other's young (Polis and Holt, 1992) is one mechanism which may increase the non-linearities in ecological systems (Holt and Polis, 1997; Takimoto et al., 2007) and thus the addition of another potential player in the trophic interactions of the North Sea is likely to add complexity to the already ongoing shifts in the North Sea community (Beaugrand, 2004; Daan et al., 2005; Payne et al., 2009).

CONCLUSIONS

This study of anchovy diet in the North Sea has confirmed their zooplanktivory, the expectation that samples taken close in time and space are more similar than distant samples was corroborated, and it was shown that methodological choices made during the analysis may influence the biological conclusions. The observed diet similarity with the diets of other clupeids such as herring and sprat, and that the diet contained clupeid fish larvae, gives potential for two strong interactions between the new anchovy population and the pre-existing clupeids.

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CHAPTER 3

Dietary overlap between the potential competitors herring, sprat and anchovy in the North Sea

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ABSTRACT

European anchovy *Engraulis encrasicolus* increased its abundance and distribution in the North Sea during the mid-1990s and may consume similar zooplankton to and/or compete with other occupants of the North Sea like herring *Clupea harengus* and sprat *Sprattus sprattus*. The diets of adult anchovy, sprat and juvenile herring of comparable sizes, sampled close in time and space, were compared to understand how the 3 species prey on zooplankton and establish whether their diets overlap or not. Anchovy was found to be more generalist, consuming a higher diversity of prey items. Herring was more specialized, with low diversity of food items. Sprat was intermediate between anchovy and herring. The dietary overlap between anchovy and sprat was highest, followed by herring and sprat before anchovy and herring. The mean weight of stomach contents did not differ between species. We conclude that of the 3 species, anchovy is likely to be the least affected by changing plankton communities.

INTRODUCTION

The North Sea is a dynamic system and has undergone documented changes in its fish community over the last decades (Daan et al. 2005, Heath 2005, Engelhard et al. 2011). Of interest is the spread of European anchovy *Engraulis encrasicolis* across the North Sea (Armstrong et al. 1999, Beare et al. 2004a) concurrent with the reported pattern of increase in species of southern geographic affinities (Beare et al. 2004b, Perry et al. 2005, ter Hofstede et al. 2010). The ecological interactions involving anchovy in the North Sea are not well understood, likely due to its past restricted distribution and low abundance; although anchovy were present in the Dutch coastal areas of the Oosterschelde and Wadden Sea (Boddeke & Vingerhoed 1996), expansions beyond these areas were reported to be unusual (Aurich 1950, Beare et al. 2004a). While the effect of the increased anchovy population on higher trophic levels remains unknown, partially due to a lack of predators' stomach data, its potential trophic interactions with lower trophic levels are starting to be addressed.

European anchovy is a confirmed zooplanktivore in both the North and Baltic Seas (Schaber et al. 2010, Raab et al. 2011), just like in other parts of its distribution, e.g. the Bay of Biscay (Plounevez & Champalbert 1999), the Mediterranean (Tudela & Palomera 1995, 1997) and in the Benguela system (van der Lingen et al. 2006). This implies that the North Sea anchovy population may interact with other planktivores such as herring *Clupea harengus* and sprat *Sprattus sprattus*. Herring diet is characterised by various copepods (*Calanus* and *Temora* species), sandeel larvae (*Ammodytes* spp.), chaetognaths and larvaceans (Hardy

1924, Bainbridge & Forsyth 1972, Daan et al. 1985, Last 1987). Sprat feed mainly on copepods and less on larger planktonic prey (Ellis & Nash 1997, Tičina et al. 2000, Casini et al. 2004, Möllmann et al. 2004) and have a very similar diet to North Sea herring (De Silva 1973). Anchovy in the North Sea consume mainly copepods and malacostracans, with other items like fish, chaetognaths, larvaceans, gastropods and cephalopods also being found (Raab et al. 2011), and the species also has a varied diet in the western Baltic Sea (Schaber et al. 2010). Clupeids can eat both fish larvae and eggs (e.g. herring: Huse & Toresen 1996; anchovy: Raab et al. 2011), and anchovy has been observed to be cannibalistic in other systems (Valdés Szeinfeld 1993, Plounevez & Champalbert 2000, Takasuka et al. 2004,), though in some instances this may be due to cod-end feeding (suggested by Borme et al. 2009). The interactions between anchovy, herring and sprat may be manifold. In addition to possible competitive interactions, intra-guild predation (Polis & Holt 1992) may also occur, and this is likely to be an important factor in the dynamics of small pelagic fish (Valdés Szeinfeld 1991, Irigoien & de Roos 2011).

Interactions with herring are of particular interest as herring is one of the main commercial species of the North Sea and has suffered low recruitment since 2000, likely due to environmental changes rather than overfishing (Payne et al. 2009, Fässler et al. 2011). North Sea herring has been suggested to have density-dependent growth (Heath et al. 1997, Nash et al. 2009; although see Brunel & Dickey-Collas 2010). Density dependence may be caused by habitat or food limitation of a population. While single-species studies address intra-specific density dependence, inter-specific density dependence may also occur (e.g. as suggested by Casini et al. 2010 between Baltic sprat and herring). The juvenile stage of North Sea herring seems to be the most crucial in determining its growth in later life, thus influencing later reproductive potential since this depends on fish size (Birkeland & Dayton 2005). Therefore, if food limitation occurs at the juvenile herring stage (when the herring are at a similar size and location as anchovy), then, at a later stage, reproduction and stock productivity of herring could be affected by this inter-specific interaction.

Diet studies of North Sea herring, sprat and anchovy are sparse; therefore, comparing diets reported in the literature is suboptimal, since the zooplankton prey of fish can change across time and space (Young et al. 2009). Studies of North Sea herring diet were carried out prior to the anchovy increase (e.g. Hardy 1924, Last 1989) and also before recent changes in the zooplankton community (Beaugrand 2004). The most recent studies of sprat diet come from the Baltic Sea (e.g. Cardinale et al. 2002, Casini et al. 2004) or other systems (e.g. the Adriatic: Tičina et al. 2000). To understand the inter-specific interactions there is a need to compare these clupeids' diets in the same area and at the same time. Anchovy is perceived

as a newcomer and few appropriate information sources exist for this species; however, we use a stomach content dataset from the German Bight (SE North Sea) where all 3 species were sampled at the same time.

The aim of this study was to describe and compare the diets of the co-occurring potential competitors anchovy, juvenile herring and sprat, as well as establish the level of dietary overlap between these species.

MATERIALS AND METHODS
Data collection

Anchovy *Engraulis encrasicolus*, herring *Clupea harengus* and sprat *Sprattus sprattus* were sampled in the spring and summer of 2004 as part of the Global Ecosystems Dynamics (GLOBEC, www.globec.org/) Germany project. Fish stomachs were extracted onboard and preserved in 4% buffered formaldehyde. For the analysis presented here, only those individuals caught during the same cruises were kept, in an attempt to ensure that all fish were likely to have encountered the same environmental conditions. Since the main interest was the trophic impact of anchovy, we only analysed and compared fish from the cruises where anchovy were caught, and only at stations close to those where anchovy were caught (east of longitude 7°E; Fig. 1). Fish diet changes with size (e.g. Casini et al. 2004); thus, only fish of comparable size (12 to 19 cm) were analysed. The size ranges of fish were 12 to 13 cm for sprat (33 adults), 12 to 15 cm for herring (35 juveniles) and 15 to 19 cm for anchovy (34 adults). This left a relatively small data set originating from May to August 2004. However, it was likely that these fish encountered similar environmental/prey conditions, as factors such as temporal and spatial variation in prey fields and/or size-dependent changes in diet were minimized.
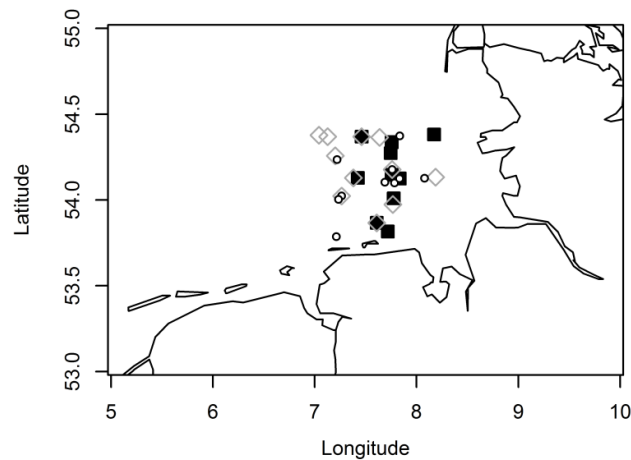
Fig. 1. Sampling stations for anchovy *Engraulis encrasicolus* (black squares), herring *Clupea harengus* (grey diamonds) and sprat *Sprattus sprattus* (white circles) in the German Bight in late spring/summer 2004

Stomach contents were weighed and prey items identified to the lowest taxonomic and developmental stage possible and counted using a binocular microscope when items represented more than half of an identifiable organism. The copepods *Paracalanus* spp. and *Pseudocalanus* spp. were recorded jointly (following the example of the Continuous Plankton Recorder Survey; Warner & Hays 1994) as 'Parapseudocalanus' due to the difficulty in separating these species. An estimate of the volumetric percentage of highly digested items was recorded as these could not be quantified in numbers. We assumed the countable items were also representative for the digested portion of the stomach contents. Counted prey items were grouped into prey categories as often done with stomach analyses (e.g. Möllmann et al. 2004) based on the pooled categorization scheme used in a previous analysis of anchovy diet (Raab et al. 2011). These categories were: *Acartia* spp., *Calanus* spp., *Centropages* spp., chaetognaths, cladocerans, copepods, fish, malacostracans, *Oikopleura* spp., Parapseudocalanus, *Temora* spp. and 'other', which included unidentified items. For each stomach, abundances

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(numbers), proportions (numerical percentages) and presence–absence of each prey category were calculated providing information on different aspects of the diet. Abundances give information on the absolute quantity of items consumed, proportions tell whether the diet is dominated by certain prey items and presence data simply give information on whether prey composition is the same or not. Abundance and wet weight per individual stomach were corrected for fish size by dividing these 2 variables by the cube of individual fish length (as proxy for fish volume). One anchovy was of unknown length; therefore, average length of all other anchovies was used for this scaling.

Diet description

The 5 most important categories by abundance (scaled by size), proportions per stomach and frequency of occurrence for each species were extracted. To improve our understanding, the abundance data (scaled by size) were back-translated for a hypothetical 'standard fish' of 14 cm (the average length of all individuals across the species).

Principal components analysis (PCA; described in Legendre & Legendre 1998) was carried out on stomach contents to visualize the differences between species. Proportions were arcsine-transformed ($x' = \arcsin[\sqrt{(x)}]$) before analysis, and PCA was carried out in R (R Development Core Team 2008) using singular value decomposition. Data were centred, and scaling was done only on the abundance data.

Species differences and dietary overlap

Abundance of prey items per stomach and wet weight of stomach contents (in grams and scaled by fish size) were compared between species using the Kruskal-Wallis test. Dietary overlap between species pairs was calculated for each species pair using the Morisita index of similarity. This index is almost independent of sample size (Wolda 1981, Krebs 1999) and only applicable on abundance data. Another commonly used index of dietary overlap is the percentage overlap, also called Schoener's index and the Renkonen measure (Krebs 1999); thus, for comparability with other studies we include this measure as well. Confidence intervals for the overlap indexes were obtained by bootstrapping, using the accelerated bias-correction method (Efron & Tibshirani 1993). Fish caught in the same hauls were also compared for diet similarity (percentage overlap and Morisita index) in order to investigate whether these fish, which had more similar feeding conditions, showed the same results as in the overall analysis. However, the number of hauls in which >1 of the species was caught was very low: 2 hauls with

anchovy–herring, 2 hauls with herring–sprat and 1 haul with anchovy–sprat (the latter with only 1 anchovy in it; see Table 1 for details). Therefore, no further statistical analysis was carried out, and only the range of diet overlap was shown as an indication of variability.

The average diet breadth as used in the above population-level measures can represent many individuals using the whole breadth, or it can represent a range of individuals that are specialized on different parts of the range of items represented (Bolnick et al. 2003). Since many ecological mechanisms occur at an individual level, it is important to understand the diet at an individual level as well; therefore, the numerical percentage was calculated for each individual stomach. Numerical percentages were then sorted in decreasing order and averaged across all stomachs of the same species. The resulting average indicates whether the species consists of individual generalists or individual specialists within the sample population (when considering it relative to the other species). In the latter case, few categories suffice to account for a high percentage of stomach contents in each of the stomachs. In the former case, a relatively larger number of prey categories accounts for the same percentage of stomach contents. The Shannon diversity index of each stomach's content was calculated using the diversity function of the vegan library of statistical software R (R Development Core Team 2008) on prey abundances (scaled by fish size). Mean diversity per stomach was then compared between species by using the Kruskal-Wallis test.

Table 1. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Overview of collected samples' origins per species and per species pair: number of cruises, stations, hauls, and time span (dates and time of day) of stomach collection

Species or species pair	Cruises	Stations	Hauls	Dates	Time of day (h)
Anchovy	3	10	10	16 May–10 Aug 2004	6:28 (May)– 18:36 (Aug)
Herring	2	11	11	15 May–29 Jun 2004	08:44 (May)– 18:05 (May)
Sprat	3	10	10	16 May–16 Aug 2004	08:50 (Jul)– 16:03 (Aug)
Anchovy– Herring	2	2	2	16-May-04 27-Jun-04	12:30 09:00
Anchovy–Sprat	1	1	1	01-Jul-04	12:17
Herring–Sprat	2	2	2	27-Jun-04 18-May-04	15:55 13:05

Table 2. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus.* Prey categories by abundance, proportion and frequency of occurrence (expressed as percentages) in order of decreasing importance for anchovy, herring and sprat. For abundance, the scaled values back-calculated for a 14 cm fish are given. Parentheses in header line indicate the volumetric percentage of uncountable digested material

Anchovy (+55%)	Percent	Herring (+90%)	Percent	Sprat (+90%)	Percent
Abundance per stomach for a 14 cm fish (SD)					
Temora spp.	79 (94)	*Calanus* spp.	25 (78)	*Temora* spp.	61 (97)
Centropages spp.	47 (92)	*Temora* spp.	17 (40)	*Calanus* spp.	17 (41)
Oikopleura spp.	13 (44)	*Acartia* spp.	5 (22)	Parapseudocalanus	15 (53)
Parapseudocalanus	9 (15)	Malacostracans	5 (8)	Cladocerans	11 (35)
Acartia spp.	9 (17)	Parapseudocalanus	2 (5)	*Centropages* spp.	9 (20)
Other	7 (12)	*Centropages* spp.	0 (1)	*Acartia* spp.	6 (15)
Malacostracans	7 (9)	Copepods	0	Fish	4 (16)
Copepods	6 (13)	*Oikopleura* spp.	0	Malacostracans	2 (5)
Calanus spp.	6 (15)	Other	0	*Oikopleura* spp.	1 (3)
Fish	5 (11)	Chaetognaths	0	Copepods	0 (1)
Cladocerans	3 (6)	Cladocerans	0	Other	0 (1)
Chaetognaths	3 (13)	Fish	0	Chaetognaths	0
Mean proportion per stomach (SD)					
Temora spp.	47 (28)	*Calanus* spp.	37 (40)	*Temora* spp.	50 (34)
Centropages spp.	12 (21)	*Temora* spp.	33 (39)	Cladocerans	16 (27)
Oikopleura spp.	9 (26)	Malacostracans	16 (28)	Parapseudocalanus	9 (21)
Malacostracans	7 (7)	Parapseudocalanus	6 (14)	*Centropages* spp.	8 (15)

Acartia spp.	5 (8)	*Acartia* spp.	5 (18)	*Calanus* spp.	7 (13)
Other	5 (9)	*Centropages* spp.	2 (7)	*Acartia* spp.	6 (12)
Parapseudocalanus	5 (6)	Copepods	0	Fish	2 (8)
Copepods	3 (5)	*Oikopleura* spp.	0	*Oikopleura* spp.	2 (9)
Fish	3 (5)	Other	0	Malacostracans	1 (21)
Calanus spp.	2 (3)	Chaetognaths	0	Other	0 (2)
Chaetognaths	1 (5)	Cladocerans	0	Copepods	0 (1)
Cladocerans	1 (1)	Fish	0	Chaetognaths	0

Frequency of occurrence

Temora spp.	88	*Calanus* spp.		*Temora* spp.	94
Malacostracans	85	*Temora* spp.		*Centropages* spp.	58
Centropages spp.	76	Malacostracans		Cladocerans	49
Other	76	Parapseudocalanus		*Acartia* spp.	36
Copepods	74	*Centropages* spp.		*Calanus* spp.	30
Acartia spp.	68	*Acartia* spp.		Parapseudocalanus	30
Parapseudocalanus	68	Copepods		Malacostracans	21
Fish	62	*Oikopleura* spp.		*Oikopleura* spp.	15
Cladocerans	53	Other		Copepods	12
Calanus spp.	38	Chaetognaths		Fish	12
Oikopleura spp.	29	Cladocerans		Other	6
Chaetognaths	21	Fish		Chaetognaths	0

RESULTS

Regardless of measure type (abundance, numerical percentage, or frequency of occurrence), *Temora* spp. was dominant in the stomachs of both anchovy *Engraulis encrasicolus* and sprat *Sprattus sprattus* (Table 2). In an average anchovy stomach, 47% of items were *Temora* spp., and 88% of anchovy stomachs contained this copepod. In the average sprat stomach, 50% of items were *Temora* spp., and *Temora* spp. occurred in 94% of stomachs. A standard size anchovy (14 cm) would contain 79 *Temora* spp., while a standard size sprat would contain 39 *Temora* spp. items. *Centropages* spp. were important in abundance and frequency for anchovy. A 14 cm anchovy would contain 47 *Centropages* spp., and 76% of anchovy stomachs contained *Centropages* spp. *Calanus* spp. were important prey for herring *Clupea harengus*. A 14 cm herring would contain 15 *Calanus* spp., as well as 15 *Temora* spp. items. *Calanus* spp. were more important than *Temora* spp. by proportions (37 and 33%, respectively) and frequency of occurrence (71 and 63%, respectively). The PCA showed different patterns according to whether abundance, proportions or presence–absence was used and explained between 51 and 68% of the dataset's variance with the first 3 dimensions (Table 3). The number of prey items in each anchovy stomach differed from those of herring and sprat (Fig. 2a). The pattern was driven by the categories 'other', *Calanus* spp. and Parapseudocalanus, with anchovy varying most along PC1 (representing 'other') and herring and sprat varying most along PC2 (*Calanus* spp.). Herring was dissimilar from the other 2 species in the proportions of data, with most of the variation explained by the categories *Temora* spp., *Calanus* spp. and malacostracans (Fig. 2b). Prey category composition in stomachs was similar in the 3 species, though anchovy appeared to have a broader range of species in its diet (Fig. 2c).
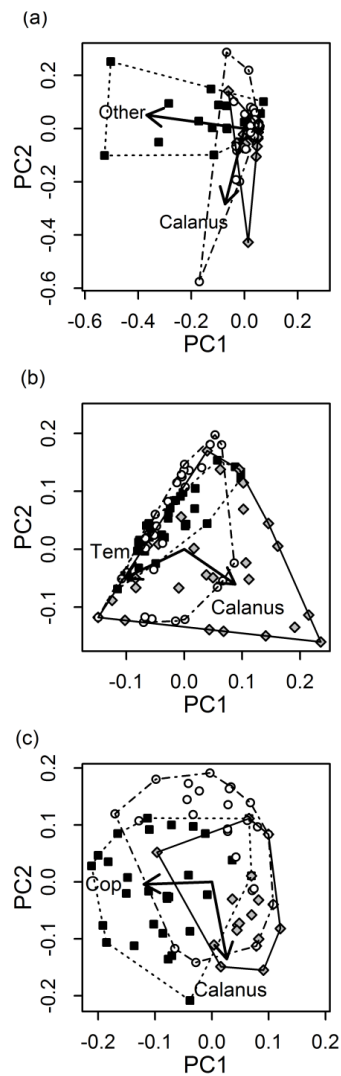
Fig. 2. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Results of principal components (PC) analysis on (a) abundance, (b) proportions and (c) presence–absence of prey categories in the stomachs of anchovy (black squares, dashed line), herring (grey diamonds) and sprat (white circles). Arrows represent the highest absolute loadings on PC1 and PC2. Tem: *Temora* spp.; cop: copepods

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Table 3. Results of principal components (PC) analysis on abundance (scaled for fish length), proportions and presence–absence data: proportion of variance explained by the first 3 principal components (expressed as percentage). For each principal component, the prey category representing the highest absolute loading is given

	Variance explained (%)			Categories with highest absolute loading		
	Abund.	**Prop.**	**Pres.–Abs.**	**Abundance**	**Proportions**	**Presence–Absence**
PC1	31	38	38	Other: –0.47	*Temora* spp.: –0.75	Copepods: –0.38
PC2	11	19	14	*Calanus* spp.: –0.60	*Calanus* spp.: –0.63	*Calanus* spp.: –0.72
PC3	9	11	10	Parapseudocalanus: –0.51	Malacostracans: –0.88	Malacostracans: –0.48
Total	51	68	62			

The total number of items per stomach corrected for fish length differed between species (Fig. 3a; Kruskal-Wallis test, H = 13.5; df = 2; p = 0.001). Median abundance per stomach was higher for a 14 cm anchovy (103 items) than for a sprat (67 items) and higher still for a herring (26 items). Stomach content weight did not differ statistically between the 3 fish species (Fig. 3b; Kruskal-Wallis test, H = 4.5; df = 2; p = 0.106). Median stomach content weight of a 14 cm fish would be 0.113 g for anchovy, 0.182 g for herring and 0.082 g for sprat. The median percentage of highly digested items was 55% for anchovy and 90% for both herring and sprat.
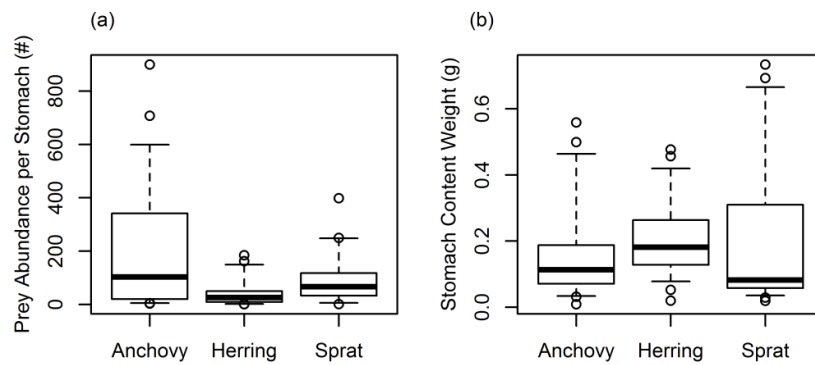

Fig. 3. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Boxplot showing (a) median prey abundance per stomach and (b) median wet weight (g) of stomach contents in anchovy, herring and sprat stomachs back-calculated to a 14 cm standard fish size. Boxes show the medium value (horizontal lines), interquartile range (boxes); the 5th and 95th percentiles (whiskers) and outliers (lowest and highest 5 percentiles, circles)

Dietary overlap, measured as percent overlap and by the Morisita index, was the highest between anchovy and sprat according to both measures used (67.2% and 0.883, respectively) and lowest between anchovy and herring (47.5% and 0.540, respectively). Herring and sprat overlapped by intermediate values (55.9% and 0.734, respectively; Table 4a). The species pairs caught in the same hauls (Table 4b) confirmed that at the within-haul level, anchovy–herring overlap (29.0% and 0.364, respectively) was lower than herring–sprat (42.4% and 0.525, respectively) too. The dietary overlap between anchovy and sprat (21.7% and 0.343,

respectively) was lower than that of the other 2 species pairs. Anchovy diet was generally more diverse than that of herring and sprat as measured by the Shannon diversity index. Individual variation among the cumulative abundance curves shows that most anchovy stomachs contained many items, while most herring stomachs contained few items of the same prey category (Fig. 4). Among herring, 2 categories on average made up >95% of all prey items, while in sprat and anchovy ca. 3 to 6 categories made up 95% of prey items. Stomach content diversity after correcting for fish length also differed between the 3 species (Fig. 4d; Kruskal-Wallis test, $H = 25.6$; df = 2; p < 0.001), with anchovy having a higher median diversity index (1.17) than sprat (0.74) and herring (0.47).

Because of the particular interest in possible direct feeding on each other of the 3 clupeids (intraguild predation and cannibalism), we explicitly report the 'fish' category (which includes eggs and larvae). Mean abundance of these items per stomach for a 14 cm fish was 5 for anchovy, 3 for sprat and 0 for herring, and the average percentage was 3 for anchovy, 2 for sprat and 0 for herring. A high number of anchovy stomachs contained fish eggs and larvae (21 out of 34 stomachs), which was higher than for sprat and herring (4 out of 33 for sprat; 0 herring out of 35).
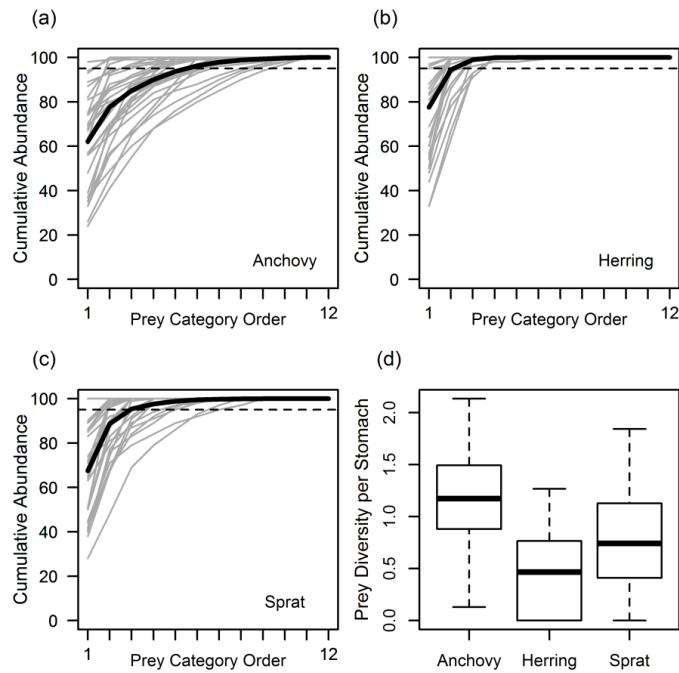
Fig. 4. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Diversity in prey items consumed by (a) anchovy, (b) herring and (c) sprat. Cumulative abundance of each individual stomach's prey items (grey) and the average (black) arranged in decreasing order of importance in numerical percentage on the *x*-axis. Thus, the *x*-axis can represent different prey categories for different individuals. The 95% level is indicated by a horizontal dashed line. (d) Boxplot of mean diversity per stomach (details as in Fig. 3)

Table 4. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus.* Estimated dietary overlap between the 3 species pairs. Percentage overlap and Morisita's index with (a) 95% confidence intervals (CI) as estimated by the accelerated bias-correction methodor (b) based only on stomachs from the same haul, with the range of resulting dietary overlap values; the number of pairs and stomachs are given.. A: anchovy; H: herring; S: sprat

Species Pair	Percentage Overlap (95% confidence interval)	Morisita Index (95% confidence interval)	
Anchovy-Herring	47.5 (42.4 - 49.1)	0.540 (0.518 - 0.560)	
Anchovy-Sprat	67.2 (65.9 - 68.7)	0.883 (0.873 - 0.906)	
Herring-Sprat	55.9 (50.8 - 57.5)	0.734 (0.654 - 0.746)	
	Percentage Overlap (range)	**Morisita Index (range)**	**Nb Pairs**
Anchovy-Herring	29.0 (0 - 70.7)	0.364 (0 - 0.862)	9 (6A + 3H)
Anchovy-Sprat	21.7 (20.0 - 25.1)	0.343 (0.297 - 0.385)	3 (1A + 3S)
Herring-Sprat	42.4 (12.3 - 73.5)	0.525 (0.158 - 0.896)	36 (8H + 8S)

DISCUSSION

The results suggest that anchovy *Engraulis encrasicolus* is more generalist a planktivore than the other 2 clupeids. Both at the population and at the individual level it consumed a higher number of different prey items than both juvenile herring *Clupea harengus* and sprat *Sprattus sprattus*. While anchovy consumed mainly *Temora* spp. and a number of other items including *Centropages* species, malacostracans, appendicularians and other copepods, juvenile herring was more specialised on *Calanus* and *Temora* species regardless of which measure of importance was used (abundance, numerical percentage or frequency of occurrence). Sprat too showed *Temora* to be their most important prey, but other copepods and cladocerans were also important. The anchovy's generalist diet also explains why the category 'other' explained much of the variance between stomachs in the multivariate analysis; this was the category that was more abundant and more frequently found in the stomachs of anchovy than in the stomachs of sprat or herring. PCA results from proportions data are more consistent across different categorisation schemes (Raab et al. 2011), suggesting that this may be a more robust measure when semi-arbitrary categorisation schemes are used.

Although there was substantial intra-specific variation in diet, the population level comparison revealed clear differences in diet among the species. Anchovy showed a more diverse diet, whereas sprat and particularly herring showed a more

specialised diet. It is well known that predator–prey interactions are affected by the relative size of the predator and prey, but the size dependence may be less prominent in small pelagic fish. It has been found that mean food size (van der Lingen et al. 2009) or wet mass and prey composition (Plounevez & Champalbert 2000, Schaber et al. 2010) do not relate to the size of adult anchovy, nor was any relationship found between anchovy length and maximum prey size: larvae, juveniles and adults fed on the same plankton size classes (Borme et al. 2009). Therefore, we do not expect the higher diversity observed in the anchovy diet to result from the size distribution of fish in our sample. The diet of adult North Sea sprat also seems relatively independent of fish size; they continue consuming medium-sized copepods when herring, in contrast, changes to increasingly larger items (Last 1987).

Percentage overlap between 0.25 and 0.75 is considered to be intermediate (arbitrarily defined in e.g. Pedersen 1999), and thus all species pairs overlap (except the intra-haul anchovy–sprat comparison) and values fall in the 'intermediate' range. The Morisita index is considered more robust than the percentage overlap measure and shows that anchovy and sprat have relatively high dietary overlap. Anchovy–herring had the lowest dietary overlap, which suggests that of the 3 species pairs, this one has the least potential for dietary competition if they are in the same place. The likelihood of anchovy and sprat interacting seems higher. The order of dietary overlap among species pairs does not completely correspond when using intra-haul comparisons compared to all samples. This is because the anchovy–sprat overlap was calculated based on only 1 anchovy stomach which happened to be the one filled with fish larvae, constituting an outlier to the remaining samples. Discounting this species pair, the order of dietary overlap among species pairs remains the same, with the anchovy–herring still being lower than the herring–sprat overlap. A percentage overlap of 42.3% between herring and sprat was found in the Baltic Sea, and it was highest in spring and summer (Möllmann et al. 2004). Assuming a similar seasonality in feeding by planktivorous clupeids between the North and Baltic Seas, the overlap found in this study would be relatively high compared to other periods of the year since the analysed stomachs came from late spring/summer sampling events. So the impact on trophic interactions or potential competition by anchovy is dependent on whether the food-limited period in its life history is during summer or another time. The details of spatial overlap between these species are not known. Anchovy is distributed throughout the North Sea (in Quarter 3, International Bottom Trawl Data) and sprat is in the southern North Sea (ICES 2011), and both spawn in the German Bight, but appear to separate spatially (Alheit 2007). Most North Sea herring spawn in autumn/winter; therefore, spatial overlap with anchovy and sprat

probably occurs when herring is already juvenile and has returned to the eastern North Sea again (ICES 2006). The main feeding time of North Sea herring is from April to June (ICES 2006), and anchovy and sprat spawning activity is also during the sampling time, so if these latter species consume food to cover their increased energetic requirements, the trophic overlap at this time of year is the most relevant to assess. Dietary overlap has been used to suggest trophic competition by several authors (Huse & Toresen 1996, Möllmann et al. 2004), but the former does not necessarily imply the latter (Holt 1987). For trophic competition to occur, there needs to be trophic niche overlap in time and space combined with insufficient food availability through either low food or high consumption by high numbers of consumers. We assumed that the analysed fish did overlap in time and space, they were selected for that reason, but since the spatial scales of feeding ranges and of plankton prey patchiness are unknown, this work could benefit from a study addressing these issues (see e.g. Young et al. 2009). In addition, we assumed that there is an increase in consumption due to an increase in anchovy population. Trophic niche overlap requires more than just co-occurrence. When species co-occur, the criteria used by each species in food selection must also result in similar food being consumed. Although the characteristics of importance to each species' feeding can predict diet quite well (Sibbing & Nagelkerke 2001), these are often unknown. Current work on comparing the feeding morphologies of anchovy sprat and herring in the North Sea indicates that, although the individual morphological characteristics of the jaw do not differ significantly, the measure of their integrated impact, the filtration area, is significantly larger in anchovy (Raab & Nagelkerke, unpubl. data). Anchovy (van der Lingen et al. 2006) and herring (Gibson & Ezzi 1990) are known to be able to change from filter feeding to particulate feeding depending on feeding conditions, while it has been suggested that sprat, at least in the Baltic, rely more on particulate feeding (Möllmann et al. 2004) but are also capable of filter feeding. Even when there is dietary overlap, behavioural adaptations for resource partitioning can lead to a low potential for competition (even between similar species like Japanese anchovy *Engraulis japonicus* and Pacific round herring *Etrumeus teres*; Tanaka et al. 2006). Sampling in the same restricted place/time does not necessarily mean that the sampled fish are using the same exact habitat prior to sampling, but it is more likely than if they are caught at a greater distance in time and space. Young herring are known to prey on fish eggs (Last 1989, Segers et al. 2007), on sprat larvae (Last 1987), on *Ammodytes* spp. and on herring itself (Hardy 1924), as well as on plaice and cod eggs (Daan et al. 1985, Ellis & Nash 1997). Sprat also prey on fish eggs (Ellis & Nash 1997), and anchovy can consume fish larvae too (Plounevez & Champalbert 2000, van der Lingen et al. 2006). In this study, anchovy had slightly more fish in their stomachs than sprat.

No herring had fish larvae in their stomachs. Sprat, anchovy and sardine larvae are found in the German Bight in June and July (Kanstinger & Peck 2009) and anchovy spawn in May and June. So during the summer they are available to herring, but herring do not consume ichthyoplankton if zooplankton is readily available (Segers et al. 2007). We conclude that direct feeding interactions between all 3 species are possible, but there may be some habitat partitioning which is hidden here by the fact that we specifically chose to analyse the overlapping area. We tried to address this issue by analysing the diets of individual fish caught in the same hauls, but due to very low intra-haul overlap the results are indicative only. However, they confirm the general pattern of anchovy–herring overlap being lower than herring–sprat overlap. No conclusion can be made about anchovy–sprat overlap due to the low sample size (n = 1). More detailed and targeted studies comparing the diet of co-occurring and non-co-occurring populations of these species would offer a way to address this question in the future, as has been done for herring and walleye pollock (see Sturdevant et al. 2001).

The anchovy diet, broad as it is, includes the most important prey items of juvenile herring (*Calanus* and *Temora* species). If these copepods decline, anchovy can continue feeding on other prey. *C. finmarchicus* populations are decreasing in the southern North Sea, while *Temora* species and *C. helgolandicus* have increased between 1958 and 2003 (Pitois & Fox 2006). *C. finmarchicus* is of greater importance by biomass than *C. helgolandicus* in that area, so assuming herring have no preference for either species, the decline would outweigh the increase in its impact on food availability. In the event of a lower abundance of potential prey for herring, it is unclear whether feeding on the second main item (*Temora* spp.) would be sufficient to maintain herring populations, but, given that this species feeds on many copepods in other systems, it seems likely.

Although anchovy stomachs contained slightly more items by abundance, the 3 species compared contained a similar amount of food by wet weight with some overlap (especially between anchovy and sprat). The clearest difference found was the degree of specialization: highest in juvenile herring and lowest in anchovy. Returning to the idea that anchovy may consume the same food as juvenile herring, it seems that, although diets overlap to some extent, anchovy can consume so many more items that it seems unlikely that there would be any particular trophic effect of the new anchovy population on the herring population. This study forms part of a burgeoning body of literature on North Sea anchovy that seems to indicate that its increase is related to habitat changes (Petitgas et al. 2012) rather than strong changes in trophic interactions. Its existence underlines the value of data collection on non-commercial species which may be required for ecological understanding that may become crucial to implementing an ecosystem approach to fisheries.

Acknowledgements

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CHAPTER 4

Anchovy increase in the North Sea

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ABSTRACT

The abundance and spatial occupation of European anchovy (*Engraulis encrasicolus*) have increased in the North Sea since the mid 1990s. This paper investigates three hypotheses about the cause of change in this species using a cross-disciplinary approach combining genetics, transport modelling, survey time series analyses and physical oceanographic modelling. Evidence from connectivity studies suggests that the population of North Sea anchovy is separate from that in the Bay of Biscay. The recruitment pulses observed in survey data fit a life cycle which includes spawning in early summer and larval development in late summer. It also supports the concept of population expansion originating from local remnant population(s). In terms of growth physiology, suitable thermal windows have expanded making conditions more favourable for life cycle closure and population persistence/productivity. In addition to the increased frequency of warm summers, which favour larvae and juvenile growth, the decrease in severe winters is also likely to improve overwinter survival. Overall, the evidence supports the hypothesis that the increase in anchovy abundance originated from an improved productivity of existing populations. This increase was associated with an expansion in thermal habitats and is probably not due to a northward shift in the distribution of southern conspecifics.

INTRODUCTION

Climate change has affected the distribution of fish populations by different mechanisms including direct displacement of populations into novel areas and increased productivity of fringe components of populations (Beare *et al.*, 2004a; Rijnsdorp *et al.*, 2009). The European anchovy (*Engraulis encrasicolus*) has recently been identified as a species that may have exhibited climate driven changes of this nature in the North Sea, the northern boundary of this Lusitanian species (Engelhard *et al.*, 2011). Anchovy abundance in the North Sea has fluctuated with periods of high abundance being followed by periods of near absence (Aurich 1953). Interestingly, the periods of appearance coincide with warm phases of the Atlantic Multi-decadal Oscillation (AMO) in the last century indicating that climate variability likely plays an important role in anchovy dynamics in the North Sea. Data from trawl surveys and commercial information landings have indicated a dramatic increase in anchovy abundance after a period of absence (Beare *et al.*, 2004a). However, the mechanisms leading to this phenomenon are not known. The aim of this study is to evaluate different hypotheses explaining why anchovy has exhibited its particular dynamics in the North Sea, to synthesize available knowledge, and provide evidence in support of the most probable scenario explaining the recent increase of this species in that ecosystem.

THE CONTEXT OF CHANGE

A changing environment

To investigate how the physical environment of the North Sea has changed over the last 50 years, we used a multi-decadal (1948-2007) hindcast of the hydrodynamic model "HAMSOM" (Pohlmann, 2006; Meyer *et al.*, 2011). The model was driven by 6-hourly air temperature, humidity, cloud cover, precipitation, sea level pressure and near-surface wind speed and direction from the NCEP/NCAR global atmospheric reanalysis. The annual heat content of the North Sea varied between 330 and 366×10^6 J m^{-3} with mean values being highest in the summer and lowest in the winter months. Inter-annual variation was highest during the winter and spring seasons. A period of increased heat content started in the late nineties. Changes in North Sea- sea surface temperature (SST) from 1949 to 1987 were relatively small (less than 0.1 °C decade^{-1} negative trend), whereas a strong increase of up to 0.5 °C decade^{-1} occurred from 1987 to 2007. The strongest warming occurred in the German Bight (1.0 °C for 1987 to 2007), compared to smaller increases in the central (0.3 to 0.4 °C) and the northern (0.1 to 0.3 °C) North Sea (ICES, 2010). However, unlike general heat content and SST, no long-term (or recent) changes in the dynamics of the thermocline strength (defined here as the maximum vertical temperature gradient with a threshold at 0.1 °C m^{-1}) were observed in the modelled time series (Meyer *et al.*, 2011). This lack of change in the North Sea thermocline dynamics partly explains why time series analyses have not found strong phenological shifts in primary production though changes in the dominant phytoplankton groups have been reported (see references in ICES, 2010).

A shift in zooplankton from a typical cold-boreal to a warm-temperate community occurred in the late 1980's (e.g., Beaugrand *et al.*, 2004; Kirby *et al.*, 2007). This included a shift in the dominant *Calanus* congener, an influx of oceanic species, an increase in warm water zooplankton species and a shift from holoplankton to meroplankton dominance. Changes in zooplankton species composition have also been associated with phenological changes potentially affecting the match-mismatch dynamics between zooplankton and their predators (Alheit *et al.*, 2005). Within upper trophic levels, shifts in fish species have also been documented with an increase in species with southern affinities and or movements of some species to greater depths (Perry *et al.*, 2005; Rijnsdorp *et al.*, 2009). These changes in physical and biological factors defined a regime shift in 1988/89 (Weijerman *et al.*, 2005), and coincided with an abrupt change in the winter North Atlantic Oscillation (NAO) index. The NAO is the most pronounced signal describing climate-driven variability on decadal time scales in the region (Hurrell and Deser, 2010). After the mid 1990's the pressure centers of the NAO (Icelandic Low and the Azorian High) moved north-eastward. These atmospheric

processes were accompanied by simultaneous changes in a number of large-scale water currents in the northeast Atlantic (Häkkinen and Rhines, 2009).

Although no causal relationship can be ascertained, climate-driven changes in various ecosystem components appear significant. Local and large-scale changes occurred in the North Sea environment. In addition, temperature changes in water appeared to be associated with several of these profound ecosystem changes and will be investigated in the present study as the potential environmental driver.

Fluctuations in anchovy catches and abundance

Anchovy has historically occurred in the North Sea (Aurich, 1953). In recent, more temperate times, the largest northern anchovy spawning area was in the Zuiderzee (area magnified in Figure 1). This estuary supported a dedicated anchovy fishery from at least the 19th century until 1932, when the estuary was closed off from the sea (Cunningham, 1890; Boddeke and Vingerhoed, 1996). Despite high inter-annual variability, yearly catches occasionally exceeded 10 000 tonnes. Anecdotal evidence suggests that anchovy was also caught off the south coast of England at the end of the 19th century (Cunningham, 1890) and was spawning in the German Bight in the late 1940s (Aurich, 1953). After the closure of the Zuiderzee, smaller anchovy spawning areas persisted in the Oosterschelde estuary in the Netherlands and in the western Dutch Waddenzee (Boddeke and Vingerhoed, 1996; Figure 1) with annual catches up to 1 000 tonnes between the 1930's and 60's (Figure 2). Anchovy was also recorded in Danish waters (the Belt area) during the 1930s and 1940s (Heegaard, 1947). All landing records from the 20th century confirm high inter-annual variability (Figure 2).
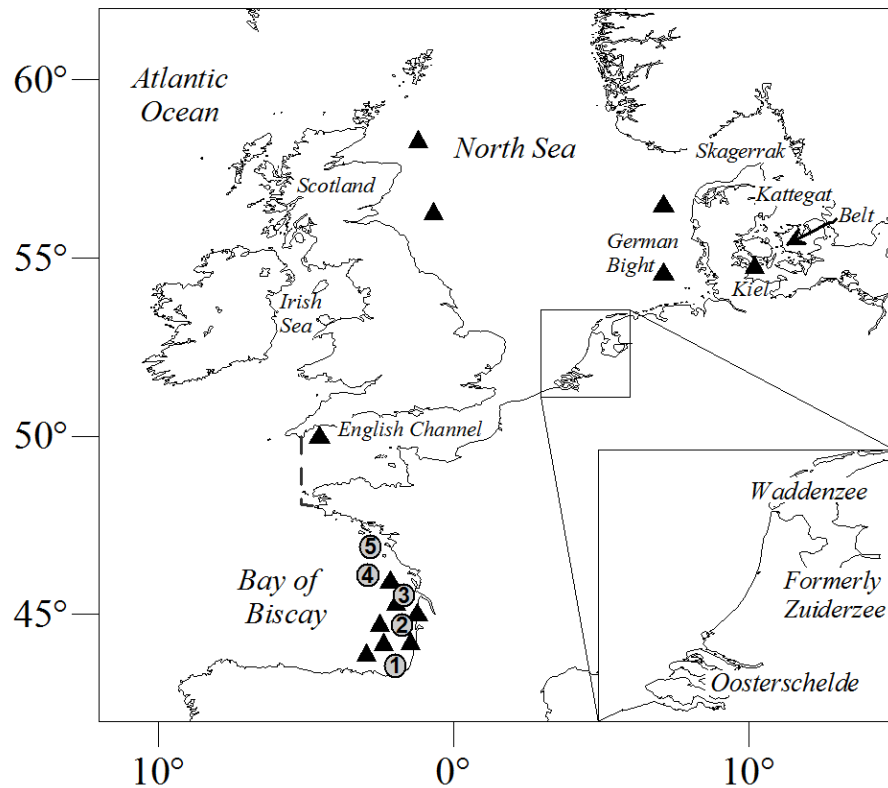
Figure 1. Map of the study area, including the North Sea and Bay of Biscay, with a magnified Dutch coastline showing area where the small local persistent population was found. Five release locations for the ichthyoplankton transport modelling are shown (1-5). The triangles denote the location of anchovy sampled for genetics analysis. Dashed line represents the boundary between the English Channel and Bay of Biscay.

In the latter half of the 20th century, anchovy was only rarely found in the North Sea. Research survey time series suggest low numbers between 1930s and 1960s and from the 1970s onwards (Beare *et al.*, 2004). In the 1990s, abundance appeared to increase again in the North Sea (Figure 2d; Beare *et al.*, 2004) as well as in adjacent regions (Armstrong *et al.*, 1999). The species is now regularly caught in the International Bottom Trawl surveys of the North Sea (Figure 2d). Anchovy in the north of its distribution appears to exclusively spawn in near-shore and estuarine areas where young larvae have been captured in good condition (Kanstinger and Peck, 2009).
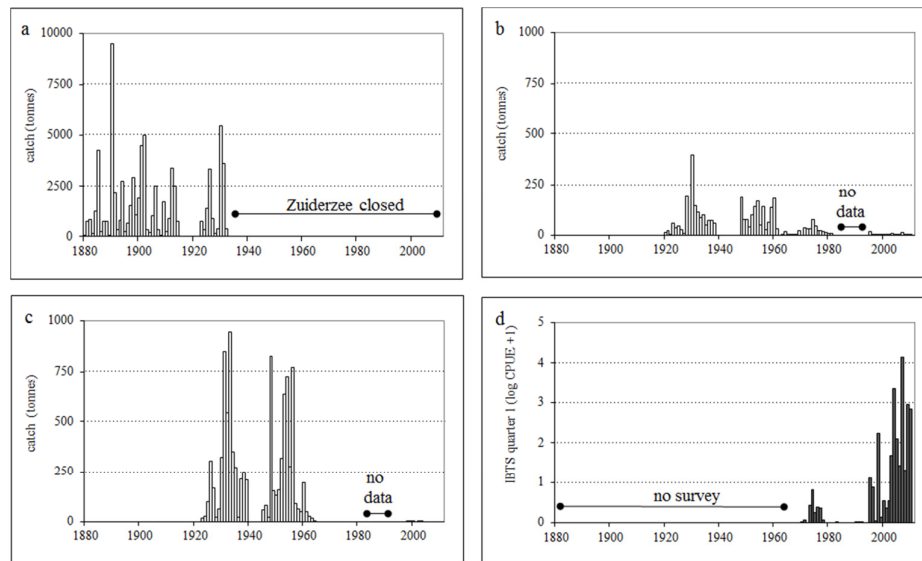
Figure 2. Long-term anchovy records in the North Sea: annual landings by Dutch coastal fisheries from 1880 to 2010: a) Zuiderzee, b) Waddenzee, c) Oosterschelde (see Fig. 1); and d) catch per unit effort from the international bottom trawl survey (IBTS, quarter 1).

Hypotheses for dramatic increase of anchovy abundance

We treat the observed increase in abundance of anchovy in the North Sea as a colonization event. The spatial expansion of a species can be explained by allopatry (colonizers coming from elsewhere), or sympatry (recruitment pulses of an adult local remnant population). In the case of North Sea anchovy, allopatric colonization can occur through passive transport of eggs or larvae that originate from areas outside the North Sea (Figure 1), or by actively migrating adults. The sympatric hypothesis amounts to the increased survival of progeny that resulted from spawning in the North Sea, leading to life cycle completion and an increase in numbers of adult fish. To test which of these three hypotheses applies to the North Sea anchovy scenario, we translated their implications into the specific life cycle dynamics of anchovy:

H1. A remnant population exists in the North Sea which has recently exhibited increased recruitment pulses.

In this case scenario, anchovy would have been able to complete its full life cycle in the North Sea. It would have been present in low numbers and in isolated areas before the newly recorded increase. The first signal of increased abundance would be in the recruits (i.e., smaller length classes would exhibit the first increase). Genetic differences would be expected between the North Sea and Bay of Biscay stocks. There would be no evidence of connectivity between the populations.

H2. An allopatric population has seeded the North Sea by an introduction of early life stages.

The first signal of increased abundance would be in the recruits, i.e. smaller length classes would show the first increase. There would be no genetic differentiation between the North Sea and Bay of Biscay stocks. Lagrangian drift model simulations would predict larval transport into the English Channel and eventually the North Sea from the Bay of Biscay.

H3. An allopatric population has seeded the North Sea by active adult migrations.

The first signal of increased abundance would be in the adults, i.e. larger length classes would show the first increase. There would be no genetic differentiation between the North Sea and Bay of Biscay stocks. But Lagrangian drift model simulations would predict larval transport into the English Channel and eventually the North Sea from the Bay of Biscay.

We assessed the validity of each of the three hypotheses by compiling evidence from genetic studies, larval transport modelling, survey time series and physical models. Also we investigate how suitable thermal habitats for anchovy spawning and larval survival may have increased in the North Sea based on physiological considerations. Each approach is considered one at a time in the following sections, building evidence for and against each hypothesis. This weight-of-evidence approach allows us to synthesize likely explanations for the observed increase in North Sea anchovy abundance in recent years. This cross-disciplinary approach used the best data sources available, but given the limited number of dedicated studies targeting anchovy in the North Sea, we made extra effort in validating the data.

EXPLORATION OF HYPOTHESES

Connectivity

We used two approaches to explore connectivity: between-population genetic structure and dispersal of early life stages (ichthyoplankton).

Genetic structure among European anchovy populations in the Mediterranean basins and adjacent waters, including Bay of Biscay, has been studied using mitochondrial DNA (Magoulas *et al.*, 2006), allozymes (Tudela *et al.*, 1999; Sanz *et al.*, 2008) and DNA microsatellites (Zarraonaindia *et al.*, 2009). These studies have shown differentiation between populations among the Mediterranean basins but similarity between Bay of Biscay and the NW Mediterranean. A geographically more extensive analysis was conducted, which included the English Channel and North Sea and which was based on Single Nucleotide Polymorphism (Morin *et al.*, 2004). A panel of 49 nuclear SNPs characterized by Zarraonaindia et al. (in press) was used here on a total of 797 individual fish, sampled in various locations in the Bay of Biscay and the North Sea (Fig. 1). Genetic divergence between North Sea and Bay of Biscay populations was assessed by applying the F_{ST} statistics (Weir and Cockerman, 1984) using FSTAT software (Goudet, 1995; 2001). In addition, the Bayesian model-based clustering algorithm implemented in the software STRUCTURE v2.3.3 (Pritchard *et al.*, 2000) was used to classify individual fishes in homogeneous groups, assuming a mixed ancestry model and correlated allele frequencies (Falush et al., 2003). The clustering algorithm was run considering different group numbers (K=1 to 10). Results indicated that the North Sea and English Channel samples were genetically homogeneous (F_{ST}= 0.002±0.003; p= 0.179), and so were those within the Bay of Biscay (F_{ST}= 0.001±0.002; p= 0.211). But significant genetic differences were found when comparing North Sea/English Channel samples with the Bay of Biscay ones (F_{ST}= 0.030±0.011; p< 0.001). In addition, best clustering statistics were obtained when considering two groups (K=2) which resulted to be one formed by the fishes from the Bay of Biscay samples and the other by the that of the North Sea/English Channel samples (Figure 3a). In addition, the genetic difference between Bay of Biscay and North Sea/English Channel populations was larger than between Bay of Biscay and NW Mediterranean populations (F_{ST}=0.020±0.009; p< 0.001). The fact that English Channel samples were grouped in a homogeneous cluster with that of the North Sea tends to reject the idea that the English Channel would comprise a transition zone between the Bay of Biscay and North Sea populations, since intermediate allele frequencies would then be expected in this area.
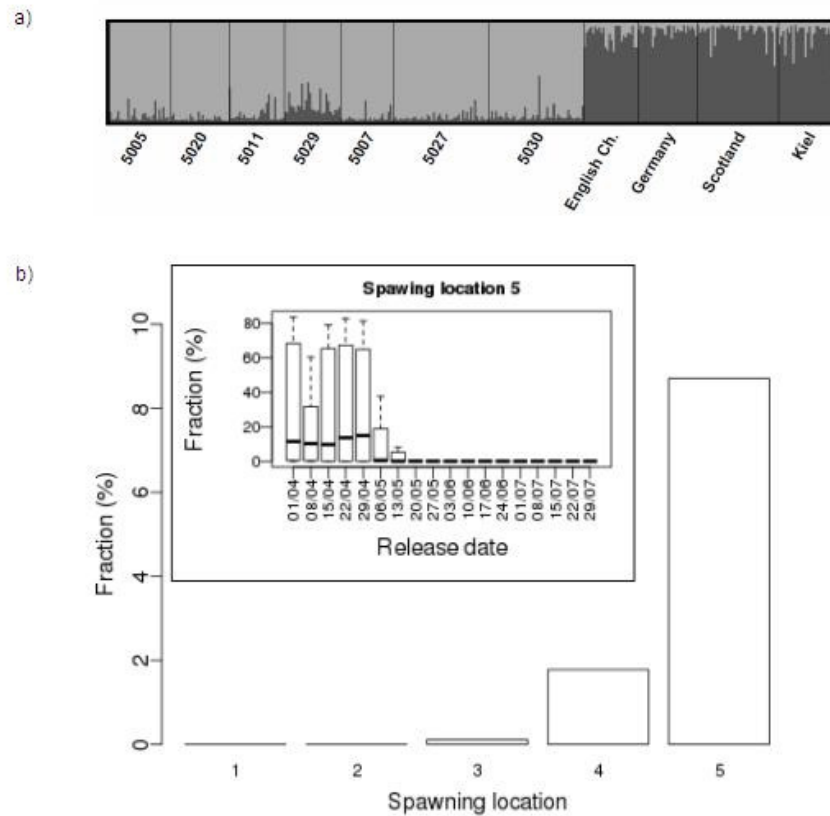
Figure 3. Exploration of connectivity between the Bay of Biscay and North Sea anchovy populations. a) Genetic population structure for K= 2 groups inferred with STRUCTURE v2.3.3 software. The different geographic areas that were sampled are separated by vertical lines. Numbers 5005, 5020, 5011, 5029, 5007, 5027, 5030 refer to Bay of Biscay sample stations (see Fig. 1). Each vertical bar represents an individual fish. The grey and black portions of the bar correspond to the individual's estimated membership fractions to the two clusters. b) Statistics from the Lagrangian particle tracking modeling from simulations over the period 1996-2009. The fraction of particles transported into the English Channel from the Bay of Biscay spawning grounds by release location (see Figure 1), and for site 5 over the season.

Oceanographic connections and transport of ichthyoplankton from the Bay of Biscay into the English Channel have already been reported (e.g., Kelly-Gerreyn *et al.*, 2004). Anchovy eggs spawned in the Bay of Biscay have the potential to be transported into the English Channel (Huret *et al.*, 2010). Here, we specifically

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estimated the loss of Bay of Biscay anchovy eggs into the English Channel using a Lagrangian particle tracking model described in Huret *et al.* (2010). Five spawning areas were chosen for release of particles (1-5, Figure 1). Most of the spawning takes place in the south (areas 1-3, Figure 1), particularly during the peak spawning season (May-June). Spawning in the northern areas takes place towards the end of the season (Motos *et al.*, 1996). Particle release was simulated every week over the spawning season (April to August), and tracked for 50 days, which is considered the mean age at metamorphosis for Bay of Biscay anchovy (Pecquerie *et al.*, 2009; Aldanondo *et al.*, 2010). The model was run over the period 1996 to 2009. Connectivity into the English Channel was measured as the fraction of particles arriving in the area North of 48°N and East of 5°E (Figures 1 and 3b). The mean fraction of particles arriving in the English Channel was generally low, between zero for spawning grounds 1 to 3, and 10% for the northern most location. The model also showed inter-annual and seasonal variability in the connectivity from the Bay of Biscay into the English Channel. For the northern spawning grounds (4 and 5), modelled connectivity occurred early in the season (until mid-May). However, very little spawning is reported by the French PELGAS survey in April-May north of 46°N, which is also suggested by Motos *et al.* (1996). Modeled connectivity is null from mid-May onwards. So the modelling exercise suggests that potential larval connectivity from the Bay of Biscay into the English Channel results from spawning in the northern part of the Bay, and only at the beginning of the spawning season, when spawning in fact does not occur in the North. Thus considering the observed spatio-temporal spawning pattern (shift to the North as the season progresses), connectivity through ichthyoplankton transport may be considered as highly unlikely.

Larval connectivity from the Bay of Biscay to the English Channel/North Sea areas is argued to be negligible using larval transport modelling. The other source of connectivity is via vagrant adults. But the genetics study showed high differentiation between the two areas. Therefore adult connectivity must also be considered negligible. These results provide evidence in favour of the Hypothesis of an increase in abundance of local North Sea populations (H1), rather than a northward expansion of Bay of Biscay populations via larval transport (H2) or adult migration (H3).
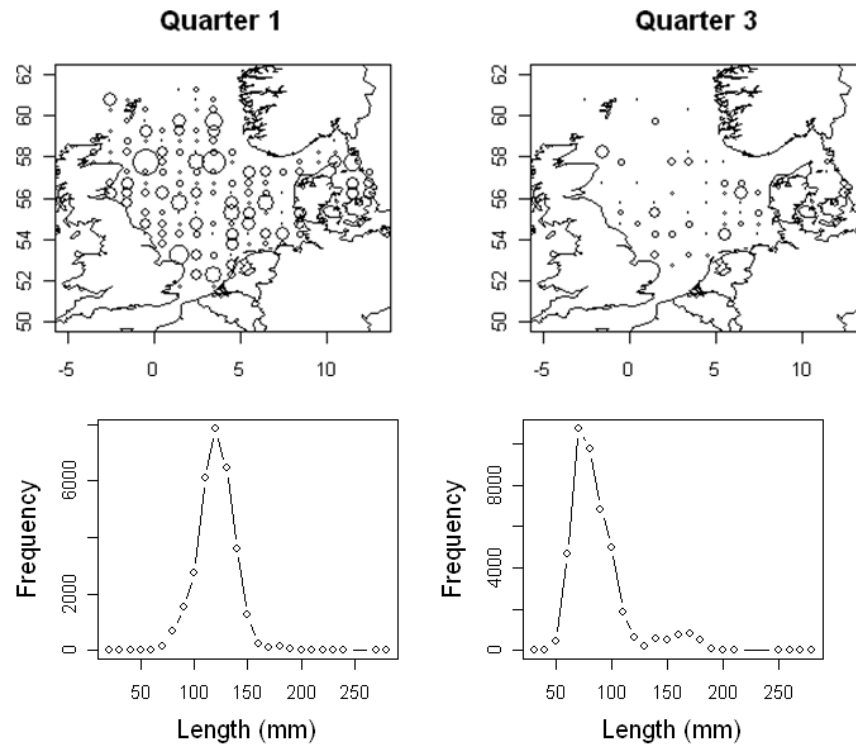
Figure 4. Top: Probability of presence (mean count >2 individuals per ICES statistical rectangle) in Q1 (left: 1973 to 2010) and Q3 (right: 1990 to 2009). Bottom: Average length class frequencies of anchovies in Q1 (left) and Q3 (right) in North Sea IBTS catches. Q refers to a year quarter (3 months). Q1 is from January to March and Q3 from July to September.

First appearance of anchovy expansion: adults or recruits?

To address this question, we analysed the spatial distribution and length structure of anchovy in the North Sea International Bottom Trawl Surveys series (IBTS). The data were extracted from the ICES website portal as anchovy catch per unit effort (numbers at length) by ICES rectangle. These data are available for quarters 1 and 3 of each year (Q1 and Q3 hereafter); since the two quarters can give insight into different periods of the life cycle, both were used in the analysis. Establishing whether the first expansion is due to adults or juveniles using survey data is difficult as survey catches can be unreliable when fish have a low abundance. We therefore focused on the surveys with average Log CPUE > 0.5.

The averaged spatial distribution (Figure 4) indicated that anchovy was more widely distributed across the North Sea in Q1 than in Q3, when they were more restricted to the southern North Sea and British coast. Anchovies in Q1 had generally one peak in length (ca 12cm) while the length distribution of anchovy in Q3 was slightly bimodal with a strong peak at ca 7cm and a weaker peak at ca 17cm (Figure 4). Lengths in Q3 were more variable across years, probably reflecting variability caused by recruitment pulses. Egg surveys along the Dutch coast show that anchovy spawn in early May. In the now extinct Zuiderzee populations, which spawned in early May, anchovy reached sizes of 6 to 8 cm in 90 to 120 days (Arné, 1931). Given that anchovy within the Bay of Biscay can reach 7 to 8 cm within ca 60 to 80 days, it seems likely that the anchovies caught in Q3 in the North Sea were juveniles hatched during late spring of the same year. Moreover, the otoliths of individual anchovies caught along the Dutch coast in 2010 (May-June) were aged and their length-at-age matched the growth pattern of Bay of Biscay anchovy (Figure 5). The time series of annual anchovy catches (survey CPUE) shows that although low numbers of anchovy were present in the 1970s and early 1990s (Figure 2d), the first large increase in abundance occurred in the mid-1990s. The first time anchovy was captured in the North Sea since the 1970s was in Q3 of 1992 (Table 1). In that year, a recruitment signal was detected (length mode < 12cm), but as abundance in Q1 of the subsequent year (1993) was low, these recruits did not survive the winter. The next recruitment signal was in Q3 of 1994 and an over-winter survival of recruits is inferred from the higher abundance in Q1 of 1995. This event, 1994-1995 was the first large-scale colonization / recruitment by anchovy in the North Sea since the 1970s. Subsequently, there were several years of higher abundance (1994-95, 1997-98, 2002-03), and in each case a Q3-increase preceded an increase in Q1 of the next year (Table 1), suggesting over-wintering of recruits (sub-adults). The probability that large anchovy catches (i.e., event X: Log CPUE > threshold) in summer (Q3) were followed by large anchovy catches in the subsequent winter (Q1), was high (Table 1): $P(Q1_t=X|Q3_{t-1}=X)=9/13=69\%$. However, poor over-winter survival also occurred (i.e., event 0: Log CPUE < threshold) with a 40% probability $(P(Q1_t=0|Q3_{t-1}=X)=2/5=40\%)$, although it was estimated using a smaller number of observations since 1992. This pattern suggests that recruitment pulses in Q3 together with over-wintering survival are necessary for high catches to occur in Q1 of the following year.
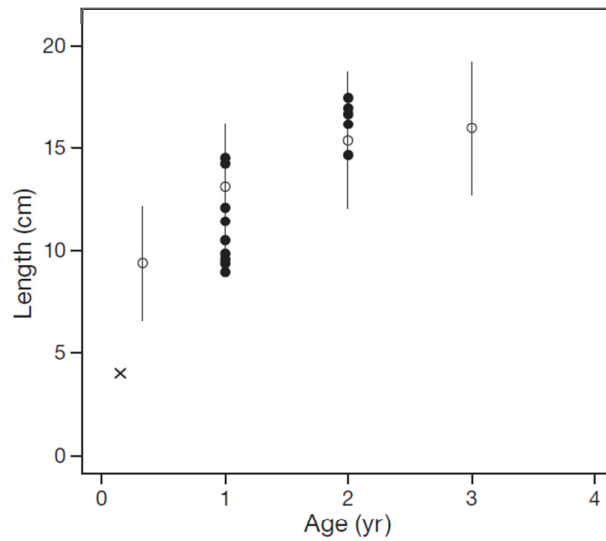
Figure 5. Growth pattern of Biscay and North Sea anchovy. Filled circles: North Sea anchovy. Unfilled Circles: average length of Bay of Biscay anchovy obtained from 2000 to 2008 spring and autumn acoustic French surveys. Bars: 95% Gaussian confidence interval around the mean. Cross: Length at metamorphosis.

Table 1. Sequence of surveys with mean Log CPUE >0.5 in quarters 3 and 1 (event X). The symbol "-" indicates that no survey data was available. Note that surveys prior to 1990 are not displayed as few anchovy were caught (mean Log CPUE<0.5).

Year	Quarter 3	Quarter 1
1990		
1991		
1992	X	
1993		
1994	X	
1995		X
1996		X
1997	X	
1998	X	X
1999	X	
2000		X
2001		
2002		X
2003	X	X
2004	X	X
2005	X	X
2006	X	X
2007	X	X
2008	X	X
2009		X
2010	-	X

Thermal habitats

One consequence of the summer warming, documented for the southern North Sea, may be a spatial and temporal expansion in favourable growth habitats. In theory, this would increase rates of larval growth and survival during summer allowing a greater number of juveniles to grow to sufficient sizes to better survive through the winter. We examined the eco-physiology of European anchovy with emphasis on optimal and sub-optimal thermal windows for growth and survival. Since the North Sea represents the upper limit of the latitudinal range in distribution of European anchovy, we also discuss survival constraints potentially imposed by the long duration of the winter period. Studies on other marine fish species have identified two principal agents affecting over-winter mortality: direct

thermal stress and starvation (Hurst, 2007), both of which may be size-dependent particularly for young-of-the-year fish. In most cases, obtaining large body sizes prior to the over-winter period increases the probability of survival (e.g., Cargnelli and Gross, 1997). The lower threshold temperature for anchovy spawning appears to be 14°C in the European Atlantic waters, based upon observations made throughout Europe including the Bay of Biscay (Ibaibarriaga *et al.*, 2007), although spawning starts with warming rather than at an absolute temperature (Motos *et al.*, 1996). Optimum larval growth temperatures are above 16 °C (Urtizberea *et al.*, 2009). At these temperatures, larvae would require 40 to 50 days to metamorphose (4 to 5 cm) and 60 to 80 days to reach a size of 7 to 8 cm (Pecquerie *et al.*, 2009; Aldanondo, *et al.*, 2010). In the Bay of Biscay pre-winter juveniles would require to reach a body size of 6.6 cm (ICES, 2009) with a condition threshold ~5 kJ g wet mass^{-1} (Dubreuil and Petitgas, 2009) to ensure over-winter survival.

As anchovy has continuously been recorded in the Wadden Sea (Boddeke and Vingerhoed, 1996), we assumed that local thermal conditions represent the minimum requirements for successful growth and survival (Figure 6a, as per van Aken, 2008). We also used long-term (1948-2007) temperature simulations from the HAMSOM oceanographic model (Meyer *et al.*, 2011), to calculate the period (in days) during which the southern North Sea water temperatures were above and below specific high (Figure 6b) and low (Figure 6c) thresholds. The simulated temperatures of the southern North Sea (defined as <55°N and <50m deep) suggested windows of suitable spawning temperatures (T >14°C) and larval growth temperatures (T >16°C) of 3 to 4 and 2 to 3 months, respectively. Wadden Sea temperature records suggested the same thermal durations. In comparison, spawning and growth windows in the South of the Bay of Biscay lasted 7 and 5 months, respectively (Figure 6a). In the southern North Sea, both the thermal spawning and growth windows have increased by ca. 2 to 6 weeks in most years between 1989 and 2007. At the same time, the severity of winters (defined here as mean water temperatures below 6°C for 60 days) has markedly declined: between 1989 and 2007, only 5 years experienced severe winters, compared to 70% of the years between 1948 and 1988. Assuming that thermal requirements for North Sea and Bay of Biscay anchovies are similar (which may not be the case due to plasticity in life history traits), suitable thermal habitats now regularly exist in the southern North Sea. Such favorable spawning and growth conditions are prerequisites for population persistence and productivity.
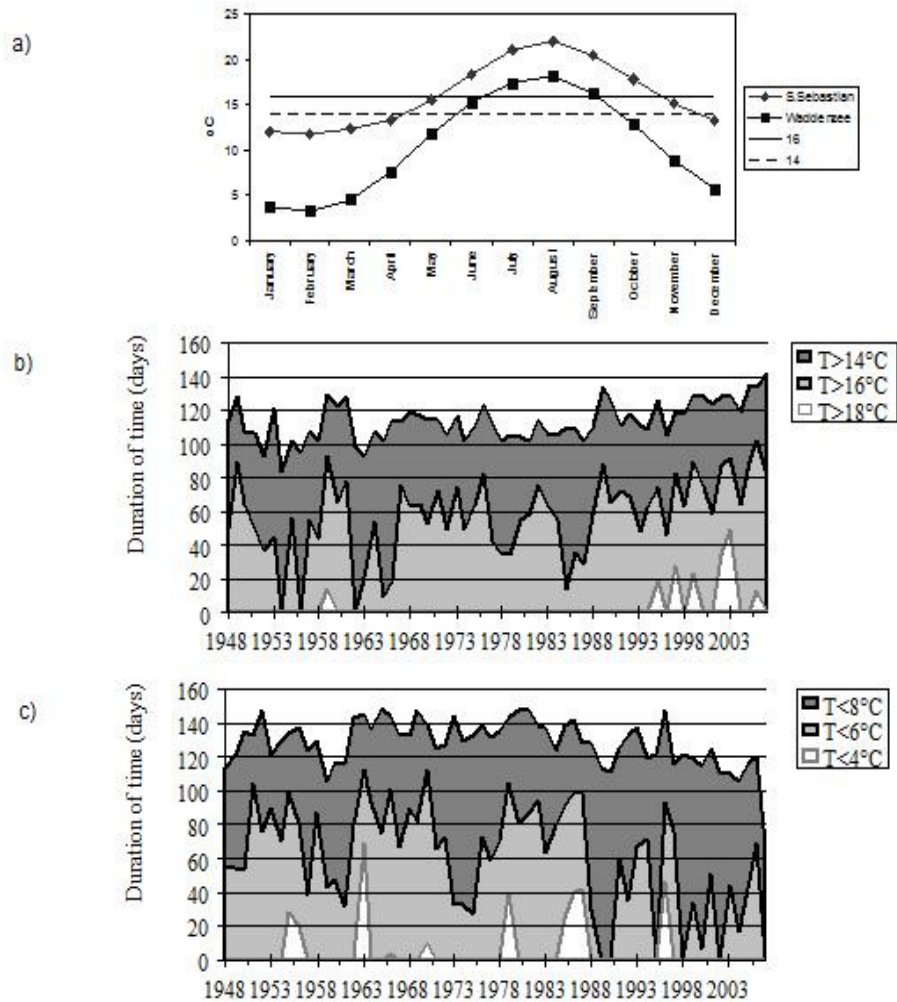
Figure 6. Observed and model-derived thermal environments for the southern North Sea and southern Bay of Biscay. a) Monthly climatology (1947-2005) observed temperature in the Waddenzee and San Sebastian. The horizontal lines indicate the lower limits for anchovy spawning (14°C) and larval growth (16°C) in the Bay of Biscay. b) Number of days (y axis) per year for the period 1948-2007 (x-axis) where temperature exceeded specific thresholds (14°C, 16°C and 18°C). c) Number of days per year in Wadden Sea where temperature was lower than specific thresholds (8°C, 6°C and 4°C).

The results of this exploration of eco-physiological habitats suggest that spatio-temporal variability in the width of thermal windows may strongly influence spawning, larval and juvenile- survival and ultimately the recruitment success of North Sea anchovy. The optimum thermal window for growth has widened in the southern North Sea since 1989. Given the thermal biology of this species, extreme warm events are unlikely to be detrimental. However, extreme (short-term) cold events have been correlated with massive winter mortality of some North Sea fish species (Pörtner and Peck, 2010), and could also apply to North Sea anchovy.

DISCUSSION

Previous genetic studies have identified potential differentiation within the Bay of Biscay (Sanz et al., 2008; Zarranoaindia et al., 2009). Here, such differentiation was probably out weighted by the larger difference between North Sea/English Channel and Bay of Biscay samples that appeared using SNP markers. Here, the transport modelling and genetic studies both suggest that North Sea and Bay of Biscay anchovy are separate populations. An additional piece of information is given by otolith chemistry performed on 4 fishes from the Bay of Biscay and 3 from the North Sea (Scotland, Fig. 1) sampled in 2009. The elements (Sr, Si, K, P, Mg, Cr, Mn, Ba, Zn, Co) of the otolith core were measured following methodology documented in Aldanondo *et al.* (2010). A cluster analysis (Ward method, Euclidean distances) based on the concentration of the different elements clearly differentiated individuals collected off the North Sea coast of Scotland from those captured in the Bay of Biscay (not shown). This indicates that the individuals collected in the North Sea and the Bay of Biscay originated from different spawning areas. Although 7 fish were analysed only, the results agree with the genetic and the transport analyses and add to the evidence in support of the local expansion hypothesis (H1).

The observed recruitment pulses seen in the trawl surveys suggest spring spawning and larval development in summer. It also supports the concept of population expansion from recruitment pulses originating from possible remnant North Sea population(s). In terms of growth physiology, the thermal windows required also fit to the seasonal schedule of spring spawning and summer larval development. In addition, the thermal windows have expanded, making conditions more favourable for life cycle closure and population persistence/productivity. Not only does the recently observed increased frequency of warm summers favour the growth of larvae and juveniles but the decrease in severe winters likely also favours over-winter survival. The overall evidence supports hypothesis H1, which interprets the observed increase in anchovy abundance as originating from increased productivity of a sympatric population or populations in the North Sea.

The alternative hypotheses, which proposed that the increase in North Sea anchovy abundance was due to a northward shift in the distribution of southern conspecifics, were rejected.

Self-recruiting and persistent remnant populations exist in all taxa and are often isolated and sometimes genetically distinct from other populations of the same species (e.g., Garcia, 2008; Galand and Fevolden, 2000). Isolated self-recruiting populations can continue to exist at low abundance and on a small spatial scale, depending on life-history or behavioural traits (Garcia, 2008; Nordeng, 1983). As natural collapses and recoveries of marine fish stocks are a common feature (Baumgartner *et al.*, 1992), small contracted populations can represent the way a species may persist over geological times. Several salmonid and clupeid species are known to be able to persist in adverse conditions as self-recruiting remnant populations. Examples include Arctic charr (*Salvelinus alpinus*; Nordeng, 1983), Blackwater herring (*Clupea harengus*; Roel *et al.*, 2004), Limfjord herring (Poulsen *et al.*, 2007), and Bay of Biscay herring (Alheit and Hagen, 1997). This study suggests that the North Sea anchovy should be included in that list.

Small population sizes are often the consequence of restricted habitat availability (Bertrand et al., 2004). Therefore, remnant populations of short-lived and highly-fecund species may dramatically increase in size when the extent of favourable habitats increases. This study suggests that the increase in North Sea anchovy since the late 1990s was associated with the expansion of its thermal habitats by supporting growth and survival of pre-recruits. However it does not explain how spatially-expanded habitats may be newly colonized (Petitgas *et al.*, 2010). We based our conclusion on a cross-disciplinary approach, which focused on stage-specific habitat requirements and the importance of life cycle closure.

Given the paucity of local studies on anchovy, our approach was to analyse an amalgam of data of differing quality. We used the IBTS series to investigate trends in anchovy abundance (as in Beare *et al.*, 2004). Anchovy in the Bay of Biscay are generally found relatively close to the bottom during the day (Massé *et al.*, 1996) particularly in winter (Fage, 1911). This may in part explain the higher catches in IBTS in Q1 and also suggests that the Q1 survey may more closely reflect patterns in anchovy abundance. It is noteworthy that anchovy are not found in the North Sea during summer pelagic fish surveys, probably because this species has migrated out of the survey area to inshore waters for spawning. The exclusively near-shore distribution of anchovy larvae as found on ichthyoplankton surveys in June / July supports this assertion (Kanstinger and Peck, 2009; IMARES, unpublished data). We therefore used the catch data from bottom trawl surveys and inferred likely processes from existing eco-physiological information of this species. There are however gaps in the survey time series (Figure 2) and only limited data are available on the growth and maturity of anchovy in the North Sea (Figure 5).

In this paper, anchovy has been considered in isolation. However the population dynamics of anchovy will also respond to and influence the dynamics of their prey, competitors and predators. Few studies have examined the link between anchovy and other components of the North Sea ecosystem. Anchovy are not currently included in multi-species North Sea models (ICES, 2010) because their biomass was considered too low for the species to have a substantial impact on the food web. Moreover there is no information on which predators consume anchovy since large-scale stomach content sampling programs were undertaken in 1981 and 1991 when North Sea anchovy populations were low. Recent diet research indicated that North Sea anchovy are generalist planktivores (Raab *et al.*, 2010; 2011) suggesting that this species, as opposed to sprat (*Sprattus sprattus*) and Atlantic herring, are opportunistic feeders and therefore less likely to be prey-limited.

We used an multi-disciplinary and integrative approach along the life-cycle. Our conclusions are based on coherent results obtained from different sources, though each has shortcomings individually. The present study has indicated the importance of suitable thermal habitats for spawning, larvae and juveniles (growth). And our analysis favours the hypothesis that the greater abundance of North Sea anchovy rose from expanding remnant populations, probably influenced by the expansion of their thermal habitat brought about by a combined action of AMO dynamics and global warming. Warming waters would likely benefit anchovy in a number of ways including increasing 1) the duration of spawning windows, 2) larval/juvenile growth rates, and 3) overwinter survival of juveniles.

Yet, there are still gaps in our knowledge about how the life cycle is effectively completed, in particular we lack knowledge on seasonal migrations and how these can be newly established from a remnant coastal population. Also unknown in the North Sea are the drivers on the population dynamics of anchovy. The present study has focused on the impact of thermal habitats but North Sea anchovy are likely to be affected by a variety of abiotic and biotic factors, including river plumes, primary production, zooplankton, wind stress and their combination as these factors are influential on anchovy populations in other areas (e.g., Schismenou *et al.*, 2008; García *et al.*, 1998; Palomera *et al.*, 2007; Borja *et al.*, 2008). Furthermore, beyond basic studies of population demographics, it would be beneficial to conduct targeted, eco-physiological research on anchovy, testing for potential adaptations to specific thermal habitats along a latitudinal gradient.

Acknowledgements

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CHAPTER 5

Influence of temperature and food availability on juvenile European anchovy, *Engraulis encrasicolus,* at its northern boundary

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Teal LR, Licandro P, Ruardij P, Dickey-Collas M (2013)

ABSTRACT

The European anchovy *Engraulis encrasicolus* population of the North Sea has increased and spread in recent decades, probably in response to the relaxation of limiting factors in its life history. We use models and empirical data to explore the effects of temperature and food availability during the first growing season on the adult anchovy population across the North Sea. First, we compare simulated growth during summer and autumn, from a dynamic energy budget model, with trends in the time series of anchovy survey catch per unit effort. The proportion of the area of the North Sea in which anchovy can grow to 10 cm (the potential growth habitat) correlates with the abundance of anchovy caught in surveys the following year. Second, spatio-temporal statistical modeling is used to show that anchovy abundance in surveys is related to environmental variables (temperature and food availability). Temperature explains the distribution and abundance of anchovy in the North Sea better than food availability or a combination of both environmental factors. We conclude that variations in growth during the first months of life can impact anchovy life cycle closure. Specifically for the North Sea anchovy, changes in temperature are more important than changes in food availability in allowing the fish to grow to overwintering size, under probably non-food-limited conditions.

INTRODUCTION

Species' ranges are being increasingly studied to understand animal and plant responses to anthropogenic impacts, such as climate change (Thomas & Lennon 1999, Parmesan & Yohe 2003, Perry et al. 2005). When a species expands its range, some limiting factors that affect the growth or survival of one or more of the distinct life history stages change (e.g. Rijnsdorp et al. 2009) which may increase the connectivity between the habitats of the successive life history stages, allowing life cycle closure (sensu Sinclair 1988). When the abundance of southern fish species recently increased in the North Sea, climate change was investigated as a cause (Beare et al. 2004b). However, given that the abundance and spawning of some of these species, like anchovy and sardine, was already high several decades ago (Aurich 1950, 1953), the relevant question is what aspect of the life history has changed to allow for this increase at more northern latitudes, regardless of whether anthropogenic climate change is implicated in the mechanism or not.

Here, we explore the apparent range expansion of anchovy *Engraulis encrasicolus,* a species with southern geographic affinity (Engelhard et al. 2011), in the North Sea since the mid-1990s (Armstrong et al. 1999, Beare et al. 2004a) and

consider its population dynamics in light of variability in potential limiting factors and their impact on life cycle closure (Petitgas et al. 2013).

Due to the relative novelty of anchovy in the North Sea, little is known about its life history in this northern part of its range. In a recent synthesis (Petitgas et al. 2012), hypotheses are explored based on the biology of the species in its Bay of Biscay habitat, with the conclusion that the productivity of the first growing season is probably an important control of survival during the first winter in the North Sea. Early life growth may affect fish survival (e.g. Meekan & Fortier 1996), and both temperature and food are related to early life growth in Japanese anchovy (e.g. Takasuka & Aoki 2006).

The present study aims to explore which factors during the early life stages (larval to juvenile, termed 'juvenile' from here on) determine the abundance and distribution of anchovy by using 2 modeling approaches (one bio-energetic and one statistical). First, temperature- and food availability-dependent growth of anchovy during its first 6 mo of life was modeled using the dynamic energy budget (DEB) framework (Kooijman 2010) linked to a 3-dimensional ecosystem model. This allowed for the development of an index of habitat suitability for juvenile growth in the North Sea. We expect that years in which simulated habitat suitability is high would correspond to years that have high empirical survey catches in the following winter.

Second, using independent environmental data, statistical modeling (generalised additive modeling [GAM]; Hastie & Tibshirani 1990, Wood 2006) was carried out to determine whether temperature or food variables or both encountered as juveniles covaried with the distribution and abundance of survey catches of anchovy in the North Sea and which variables provide the most parsimonious explanation of the data.

Using this 2 method approach, we carry out a robust exploration of the overarching hypothesis of the present work—that the limitations to juvenile growth in the summer were relaxed in years that preceded greater catches of adult anchovy in the North Sea.

MATERIALS AND METHODS

DEB modeling

The DEB theory (Kooijman 2010) provides a framework that allows an organism's rate of energy assimilation and utilization for body maintenance, growth and reproduction to be modeled as a function of the state of the organism itself (i.e. its age, size and amount of energy reserves) and the state of its

environment (i.e. temperature and food availability). The DEB model assumes that assimilation and maintenance are a function of surface area and body volume respectively. Assimilated energy enters the reserves, from which it is allocated to maintenance plus growth (together these are a fraction, kappa, of the reserve pool) and reproduction (1 – kappa). The reader is referred to the original theoretical literature (Kooijman 2010) for a full description of dynamic energy budgets or to van der Meer (2006) for a summary of the approach.

In a recent application of the DEB framework, spatially explicit environmental food and temperature were used as input for simulations of climate change impacts on habitat suitability as reflected in fish growth (Teal et al. 2012). The model simulates changes in the growth of a hypothetical fish and outputs body size-, food- and temperature-dependent growth rates for each North Sea grid cell (daily, 10×10 km) of the coupled ecosystem model General Estuarine Transport Model - European Regional Seas Ecosystem Model (GETM-ERSEM, www.nioz.nl/northsea_model, referred to as 'ERSEM' from here on).

Here, we use this model formulation to simulate the daily growth of juvenile North Sea anchovy for each year between 1985 and 2007. That is, for each grid cell, the starting length of the hypothetical fish is converted to volume by cubing the product of length and the species-specific shape coefficient ($_m$). Then, the volume change is calculated with DEB given environmental temperature and food values from ERSEM, the new volume after 1 d of growth is converted back to length, and the difference in lengths between days is termed the daily growth potential of the fish.

The DEB parameters used are anchovy-specific and based on empirical data from the Bay of Biscay or experiments, for lack of equivalent North Sea information (Table 1).

The timing of the growing season of anchovy has to be inferred from the sparse available empirical data. The estimated start of spawning time of anchovy in the German Bight is June/July (Alheit et al. 2007), and larvae are present in highest abundances in June to July in the Helgoland Roads in the German Bight (Alheit et al. 2012), but it is possible that spawning may continue until July/August (speculated by Kanstinger & Peck 2009). Therefore, the yearly growth simulation was carried out from 1 June (day 152 of the year) to the end of the year, and in each grid cell of the North Sea, a starting length of 0.5 cm was used to match the anchovy age at first feeding (off Portugal; Ré 1996).

Daily fish length reached by a certain date was calculated by summing all positive growth potentials across previous days in the model, as we work with the assumption that the fish cannot shrink. We use this fish length to display model results as length is a more tangible measure for comparison with empirical data and

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also more commonly used in fisheries biology than the more abstract growth potential. We also compute the proportion of the North Sea containing suitable habitat for juvenile anchovy growth. Fish habitat can be defined in many ways, but here, we define suitable habitat as those areas where anchovy can reach a specific threshold size that allows for overwinter survival, as suggested by Petitgas et al. (2012). For Bay of Biscay anchovies, having a body size of 6 to 7 cm is estimated to result in better overwinter survival, and we assume that in the North Sea this overwintering size would need to be larger due to colder winters. We therefore chose 10 cm as threshold size.

Two years from the series of analysed years (1985 to 2007) were selected to provide more detailed spatial information, i.e. to show which areas of the North Sea are the most suitable for juvenile anchovy growth: 1988 and 2003. These years had the lowest and highest mean temperatures in Quarter 3 (July to September) respectively at the Marsdiep tidal channel (Wadden Sea), and this location is representative of the southern North Sea (Teal et al. 2008) where we expect young anchovies to be located.

The environmental input data used in the growth model are the output of ERSEM. We use the ERSEM outputs of sea surface temperature (SST) between 0 and 5 m and potential food availability for pelagic fish, a measure of pelagic zooplankton production, hereafter referred to as secondary production (example output is shown in Fig. 1). ERSEM reports this measure in mg C m^{-2} d^{-1}, and we used the conversion factor of 46 to convert from mg C to Joules (Salonen et al. 1976). Food dependency f in the DEB model is modeled as $f = X/(X + X_h)$. The food density X referred to in f was calculated as the total secondary production available to pelagic fish divided by depth of the water column. The saturation coefficient X_h was set to 6.9×10^{-5} J cm^{-2}, previously used in the functional response of sole and plaice (Teal et al. 2012). Since not all the secondary pelagic production output by ERSEM is available to anchovy, total levels were calibrated to a lower proportion of the total based on the comparison between available empirical data on anchovy growth and model output for anchovy growth. The mean length of anchovies caught in Weeks 40 and 41 of 2003 (late September to early October) between 51 and 53° N and 3 to 5° E was 9.9 cm (Grift et al. 2004, our Fig. 2a). We simulated fish growth for the same geographical area so that the mean lengths reached in the included cells would be the same by that time of year in 2003 by varying the food proportions accordingly (Fig. 2b). The fraction of pelagic secondary production that gave length outputs similar to the empirical data was 1.25×10^{-6}; we therefore consider this fraction of secondary production to be available to anchovy.

Table 1. Parameter values used in the dynamic energy budget model for anchovy growth

| Symbol	Dimension	Value	Explanation	Source
$\{\dot{p}_{Am}\}$	J cm^{-3} d^{-1}	329	Maximum surface area specific assimilation rate	Freitas et al. (2010)
$[p_M]$	J cm^{-3} d^{-1}	62	Volume-specific maintenance costs	Freitas et al. (2010)
$[E_M]$	J cm^{-3}	645	Maximum storage density	Freitas et al. (2010)
$[E_G]$	J cm^{-3}	5600	Volume-specific costs of structure	Freitas et al. (2010)
K	–	0.65	Fraction of utilised energy spent on maintenance plus growth	Pecquerie et al. (2009)
M	–	0.172	Shape coefficient	Pecquerie et al. (2009)
T_A	K	9800	Arrhenius temperature	Pecquerie et al. (2009)
T_L	K	278	Lower boundary of tolerance range	Freitas et al. (2010)
T_H	K	305	Upper boundary of tolerance range	Freitas et al. (2010)
T_{AL}	K	50000	Rate of decrease at lower boundary	Teal et al. (2012)
T_{AH}	K	100000	Rate of decrease at upper boundary	Teal et al. (2012)
X_h	J cm^{-2}	0.000069	Saturation coefficient	Teal et al. (2012)
T_{ref}	K	293	Reference temperature used	Freitas et al. (2010)
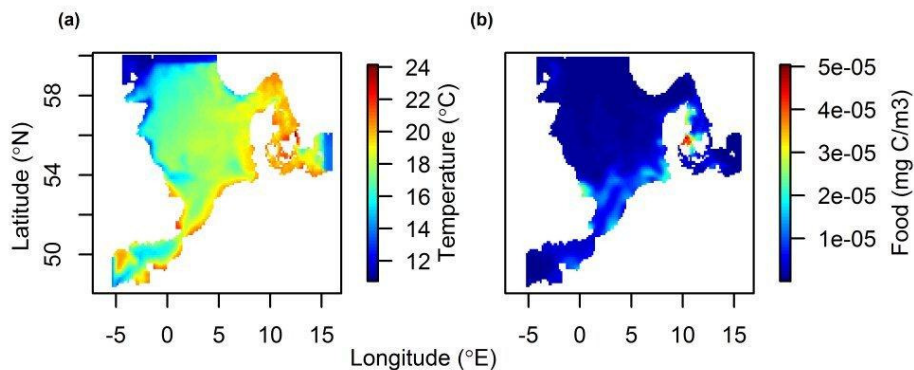
Fig. 1. Example of daily environmental data from the ecosystem model ERSEM used in the simulated growing seasons: (a) temperature and (b) food availability (calibrated to lower fraction 1.25×10^{-6} mg C m^{-3} and adjusted to water column depth) for mid-July of 2003
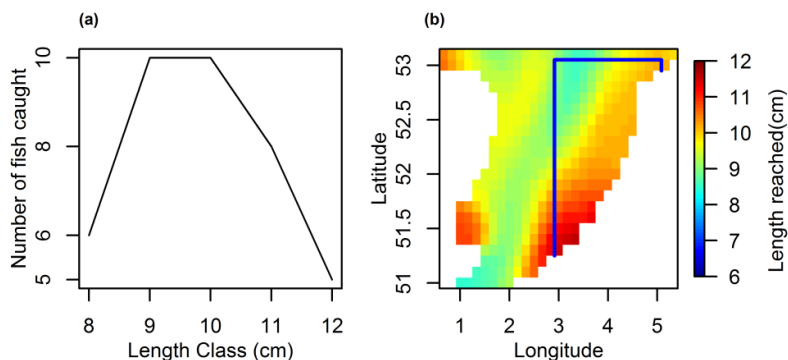

Fig. 2. Calibration of the dynamic energy budget (DEB) model: (a) empirical length frequencies of anchovy in late September to early October and (b) DEB model output by 1 October, both for the Dutch coastal zone (delineated in blue on the map in b) for the year 2003

Empirical demersal trawl data from the International Bottom Trawl Survey (IBTS) were extracted from the International Council for the Seas' website to allow for comparison with model output. Anchovy catch per unit effort (CPUE) per length class were summed across length classes for each ICES rectangle (1° longitude and 0.5° latitude), and the total abundance in Quarter 1 (January to March) of each year was calculated. Yearly habitat availability (proportion of North Sea cells having reached overwintering size) was then correlated to the next year's Quarter 1 total survey catches using Spearman's rank correlation.

All the analysis and plotting was carried out in R (R Development Core Team 2012).

Spatio-temporal modeling

The relationship between anchovy catches in the IBTS (i.e. demersal trawl data) and the potential explanatory variables affecting the catch (temperature and food) is modelled with a non-parametric regression technique, GAM, which uses multiple penalised regression splines (Wood 2006). This framework is very flexible for modeling biological processes, which are not always linear, and in addition it allows for the inclusion of spatial information into the model. Climate can act differentially in both space and time (Stenseth et al. 2002), and the effect of environment on fish populations may vary in space (e.g. Ciannelli et al. 2007, Dingsør et al. 2007). Spatial effects are taken into account by adding a variable representing space as the interaction between latitude and longitude (previous examples include Ciannelli et al. 2007, Llope et al. 2009). In this way, as much available information as possible is included into the model (rather than using averages for North Sea or across sub-areas of it, for example) since anchovy data are already sparse. The effect of variables for which we do not have information but which still shape the distribution of anchovy are implicit in the spatial variable, and their effect can thus be distinguished from the variables for which we do have data (temperature and food).

We compared 3 model formulations for data from years 1973 to 2006 (pooled), representing the influence of (1) temperature only, (2) food availability only and (3) both combined, during the anchovy growing season on anchovy abundance, using survey catches as a proxy for abundance. All 3 models included additional spatial effects. The response variable is the log-transformed survey CPUE of anchovy ('Catch') at longitude 'Lon' and latitude 'Lat' for Quarter 1 (January to March) of Year x. This was related to the co-located position, the SST ('Temp') in Quarter 3 (July to September) of Year $x - 1$, and food availability ('Food'), i.e. the total copepods in Quarter 3 of Year $x - 1$.

Model 1: Temperature only:

Catch(Lat,Lon) = $a + s_1$(Lat,Lon) + g_1(Temp) +   (Lat,Lon)

Model 2: Food availability only:

Catch(Lat,Lon) = $a + s_2$(Lat,Lon) + g_2(Food) +   (Lat,Lon)

Model 3: Both temperature and food:

Catch(Lat,Lon) = $a + s_3$(Lat,Lon) + g_3(Temp) + g_4(Food) +   (Lat,Lon)

where a is the intercept, s_1, s_2 and s_3 are 2-dimensional non-parametric smooth functions describing the effect of location on Catch, and g_1, g_2, g_3 and g_4 are 1-dimensional smooth functions describing the effect of the environment (temperature or food) on Catch. The random error term (Lat,Lon) is assumed to be normally distributed with zero mean and finite variance.

To avoid over-fitting, we limited the number of smoother knots, k, to 4 for the g (environment) functions and to 20 for the s (interaction Lat × Lon) functions. The analysis was carried out in R using the 'mgcv' package (Wood 2006) and the data outlined below.

Anchovy CPUE per ICES rectangle (as described above) from Quarter 1 were used. The survey catches dataset suffers from the classical problem of zero-inflation common in fisheries datasets: the full dataset between 1973 and 2006 contains >90% zeroes. Most likely, some of these zero observations are true zeroes (no anchovy presence where sampling occurred), and some are false zeroes (anchovy presence but not observed by sampling). While novel statistical approaches are being developed (Liu & Chan 2010, example in Yu et al. 2012) to discriminate between the 2 potential causes for zeros, we consider that in addressing a range expansion the use of historical data to distinguish true/false zeroes is not appropriate. Using a presence-absence approach would be possible, but our interest lies in what factors influence anchovy abundance when it is present, and there are 2 possible approaches to address this issue (detailed by Ciannelli et al. 2008). One is to use the 'conditional model' in which first presence-absence is modeled and only then is the species abundance modeled, conditional on the species being present. Another approach is to remove the zeroes and focus on the presence data only. We choose to exclude the zeroes because the conditional model can give contradictory results (Barry & Welsh 2002), and our interest lies mainly in what accounts for the abundance when anchovy is present rather than what allows for its presence. We try to address a combination of what factors in the growing season account for both the presence and abundance in Quarter 1.

SST (°C) data of the International Comprehensive Ocean-Atmosphere Data Set (1° enhanced) were obtained from the website of the NOAA Earth System Research Laboratory Physical Sciences Division, Boulder, CO (www.cdc.noaa.gov/). The resolution of these SST data was 1° longitude by 1° latitude, while the ICES rectangle resolution was 1° longitude and 0.5° latitude. The SST values were therefore downscaled to the ICES rectangles using loess. The degree of smoothing (value of 'span' in loess) was estimated independently for each year since the spatial structure of the data may vary from year to year. Monthly mean SST were then averaged to give the mean SST for each rectangle for the third quarter of each year as a proxy for the anchovy growing season.

Zooplankton data were obtained from the Sir Alistair Hardy Foundation for Ocean Science's Continuous Plankton Recorder (CPR) dataset. The CPR survey has provided a long-running dataset by using vessels of opportunity to collect samples that are later analysed in the lab (for a detailed description of the dataset, see Warner & Hays 1994, Richardson et al. 2006).

Recent studies of anchovy diet in the North and Baltic Seas (Schaber et al. 2010, Raab et al. 2011, 2012) indicate that anchovy is a generalist feeder as its diet varies across areas, years and seasons, but copepods make up a big part of the diet. As in previous studies (reviewed by van der Lingen et al. 2009), copepods stand out as an important prey taxon, although the percentage of copepod prey items in the North Sea anchovy diet is lower than in other regions. We therefore used the total traverse count of copepods (referred to as total copepods from now on) from the CPR, which includes copepods ≤ 2 mm, to test the effect of prey variability on juvenile anchovy. Moreover, we selected relevant plankton taxa, such as *Temora* spp. and *Centropages* spp., which are the most important items for North Sea anchovy by abundance in stomachs (Raab et al. 2011). Total zooplankton biomass (dry weight) was also utilised as a proxy of the overall available zooplankton standing stock. This was derived from CPR records by multiplying the density of 173 copepod and non-copepod taxa by the average dry weight per individual (see Llope et al. 2012 for more details). As the aim was to investigate the potential effect of environmental variability on the growth of the North Sea anchovy population, we related zooplankton records from Quarter 3 (i.e. the anchovy growing season) of a year with anchovy CPUE in Quarter 1 of the following year. Plankton data were first averaged per month and per ICES rectangle, and then the mean value in Quarter 3 was calculated.

Selection of the best version of Model 2 for food only was done by minimizing the generalised cross-validation (GCV) index, which reflects the trade-off between model complexity and fit to the data (Wood 2006 and explanation by Llope et al. 2012). This model's food measure was subsequently used in Model 3. Then, Models 1, 2 and 3 were compared and selected through minimization of GCV and removal of non-significant variables.

RESULTS

DEB modeling

We present results of the DEB model for the whole North Sea as well as for a sub-area, the southern North Sea (between 53–55° N and 3–9° E), as an example because spawning is known to take place there and to allow for comparison with other studies (e.g. Alheit et al. 2007, 2012).
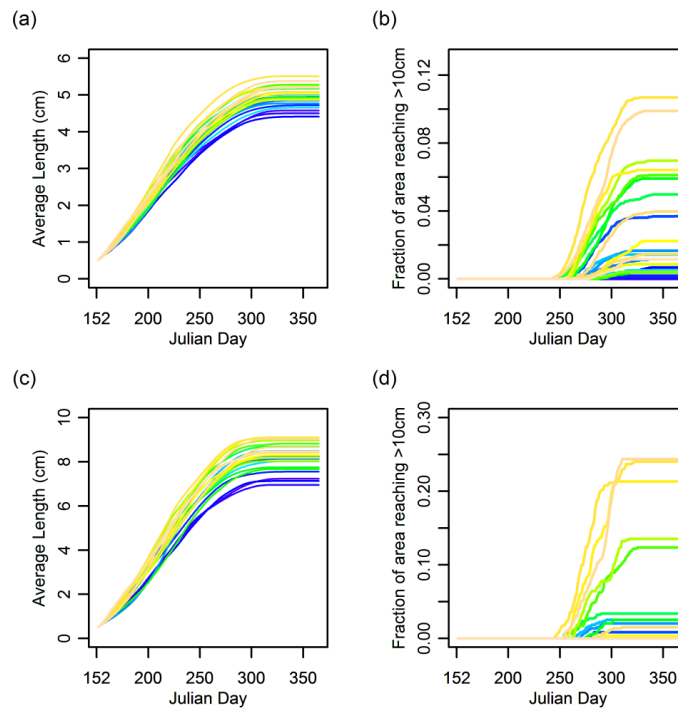
Fig. 3. Dynamic energy budget model results: (a,c) mean length attained and (b,d) proportion of North Sea where lengths above 10 cm are attained by 31 December by anchovy in (a,b) the whole North Sea and (c,d) in the Southern North Sea. Each line represents 1 year, and the colours change gradually from blue to green to yellow as years progress from 1985 to 2007
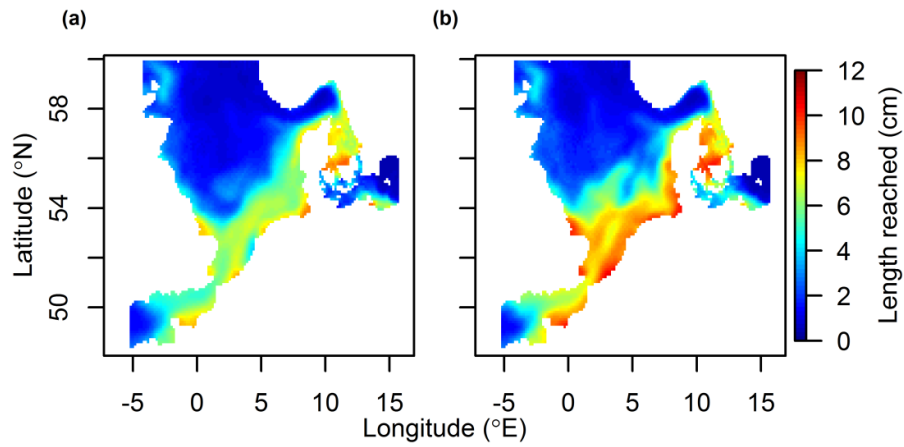
Fig. 4. Examples of (a) a low and (b) a high growth year for anchovy: lengths reached by 1 October in (a) 1988 and (b) 2003 (these years have a fraction of 0.002 and 0.107 of North Sea, respectively, where anchovy can reach >10 cm)

The mean lengths reached by anchovy in the North Sea between 1 June and the end of the year during the period 1985 to 2007 are 4.4 to 5.5 cm (Fig. 3a) and thus show relatively little variation among years (1.1 cm). Even using this overall North Sea average, however, it is clear that in early years (blue lines in Fig. 3a) in the time series, anchovy reach a lower size than in later years (yellow lines in Fig. 3a). This also applies when considering only the southern North Sea, where average lengths reached range from 7 to 9 cm (Fig. 3c).

The measure of habitat suitability, expressed as the fraction of area where fish can reach 10 cm, shows more inter-year variation: across the whole North Sea, the proportion varies between 0 in the year 1986 and 0.11 in 2003 (Fig. 3b). Only 1986 had even lower habitat suitability than the example year for cold temperatures (1988). In 1986, in no part of the North Sea did anchovies reach the overwintering size of 10 cm. In the southern North Sea, the proportion of suitable habitat varies between 0 in a suite of years (during the 1980s, 1990s and some from the 2000s) and 0.24 in 2006 (Fig. 3d).

The areas of the North Sea where anchovy would be able to reach sizes of ≥10 cm according to the DEB model are similar in cold and warm years, illustrated (in Fig. 4) by the maps for 1988 (fraction of suitable habitat: 0.02) and 2003 (fraction suitable habitat: 0.11). Growth is highest in the southern North Sea, including the Dogger Bank, and around Denmark. It also appears that most of the positive

growth has happened by 1 October and starts leveling off after this period (day 274 of the year, Fig. 3).

Simulation results and empirical abundance from the following year's first quarter, indicative of survival, are well correlated (Fig. 5; Spearman's rank correlation, $\rho = 0.78$; $p < 0.001$). When years corresponding to zero catches in the IBTS are removed (6 years total), the same significant positive relationship holds (Spearman's rank correlation, $\rho = 0.65$; $p = 0.004$).
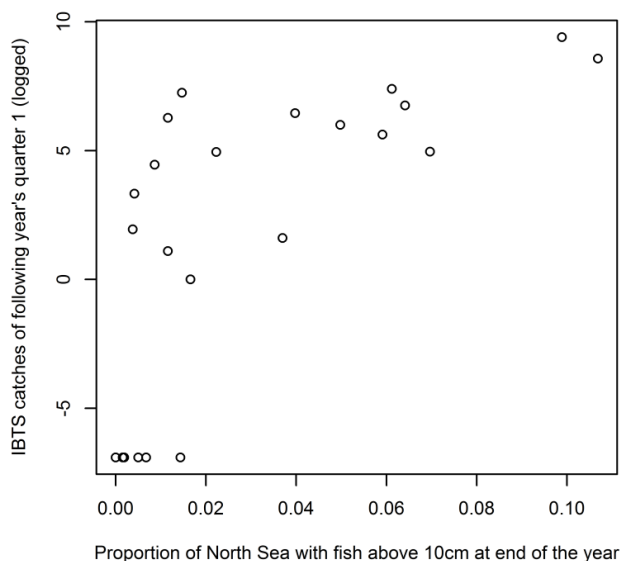

Fig. 5. Relationship between survey catches (from the International Bottom Trawl Survey) and proportion of the North Sea in the previous growing season that was suitable for anchovy (proxy used is the area where anchovy can attain >10 cm in length)

SPATIO-TEMPORAL MODELING

The best model fit for the relationship between anchovy CPUE and food variables (i.e. different versions of Model 2) in the period from 1973 to 2006 was for the model that used log(zooplankton biomass) as it had the lowest GCV, and

therefore, log(zooplankton biomass) was chosen as most appropriate zooplankton variable to represent anchovy food in Model 3.

The best model fit for the relationship between anchovy CPUE and environmental variables in Models 1 to 3 (temperature, food, or both) was for the model that included temperature only: Model 1 (GCV = 2.1835; R^2 = 0.10; deviance explained= 12.8%; Table 2, Fig. 6) based on minimization of GCV and removal of non-significant variables. Indeed, while Model 3 had a lower GCV than the other models (GCV = 2.1199; R^2 = 0.738; deviance explained =10.1%; Table 2), it included a non-significant variable (food, p = 0.186) that did not show a significant relationship with anchovy abundance and could thus be removed.

Model 2, with only food as an explanatory variable, had the lowest coefficient of determination (R^2) and accounted for the least of the deviance (R^2 = 0.05, deviance explained = 7.46% with a GCV of 2.1546; Table 2). The relationship between food and anchovy CPUE was close to zero in both Models 2 and 3 (Figs. 7b & 8b respectively) and non-significant in both (p = 0.184 and p = 0.186, respectively; Table 2).

The spatial effect found in Model 1 with only temperature (see Fig. 6a) indicates more CPUE off the Scottish coast and on the Dogger Bank, as well as around Denmark. Temperature during the previous growing season has a positive effect on anchovy CPUE (Model 1, Fig. 6b) between 12 and 15°C, a weak effect on the CPUE between 15 and 17°C and a strong positive effect again between 17 and 19°C.

The residuals did not show any particular pattern, and temporal and spatial autocorrelation were not a problem due to the low proximity in time and space between the different observations after removing the zeros from the dataset.
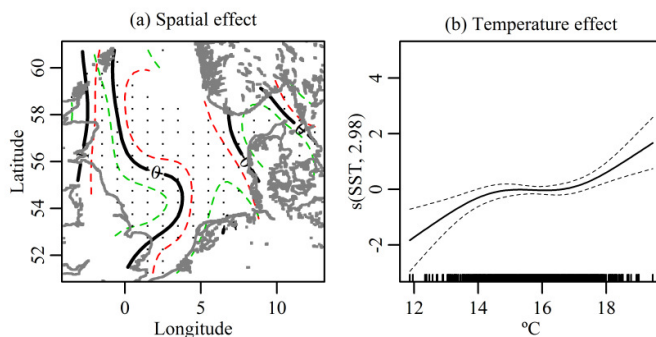
Fig. 6. Effect of space and of temperature on the survey catch per unit effort (CPUE) of anchovy in 1973 to 2006: (a) Spatial contours of anchovy CPUE with upper (red) and lower (green) confidence intervals; (b) partial additive effect of temperature (*x*-axis) on the CPUE of anchovy (*y*-axis, number in parentheses indicates the effective degrees of freedom). The dashed lines are the 95% confidence intervals. The rug plot on the *x*-axis indicates the location of observations

Fig. 7. Effect of space and of food on the survey catch per unit effort (CPUE) of anchovy in years 1973 to 2006: (a) Spatial contours of anchovy CPUE with upper (red) and lower (green) confidence intervals; (b) partial additive effect of food (*x*-axis) on the CPUE of anchovy (*y*-axis, number in parentheses indicates the effective degrees of freedom). The dashed lines are the 95% confidence intervals. The rug pl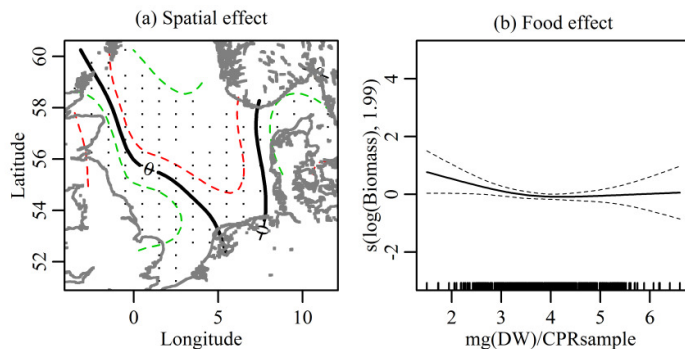ot on the *x*-axis indicates the location of observations. The original food unit is mg dry weight (DW) per continuous plankton recorder (CPR) sample, which has a nominal volume of 3 m^3
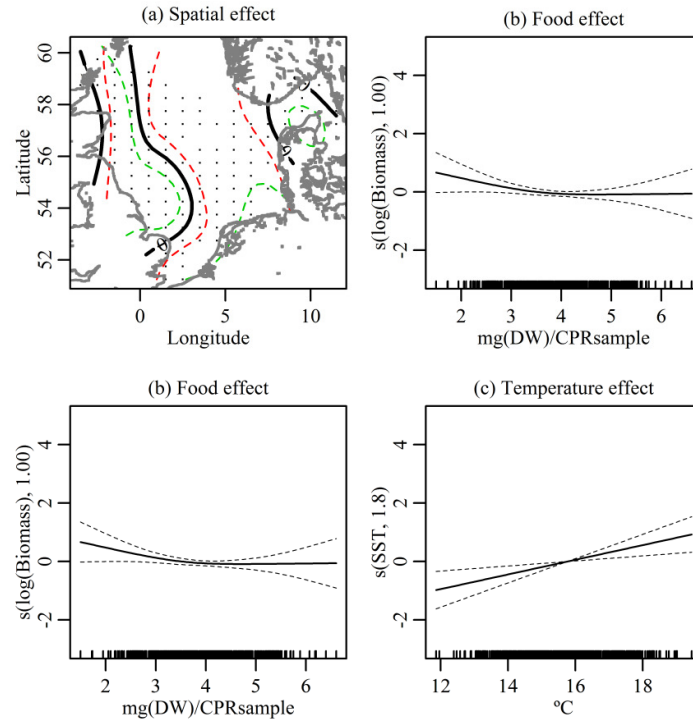
Fig. 8. Effect of space, food and temperature on the survey catch per unit effort (CPUE) of anchovy in 1973 to 2006: (a) Spatial contours of anchovy CPUE with upper (red) and lower (green) confidence intervals; (b) partial additive effect of food (*x*-axis) and (c) partial additive effect of temperature (*x*-axis) on the CPUE of anchovy (*y*-axis, number in parentheses indicates the effective degrees of freedom). See Fig. 7 for more details

Table 2. Generalised additive modelling: intercept, effective degrees of freedom (edf) and significance (p-value) of the spatial and environmental covariables in each of the 3 models. Coefficient of determination (R^2) and generalised cross validation (GCV) score are given per model.

	Model 1: TEMP		Model 2: FOOD		Model 3: BOTH	
	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	1.3737	<0.001	1.3193	<0.001	1.3193	<0.001
SE	0.0620		0.0661		0.0653	
	edf	p-value	edf	p-value	edf	p-value
(Long, Lat)	13.972	<0.001	9.213	0.030	11.441	0.009
Temp	2.988	<0.001	–	–	1.807	0.002
Food	–	–	1.989	0.184	1.000	0.186
R^2	0.1		0.0525		0.738	
GCV	2.1835		2.1546		2.1199	
Deviance accounted for	12.8%		7.46%		10.1%	
n	550		481		481	

DISCUSSION

The benefit of using both the spatio-temporal modeling and DEB approaches is that while the former indicates which environmental factors co-vary in time and space, the DEB model simulates the underlying mechanisms. We find that the proportion of North Sea habitat during the anchovy growing season is positively related to the following year's first quarter's anchovy CPUE and that the temperature of the growing season best explains the spatial variation in anchovy abundance and distribution. This supports the hypothesis of expanded thermal habitats as a mechanism for increased summer growth of individuals and better subsequent overwinter survival leading to the anchovy population expansion (Petitgas et al. 2012).

In both cold and warm years, the areas where anchovy can grow best are located in the same areas in the southern North Sea. These regions include areas where a resident anchovy population is found (the Dutch coast; Boddeke & Vingerhoed 1996) and where a new anchovy spawning area was reported after the population increase (the German Bight; Alheit et al. 2007). This also corresponds roughly to the bathymetry of the North Sea and to shallower, hence warmer, areas.

Generally, the location of high anchovy CPUE found in the GAM does not correspond well to the high growth areas found in the DEB model. In the German Bight for instance, there is a low anomaly in the Quarter 1 CPUE, where DEB simulated growth is highest. CPUE is high on the east coast of the UK, on the Dogger bank and around Denmark. According to the DEB output, the east coast of the UK is a low growth area, the Dogger Bank varies depending on the year, while around Denmark, growth is always high. This discrepancy between high growth areas and high CPUE later is not completely surprising as fish are mobile organisms and often have seasonal migrations. Anchovy is known to partition its nursery and feeding grounds in other systems (e.g. Irigoien et al. 2007), so while it is possible that the fish caught in areas of low growth, e.g. off Scotland, grew there under sub-optimal growth conditions, it seems more likely that they occupied the more suitable habitat areas during the previous summer and then moved elsewhere, as indicated by earlier studies (Beare et al. 2004a, Alheit et al. 2012). In winter, the SE North Sea cools down, and anchovy may move to warmer waters in the areas supplied by Atlantic inflow of relatively warm water (Southern Bight and along the coast of Scotland and England).

The yearly variability in habitat suitability corresponds to the general increase of anchovy population over time (Beare et al. 2004a), and specifically, the habitat suitability at the end of the year is strongly correlated with the IBTS CPUE of the following year's first quarter. This supports the hypothesis (of Petitgas et al. 2012) that it is the first growing season of North Sea anchovy that determines the abundance in the following year, due to increased winter survival. A different index of habitat suitability developed for older anchovies and based on the rate of reallocation of energy from reproduction buffer to maintenance in the DEB model has shown that the spatial extent of unsuitable areas during winter has decreased for anchovies in the North Sea (Peck et al. 2009). November and December in particular showed large variability throughout the timeseries (1980 to 2004) with a decrease in the percentage of unsuitable area. Thus, it seems likely that in addition to affecting juvenile growth, winter temperatures are also a major influence on adult anchovy via reproduction.

Additional mechanisms related to reproduction and overwintering may have enhanced the population increase of anchovy under warming climatic conditions. First, a warmer growing season implies an acceleration of physiological processes, from assimilation of ingested food to maturation of oocytes and egg batch production, thus increasing the overall frequency of batch production as long as sufficient food is available. Second, under warming conditions, the length of the spawning season increases. According to a field study in the Bay of Biscay, both batch fecundity and batch frequency increase as the spawning season progresses (Motos 1996). Third, temperature since the 1990s has been higher than in the past decades (Hughes et al. 2012), and this may allow for increased overwinter survival of the individuals (see Petitgas et al. 2012).

Our study could be considered limited by the use of sub-optimal gear (a demersal trawl) to derived CPUE indices of survey abundance. One might imagine that small pelagic schooling fish are better sampled with acoustic surveys. However, the IBTS originates from the ICES young herring survey, and the GOV trawl was specifically chosen to sample juvenile clupeids (Heessen et al. 1997). The IBTS is the only comprehensive survey that has charted the population dynamics of North Sea anchovy, similar to the trends expressed by commercial vessels. This IBTS is also the CPUE series used in previous studies (Beare et al. 2004a, Petitgas et al. 2012). In fact, the North Sea acoustic survey (as mentioned by Petitgas et al. 2012) does not catch anchovy. This is thought to occur because the survey is executed in the summer (June/July) in offshore areas (ICES 2012) just

when anchovies are spawning in inshore areas (Alheit et al. 2007, 2012). So the IBTS is the only dataset that regularly records anchovy, and this survey also covers a long period of time and is spatially extensive. Anchovy have been suggested to be benthic in wintertime (Fage 1911), and a loss of reserves in winter and resulting change in buoyancy (Dubreuil & Petitgas 2009) may support or cause this change, again suggesting that the Quarter 1 IBTS survey is an appropriate and reliable index of anchovy dynamics in the North Sea.

In the spatio-temporal modeling part of the present paper, we use empirical data to disentangle the effects of temperature and food during the growing season. We find that temperature is more important than food in explaining the pattern of abundance and distribution of anchovies. In the German Bight, CPUE is generally lower, possibly because this area is rather shallow and therefore cools down substantially during winter, when anchovy move elsewhere (Alheit et al. 2012, Beare et al. 2004a). Physiologically, one may expect a positive effect of increasing temperature on fish productivity, up to a maximum and followed by a sharp decrease due to e.g. cessation of enzyme activity (Pörtner & Farrell 2008). The smoothed relationship between temperature and CPUE anomalies that we find here deviates from this expectation. The positive relationship below 15°C and above 17°C and a stable level in between may indicate that 2 processes are involved. The positive temperature effect up to 15°C may reflect the need of anchovy for warm temperatures to spawn (Motos et al. 1996). The increase between 17 and 19°C may reflect the expansion of the spawning habitat. Food availability is expected to have a positive effect on fish populations (Brandt 1993) and on young anchovy in Japan (Zenitani et al. 2007), so it seems surprising that no effect is found here. The effect of zooplankton prey on anchovy distribution may have been overridden by that of temperature because since the 1990s the temperature in the southern North Sea has been higher than in previous decades (Hughes et al. 2012). This strengthens the hypothesis that anchovy are unlikely to suffer from food limitation in the North Sea, already suggested previously due to the species being a generalist feeder compared to other likely competitors (Raab et al. 2012). Although the empirical food-availability proxy we used (total zooplankton biomass) may be crude, we consider the results robust as we tried several other measures of food availability from the CPR data based on the present understanding of North Sea anchovy diet and obtained similar results.

Growth is affected by temperature and food availability in anchovy (Basilone et al. 2004, Takasuka & Aoki 2006), and survival also depends on food (Zenitani et

al. 2007). In a comparative study of different anchovy populations in Asia, the respective importance of temperature and food varied by geographic region; however, the synthesis showed that an overall temperature relationship underlies all the relationships, making temperature more important than food availability in those areas (Takasuka & Aoki 2006). Our results support this finding.

Other factors may affect growth patterns and were not taken into account in our study. Density-dependence can reduce growth in fish (Lorenzen & Enberg 2002), but this possibility is ignored in our DEB model. Trophic competition can reduce growth, and size-selective predation may affect growth patterns. Different predator species select differently in Japanese anchovy (Takasuka et al. 2003), and cannibalism also occurs (Takasuka et al. 2004). The impacts of same-level and top-down effects on the North Sea anchovy population remain to be studied.

In conclusion, the present multiple-approach study, combining eco-physiological and ecosystem models with analysis of empirical data, provides a supportive and convincing argument about the processes that determined the recent expansion of anchovy in the North Sea. The DEB model is parameter intensive and based on a generic mechanical description of the anchovy's eco-physiology. In this case, we parameterised it using mostly Bay of Biscay anchovy values (Pecquerie et al. 2009, Freitas et al. 2010). However, the North Sea anchovy population is considered to be genetically distinct from the Bay of Biscay population (Zarraonaindia et al. 2012), and parameter values are partly under genetic control (Kooijman 2010); therefore, it is possible that some of the parameter values used in the present study may differ from those that are appropriate for North Sea anchovy. The spatio-temporal modeling approach suffers from the same issues as many empirical studies, such as possible biases in measurement or sampling, and moreover, the GAM approach we use is correlative and does not address underlying mechanisms linking the variables of interest. Statistical relationships do not necessarily imply causality, but putting all the information together gives a coherent picture. We think that together the 2 parts of the present paper support the importance of the growing season in the range expansion of anchovy in the North Sea and indicate that habitat suitability in terms of the pre-winter growth is a crucial factor.

Acknowledgements

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CHAPTER 6

Depensation in small pelagic fish, illustrated with the North Sea anchovy example

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ABSTRACT

Fish population dynamics have historically been represented using the logistic growth model. Several mechanisms have, however, been proposed which may result in negative population growth at low abundances, i.e. depensation, in small pelagic fish populations (e.g. intra-guild predation or the school trap).

European anchovy (*Engraulis encrasicolus*) increased its abundance in the mid-1990s across the North Sea but the mechanisms leading to its rather sudden increase are unclear. Here we explore the hypothesis that depensation may have played a role in the dynamics of the expansion of anchovy in the North Sea. We constructed a simple single-species model that includes depensation and explored the effect of varying assumptions about the strength of depensation, the species' mobility and the environment on the spread of a population of a small pelagic fish through space.

We aim to illustrate under which conditions it can spread out of a localized area in the South of the North Sea, where it likely existed as a resident localised population. Ultimately, the aim is to understand the impact of environmental or climate change on the potential of a population with depensation to invade a spatially heterogeneous system.

In a homogeneous continuous environment, under both logistic and depensatory growth, the population either goes extinct or spreads to the whole system. In the more realistic condition where the environment is heterogeneous, on the other hand, an intermediate type of stable distribution can also exist where only part of the North Sea is occupied. While in the logistic situation the transition between high and low abundance areas is smooth, depensation results in a more abrupt transition between these abundance states.

Under warming climatic conditions, the transition zone from high-low abundance moves North (and area occupied increases) and the latitudinal spread would be smooth if the environment is continuous, but more step-wise in a patchy environment.

INTRODUCTION

Small pelagic schooling fish are some of the most productive fish stocks worldwide and are notorious for very variable populations and changes in abundance and distribution (Lluch-Belda et al. 1989, Schwartzlose et al. 1999). The processes governing the populations and causing species alternations in these systems (Schwartzlose et al. 1999, Chavez et al. 2003) are not well understood but

some hypotheses have been put forward (e.g. differential responses to temperature Takasuka et al. 2007).

With climate change, changes in species ranges are occurring (e.g. Thomas & Lennon 1999, Perry et al. 2005, Thomas et al. 2006). In the North Sea, fish assemblage are changing in response to climate change with warmth-preferring species increasing in abundance (ter Hofstede et al. 2010, Engelhard et al. 2011). The European anchovy is one example of a warm-water species increasing its abundance in the North Sea in recent decades (Beare et al. 2004a, Beare et al. 2004b, Alheit et al. 2012, Petitgas et al. 2012).

The processes that determine the success of species' invasions of new habitats are influenced by changes in e.g. dispersal ability or propagule pressure, environmental conditions, or in vital rates or biotic interactions, such as the ranges of predator or competitors, including indirect via pathogens or parasites. Demographic Allee effects (sensu Stephens et al. 1999) "overall fitness has a positive relationship with density that results in per capita growth rate of the species being reduced at low density") are not often included in this list, but their influence in invasion dynamics is substantial (Taylor & Hastings 2005). In marine systems, studies of Allee effects have often been on component Allee effects (a decrease in some component of fitness at low density) in invertebrates, especially broadcast spawners (see Gascoigne & Lipcius 2004); and demographic Allee effects (an overall effect on population growth rate) in fished stocks using time-series analyses but without specifying mechanisms (e.g. Myers et al. 1995). The presence of a component Allee effect (e.g. in fecundity) however does not necessarily imply an overall demographic Allee effect in the population, as a particular component Allee effect may be balanced out by other mechanisms (e.g. increased survival of fewer offspring). Thus in a population-dynamical context, a focus on demographic Allee effects (net sum of all component Allee effects and counteracting mechanisms) is more relevant.

In fisheries science, positive density-dependence, through predation or reproduction, is termed "depensation" (Hilborn & Walters 1992). We're interested in depensation (i.e. positive density dependence) in fish stocks and study it in the context of anchovy increase in the North Sea.

We consider three mechanisms for depensation to be of particular interest for schooling small pelagic fish: the school trap (Bakun & Cury 1999), intraguild predation (Polis & Holt 1992) and the predator pit (Bakun 2006),. The school trap concept (Bakun & Cury 1999) rests on the assumption that small pelagic fish have

a schooling imperative resulting in a species having to school with fish of another species (mixed schools, as observed e.g. by (Fréon 1984) when its population abundance is low. This may be disadvantageous for the species and thus result in lower growth rates at these low abundances. In intraguild predation (Polis & Holt 1992) a species consumes its trophic competitor along with the food resource it shares with the competitor. If the species in question increases its abundance due to external factors (such as temperature), its predation pressure will likely reduce competitors' numbers and thus increase food availability to itself, creating a positive feedback loop for increased population growth (as more food often leads to more growth). The predator pit mechanism (Bakun 2006), which is a combination of numerical and functional responses, postulates two threshold levels in a prey's population abundance. The lower threshold influences the predator's functional response. Below it the predator takes no interest in the prey but above the threshold it switches to targeting this prey and more intensively the more of it is available. At the higher threshold the predator population satiates and thus predation pressure decreases, allowing the prey population to grow. The space between these abundance thresholds is called the predatory pit, and the prey species can only reach and overcome the upper abundance threshold by having a very high population growth rate. Once it crosses the upper abundance threshold, population growth increases.

Thus all three mechanisms may cause a positive relationship between population growth and population abundances Because these three mechanisms likely apply to small pelagic fish species, the role of depensation in the population dynamics of small pelagics may have been underestimated. Here we want to explore the role of depensation on the spread of such populations through space. By modelling the population dynamics (with depensation) of a small pelagic fish expanding in a spatially heterogeneous system, we hope to gain more insight into the processes governing range expansions of such populations. We use the example of anchovy in the North Sea which has recently appeared in increased numbers and distribution (Beare et al. 2004a). The origin of these fish is unknown but the presence of a spawning population in the southern North Sea (Oosterschelde, NL) and recent genetic analyses (Zarraonaindia et al. 2012) suggest the anchovies caught across the North Sea may be the product of a resident population that during the mid 1990s began a rapid expansion (Petitgas et al. 2012).

We hypothesize that in a depensation situation, changed environmental conditions can allow the population to spread through space despite depensation effects initially limiting it to a local area.

The specific aim of the study is to investigate under which conditions the spread from a localized area of the North Sea space can happen assuming depensatory dynamics and which factors are important in determining the spread. We simulate single species population dynamics in a spatial system and explore how the combination of depensation and dispersal affect the ability of the population to spread throughout the entire system assuming it started at equilibrium levels. Ultimately, the aim is to understand the impact of environmental or climate change on the potential of a population with depensation to invade a spatially heterogeneous system.

METHODS
Modelling the Allee effect
The anchovy increase in the North Sea is thought to result from an increase of a localized population in the southern North Sea that has been present there for a longer period of time (Petitgas et al. 2012) and we therefore assume to be at equilibrium levels.

We first represent the North Sea anchovy population dynamics using the logistic growth model with decay:

$N' = r \cdot N \cdot (1 - (N/K)) - d \cdot N$ (equ. 1)

This assumes that the population N grows at a given population growth rate r in a system of carrying capacity K (May 1973) and d represents decay. Population growth rate is always positive for r>d and slows down as the population gets closer to carrying capacity (figure 1a).

We then compare how depensatory dynamics of this hypothetical anchovy population would change the results using an Allee effect model with decay (Courchamp et al. 1999):

$N' = r \cdot N \cdot ((N/A) - 1) \cdot (1 - (N/K)) - d \cdot N$ (equ. 2)

which includes a depensation term (N/A-1) that decreases population growth at low abundances and increases it at high abundances.

Parameter A is the threshold abundance at which the depensation term is null and affects the abundance at which population growth is zero (figure 1b). Allee effect models have been used to model alternative stable states in spatial systems (van de Leemput et al. in review). Hereafter we use the terms "Allee effect" and

depensation interchangeably despite the concepts not overlapping completely (see introduction). The North Sea can be thought of as having two states of abundance of anchovy: low or no anchovy and high (close to K) anchovy. Only under certain conditions, these two abundance states can coexist in the same system, when so-called 'invasion pinning' occurs, i.e. the species' range is limited to it being unable to propagate (explained in Keitt et al. 2001).

We analyse how an increase in temperature due to climate change may impact the expected spatial range of anchovy, and for the Allee model we explore how the combination of A and dispersal (D see below) impact the spread of the population. The suggested cause of increase is an expansion in thermal habitats allowing for better summer growth of young fish and consequent increased winter survival as well as possibly increased reproduction (Petitgas et al. 2012). These processes suggested to determine the anchovy increase are related to growth which results in increased numbers the following year. We therefore choose to represent environmental temperature as variations in population growth rate (rather than carrying capacity or decay rate).
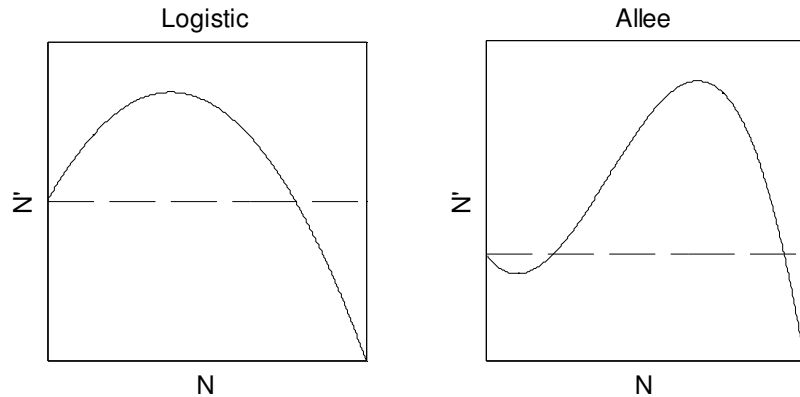

Figure 1: Population growth functions for (a) the logistic growth model and (b) the Allee effect model used.

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Spatial Models

We run the logistic and depensation models described above in a system representing the North Sea first as a homogeneous environment (situation 1 as simple example) then as a heterogeneous environment with a continuous latitudinal environmental gradient. Summer temperature is an important influencing factor in determining modelled young anchovy growth and empirical survey catches (Raab et al. in press). During summer, the southern North Sea is warmer than the North due to topography of North Sea, which is shallower in the South. Therefore, after the baseline representation of the environment as homogenous space, we then represent environmental heterogeneity as a gradient with smoothly decreasing values for maximum growth rate from the South (r_{max}) to North (r_{min}).

The way in which space is represented in a model may change the outcome; (see e.g. Keitt et al. 2001): in a patchy environment, stable range pinning is possible under wide set of parameter conditions but in a uniform environment this is not the case). Therefore, for the more realistic case of a heterogeneous environment, we model the population in both continuous space (situation 2) and discontinuous i.e. patchy, space (situation 3, see table 1 for overview).

The continuous space models represent the North Sea by a grid of 100*10 cells in which anchovy can move between cells and temperature/growth rate can differ between cells. The patchy space model represents the North Sea as a network of 40 uniform patches with its growth rate corresponding to that of the patch if it were set in the continuous environment.

To represent the resident population existing in the southern part of the North Sea, we give 10% of the system an initial population density of equilibrium K (K*), from which it may spread and simulate the population until it equilibrates. In the case of continuous space this means the southernmost 10% of cells; in the case of a patchy environment the southernmost 10% of the patches (i.e. 4 patches) are at equilibrium K (K*).

Dispersal of the population is set by a parameter D representing the proportion of the local population that leaves a given cell or patch. Through continuous space, dispersal D is simulated by a given proportion of the cell's abundance spreading to 4 adjacent cells. The edges of the system are set to have a mirror-effect, i.e. no fish are lost (to land).

In patchy space, distance between patches determines the exchange rate D following a random dispersal kernel with a Gaussian distribution (used e.g. in Etienne et al. 2002).

For each situation in continuous or patchy space, we consider logistic growth and weak and strong depensation (5% and 10 % of K), we explore how conditions of growth in the South affect what portion of the system is filled.

We assume the carrying capacity K and decay rate d to be constant throughout the modelled system (by setting arbitrary constant values of K=500 and d=0.2 respectively,) and represent changes in environment by variations in growth rate as explained above. For the gradient situations, we assume a constant value of 0.001 for r_{min}, as warming is likely to affect most strongly the shallower southern part of the North Sea (represented by r_{max}), rather than the North.

Table 1: Overview of the situations represented: spatial configuration of the model, growth model used, parameter values and corresponding figures.

Situation	Spatial configuration	Growth type	Parameters	Figure
1	Homogeneous environment, continuous space	Logistic	r=0.6	2a
		Allee	r=0.6, A=25	2b
		Allee	r=0.6, A=50	2c
2	Heterogeneous environment, continuous space	Logistic	rmax=0.3, 0.6, 0.9	3a
		Allee	rmax=0.3, 0.6, 0.9, A=25	3b
		Allee	rmax=0.3, 0.6, 0.9, A=50	3c
		Logistic	rmax=0.6, D=0.1, 0.5, 0.9	4a-b
		Allee	rmax=0.6, A=50, D=0.1, 0.5, 0.9	4c-d
3	Heterogeneous environment, patchy space	Logistic	rmax=0.3, 0.6, 0.9	6a
		Allee	rmax=0.3, 0.6, 0.9, A=25	6b
		Allee	rmax=0.3, 0.6, 0.9, A=50	6c

Homogeneous environment in continuous space (situation 1)

The logistic model has been explored in much detail elsewhere but we present a simple example for illustration with a value of r>d. For the Allee model, a low and high depensation (A=25 and A=50) example are given to illustrate the effect of A. The effect of dispersal is shown by assigning three values to D and showing the time series of the population and the end states. We show the population growth

curves and the state of the system as it changes through simulation time, i.e. at t=0, t=100 and t=1000.

Heterogeneous environment in continuous space (situation 2)

The initial population value used to represent the resident anchovy population is estimated from the homogeneous space situation. For a given K, A, d, and D, the growth rate at which the population switches from collapsing to expanding is the critical growth value r_{crit}. Solving the Allee model (equation 2), i.e. finding its higher value root, with that critical growth value gives the equilibrium population size K*. This value is used as initial population value in the heterogeneous environment situations (2 and 3).

We show the effect of varying the growth rate in the southern North Sea on the final spatial configuration of the population and on the speed of reaching the equilibrium situation for r_{max} values of 0.3 and 0.6 and 0.9. For one of these r_{max} values (0.6), we also explore the effect of dispersal on the final spatial configuration of the population and the speed at which equilibrium is reached (values of D used are 0.1, 0.5 and 0.9).

Finally we combine results for different A and r_{max} values (A between 5 and 150, r_{max} between 0 and 1) and show how these impact the latitude reached.

Heterogeneous environment in discontinuous (patchy) space (situation 3)

For the patchy space situation we use an example network of 40 patches (arbitrary number),

each patch is assigned a random x and y coordinate in a continuous spatial system of 100*10 representing the North Sea's latitudinal temperature (r growth rate) gradient for the continuous space situation. Thus each patch has a different growth rate, the further south it is located, the higher that patch's growth rate. A patch may for instance represent areas of the North Sea that are suitable for anchovy spawning and thus are very influential in determining the population reproduction. Here too we consider the situation where depensation is weak and strong (A=25 an A=50 respectively), and explore under which temperature conditions, by varying the growth in South (r_{max}), how far north the population can

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spread i.e. how it may be affected by possible warming under climate change. We vary A (between 5-100) and vary r_{max} (between 0-1) and record the effect on the northernmost patch occupied (defined as abundance>K/2). Finally we combine results for different A and r_{max} values and show how these impact the latitude reached.

RESULTS
Homogeneous continuous space (situation 1)

In homogeneous space, the population either goes extinct (not shown) or expands to all areas of the system from its initial area of distribution (figure 2). Under logistic growth, the population always expands to K for r>d (e.g. figure 2a) and goes extinct if r<d. Under depensation, for a given Allee threshold, there is a critical growth rate above which the population can expand to fill the whole system. The value of this critical growth rate can be determined by plotting the function under the chosen parameter settings. If the area under the curve between A and K is larger than the area under the curve between 0 and A, expansion is possible (e.g. figure 2b-c). If this is not the case (e.g. because r is lower, and everything else is the same), the population goes extinct (not shown). The effect of A is to restrict the population to its initial area, disabling it to expand to new areas, but higher r values can counteract this.

Warming effects under climate change i.e. an increase of r_{max} may result in expansion instead of extinction, given that A stays constant.
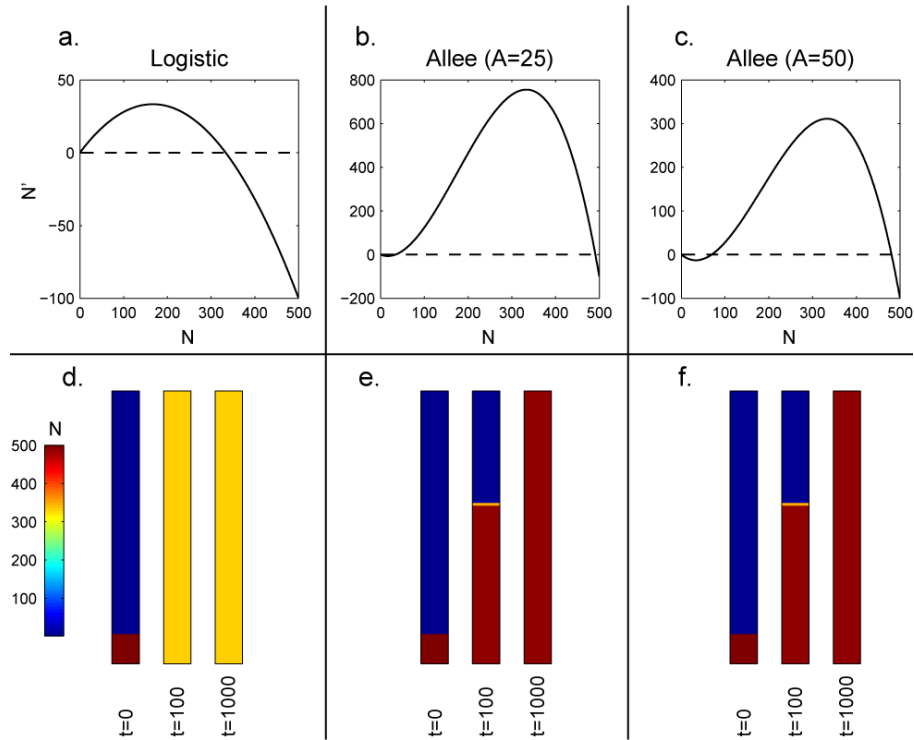
Figure 2: Population growth functions for logistic (a) and depensatory growth with low (A=25) and high (A=50) depensation. Effect of growth rate r on the expansion of a localised population through a homogeneous environment for logistic growth with r=0.3 (d) and under depensatory growth for low (e, A=25) and high (f, A=50) depensation levels. Colour bars show the anchovy population (red) in the North Sea system at the first (t=0), intermediate (t=100) and final (t=1000) time step of the simulation.

Heterogeneous continuous environment (situation 2)

For the logistic model, the population expands when r>d, whether r_{max} is low or high. (e.g. in figure 3a).

In a heterogeneous continuous environment, the population with depensation spreads or disappears in a wavelike fashion but depending on the balance of maximal growth rate in the South (r_{max}) and A it can also become limited at a certain "latitude" of the system, the so-called 'range pinning' (Keitt et al. 2001).

In the example situation where A=50, an r_{max} of 0.3 would allow the population to expand from its refugium to 60 percent of the system when decay is 0.2. When growth rate is higher, as might be expected under climate change, the percent of the system filled by anchovy increased to 80% for r_{max} of 0.6 and to 87% for r_{max} of 0.9 (figure 3c). For lower depensation intensity, population can spread further North, e.g. with A=25, for r_{max} =0.3 the population can already spread to 83 % of the system (figure 3b).

Dispersal affects the speed at which the final state of the system is reached, with low dispersal situations being slow to equilibrate and high dispersal situations reaching equilibrium in a shorter time (figure 4b, 4d). In the depensation situation(figure 4c, 4d), this effect is more pronounced than in the logistic situation (figure 4a, 4b).

Dispersal does not affect the midpoint of the shift from high-low abundance of anchovy, but the higher D is, the smoother the transition between the abundance states in the depensation situation (figure 4c). Generally, if A is lower, for a given r_{max}, higher latitudes are reached, i.e. for a given A, the effect of increasing r_{max} is to increase the final 'latitude' to which anchovy can spread (figure 5).
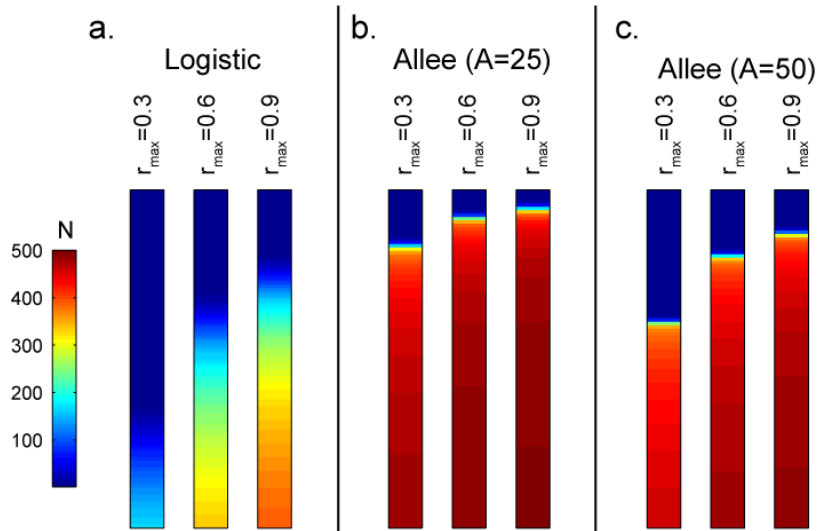
Figure 3: Effect of growth rate r and depensation intensity A on the spread of localized anchovy population through a heterogeneous environment with smooth gradient from rmax(South) to rmin(North) under climate change. For the logistic growth (a) the end state of system for different values of rmax (0.3, 0.6 and 0.9) is shown. For low (b, A=25) and high (c, A=50) depensation intensity, the effect of different temperatures in southern North Sea (rmax 0.3, 0.6 and 0.9) on the final system state are shown.
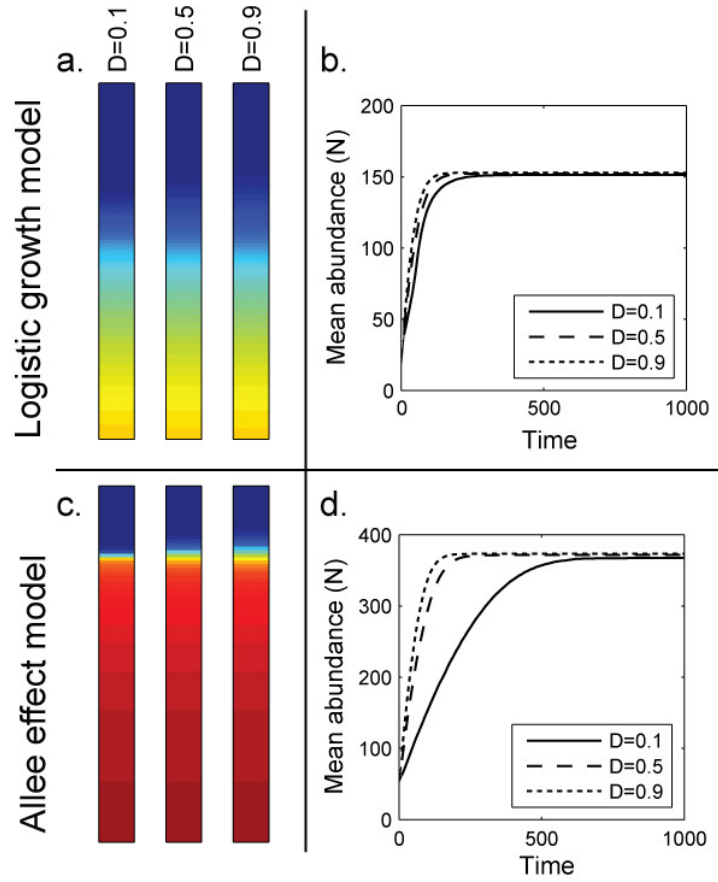
Figure 4: Effect of dispersal on the spread of localised anchovy population from the southern North Sea. Left panel: spatial configuration at end of simulations for (left-most colour bar) low D (=0.1), (middle colour bar) medium D (=0.5) and (right-most colour bar) high D (=0.9) for logistic growth (a) and depensatory growth with A= 50 (c). Right panel: development of mean cell density through time for D=0.1 (blue line), D=0.5(green) and D=0.9 (red line) for logistic growth (b) and depensatory growth with A= 50 (d).

Figure 5: Latitude reached by a population with depensation according to growth rate in the southern North Sea (rmax) for different intensities of depensation (A=5, dashed grey line; A=10, solid grey line; A=50, dotted black line; A=100, dashed black line and A=150 solid black line).
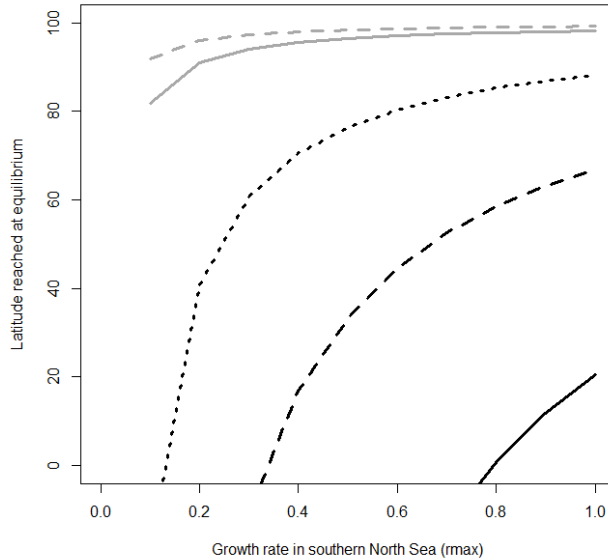
Heterogeneous discontinous environment (situation 3)

In a discontinuous (patchy) environment with logistic growth, the population spreads to nearby neighbouring patches and latitudinal abundance changes are gradual (fig. 6a). Under depensation, patches reach high or low population density and the difference in abundance between patches is higher. When A is low the population spreads further from the initial population (fig 6b) than when A is high (fig 6c). For the discontinuous (patchy) environment situation there also is a threshold value of r_{max} above which the population can spread from the South (i.e. just below r_{max} values for which the lines are displayed in figure 7). This r_{max} threshold value depends on the exact configuration of the network. Since if patches are closer together, new patches require less growth to overcome depensation effect.

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Increasing temperature affects where the most northern occupied patch lies (figure 7) the effect of temperature on the latitude of the northernmost occupied patch. While in continuous space, the increase is smooth, in patchy space the increase is in steps.
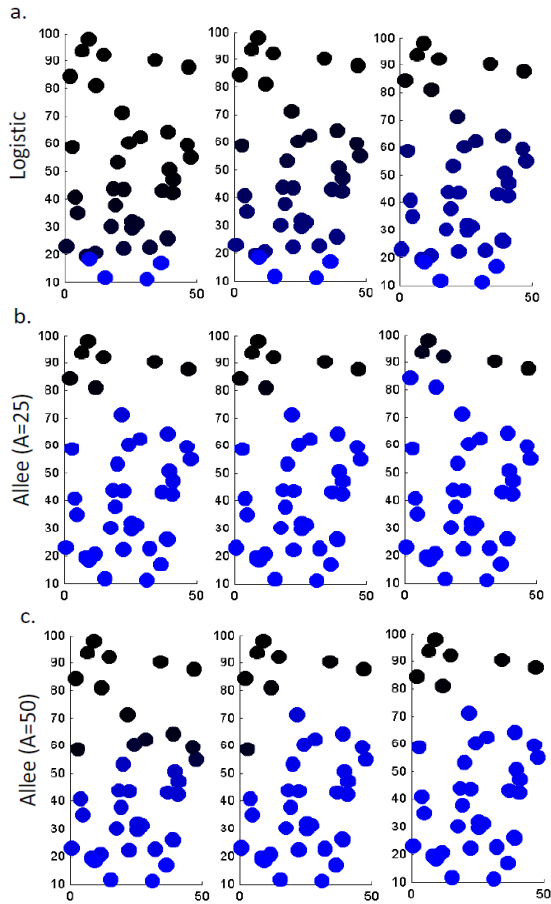

Figure 6: Effect of growth rate r on the expansion of a localised population through a heterogeneous patchy environment for logistic growth (a) and depensatory growth (low A=25, b and high A=100, c) under climate change increasing rmax from 0.3 to 0.6 to 0.9. Empty patches are represented by black dots, full patches by blue dots.

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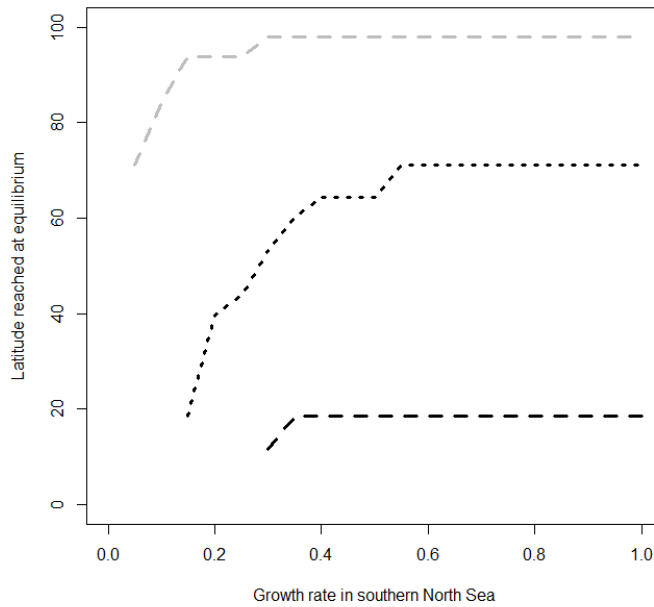
Figure 7: Effect of increasing growth rate (rmax) in the southern North Sea on the latitude reached by a localised population under different intensities of depensation (A=5, dashed grey line; A=50, dotted black line; A=100, dashed black line).

DISCUSSION

We explored the effects of assuming population growth with depensation (rather than logistic growth) in a model application based on the case of North Sea anchovy. This population has spread from a local population in the southern North Sea (Petitgas et al. 2012) and we do not purport to represent the anchovy increase in the North Sea (Armstrong et al. 1999, Beare et al. 2004a, Alheit et al. 2012, Petitgas et al. 2012) as it happened, but show the effects of including depensation in a model of the possible spatial spread of anchovy.

In a homogeneous system, both logistic and depensatory growth lead to expansion to the full system if population growth rate is above a certain threshold, and extinction if below that threshold.

In the more realistic situation of a heterogenous system, for which we chose to set a latitudinal growth gradient, when logistic growth leads to the expansion of the localized population, it spreads to parts of the system with a gradual transition between high and low abundance states. When depensation is present, so-called 'range pinning' (Keitt et al. 2001) can occur and parts of the system are occupied to high abundances and others not. The transition between the high and low abundance states is far steeper/more pronounced than when logistic growth is assumed. This implies that in a system where the population might be expected to occur at intermediate abundances with the logistic growth model, the population may not be present if there is depensation. The strength of depensation along with the population growth rate are influential in determining whether and where this range pinning occurs with low depensation effects approaching logistic growth, but under high depensation levels populations may go extinct despite the environment providing possibility for high growth rates: a counter-intuitive result.

Dispersal levels are important in determining the speed of spread and the sharpness of the transition between high and low abundance areas. In continuous space, the final configuration of the system is not affected by dispersal except at very low dispersal rate where depensation always outweighs dispersal. In patchy landscapes however, dispersal will be crucial in the spread of a localised population. This is equivalent to the distance between patches being important and this may be an issue in anchovy populations if their spawning sites are limited in the North Sea. Essentially, given suitable growth rates (i.e. where without depensation the population would be able to increase), the interaction of dispersal and depensation intensity determine the dynamics at neighbouring patches. If due to low dispersal the population cannot reach the next patch in high enough numbers to overcome depensation effects, the population becomes limited in space. Thus dispersal in relation to inter-patch distance is very important and a study in which we will vary dispersal in different example network structures is planned. The spatial configuration of the system for anchovy is therefore influential in determining where the population may reach from South to North and whether the spread happens in a smooth or stepwise way. Depending on processes involved, continuous space or patchy space may be a more appropriate representation of the anchovy population. Continuous space is more likely to be a good representation if

the limitations on growth are due to a relatively smooth environmental variable e.g. temperature or salinity. Patchy space on the other hand is more likely to be a good representation of the situation if the limitation on anchovy spawning is related to physical habitat that is patchy, such as estuaries or shallow waters. Anchovy is known to move to appropriate, often coastal, spawning locations in southern Europe (e.g. Motos et al. 1996, Bellier et al. 2007 for the Bay of Biscay or Ré 1996 off Portugal). Therefore if we assume that spawning behaviour in the North Sea is localised, similar to other populations, patchy space may be a more appropriate representation for this species. Indeed, in the North Sea spawning now occurs in the German Bight (Alheit et al. 2007, Alheit et al. 2012), which is also the mouth of the river Elbe, and in the Thames estuary in the UK (*pers. com.* Jeroen vd Kooij), in addition to the existing spawning araes in the Dutch Wadden Sea and Oosterschelde (Boddeke & Vingerhoed 1996). Generally though, monitoring for this species' eggs and larvae is sparse, so mapping its exact spawning locations is difficult.

The patchy landscape situation we describe fits well into the metapopulation biology framework (Hanski 1998)of "idealised habitat patches in which species can occur as discrete local populations connected by migration". The exact dynamics in patches are given by the population dynamics model and migration is determined by dispersal or inter-patch distance. There are several studies on metapopulations and Allee effects (reviewed by Amarasekare 1998), including on spatially explicit metapopulations (Sato 2009). So our study could be considered an application to the anchovy situation and differs from those studies because our patches have unequal growth rates, and we know that the initial population must to be located in a specific part of the system.

Dispersal is crucial and the effects of dispersal in this study can still be expanded upon. Even with more expansive analysis however, dispersal will likely remain a complicated process as it may not be constant during a range change due to either ecological or evolutionary processes playing a role (Simmons & Thomas 2004). In bush crickets for instance dispersal changed (temporarily, for 5-10 years) in populations that expanded their range beyond the core range where dispersal stayed the same, so the authors conclude that "Transient changes in dispersal are likely to be common in many species undergoing range expansion and can have major population and biogeographic consequences". In pelagic fish, an example of such transient dispersal changes might be the so-called "Density dependent migratory waves" (Fauchald et al. 2006) . These are migration "waves" of

gregarious animals that happen as a result of food abundance being low. So in addition to dispersal possibly being density-dependent, it may even be density dependent in a non-linear way, e.g. by such "waves".

Empirically testing for depensation effects in North Sea anchovy has not been undertaken here or elsewhere to our knowledge, and depensation is notoriously difficult to identify in fish stocks (Myers et al. 1995). We do however find it likely that depensation has a role to play in anchovy population as the three possible mechanisms mentioned in the introduction apply to small pelagics. An easily testable prerequisite for the school trap is that mixed schools occur at all in the North Sea. Acoustic surveys can identify schools and species membership, but a key problem in studying the North Sea anchovy increase is that the standard acoustic surveys carried out in summer in the North Sea do not cover inshore areas where anchovy occur at that period. In other systems, mixed schools of small pelagic fish are known to occur (e.g. Fréon 1984) including schools of anchovy and sardine (Radovitch 1979, Cury et al. 2000). Mixed schools seem to occur more often as relative abundance to other species decreases, as observed off South Africa and off Senegal (Cury et al. 2000). Based on the spatial distribution of forage fish in the North Sea (Engelhard et al. in press) the highest degree of spatial overlap by anchovy with other small pelagic fish in the North Sea (and thus potential mixing) is most likely to be with sprat and juvenile herring in the North Sea and adult herring around the East and South coast of Great Britain.

Intraguild predation is a common feature in small pelagic fish populations (Irigoien & de Roos 2011). Anchovy is both a potential intraguild predator as it can consume fish eggs and larvae (e.g. in the North Sea Raab et al. 2011) including its own (Szeinfeld 1993, Plounevez & Champalbert 2000, Takasuka et al. 2004), as well as being potential intraguild prey. Indeed, many small pelagic species consume fish eggs and larvae (e.g. herring Huse & Toresen 1996, Segers et al. 2007) and it seems unlikely that they differentiate by species. While intraguild predation was already suggested to play a role in anchovy - sardine dynamics two decades ago in the Benguela system (Szeinfeld 1991), we are unaware of targeted studies quantifying this process and identifying the fish larvae and eggs to species level in the North Sea fish community.

To investigate the predatory pit mechanism, the predators of anchovy and their functional and numerical responses to this particular prey item should be known and this is probably the most difficult of the mechanisms to investigate or quantify. Small pelagic fish in the North Sea such as herring, sprat, sandeel, and Norway

pout have different sources of biomass removal and make up different proportions of predatory fishes' diets (Engelhard et al. in press). Herring biomass losses in the North Sea are currently mostly to saithe (and to the fishery), while sprat losses are mostly to mackerel and horse mackerel (Engelhard et al. in press). This makes it difficult to consider these species all as one homogeneous mass, be it ecologically or in management (Dickey-Collas et al. in press). Thus assuming anchovy to be identical to any of these other small pelagic species in their role of prey to different predators, including humans, is not a very reliable option. However, one might expect that if warming continues and increases the growth of anchovy by improving thermal windows and early life growth (Petitgas et al. 2012, Raab et al. in press) this would have a positive influence on the population growth should they be in a predatory pit situation regardless of which predators are involved exactly.

The effects of climate change on each of these processes respectively is generally difficult to speculate on due to the many missing information linkages. Climate change affects fish populations at a variety of spatial scales and at different levels of biological organisation (Lehodey P. et al. 2006, Rijnsdorp et al. 2009). Actually in all depensation processes mentioned, if we assume temperature to increase North Sea anchovy growth and this channels through to population growth then the positive feedback effects are accentuated. This only applies however if other populations are constant which they are probably not.

Landings of small pelagic fish, which may be considered to reflect abundance, show high variability (Dickey-Collas et al. in press) and e.g. herring is exhibiting higher recruitment after a series of low recruitment years (Payne et al. 2009) likely to increase its population again. Predatory fish dynamics also vary in the North Sea: saithe spawning stock biomass has decreased over the past few years, mackerel population is mostly in upward trend while catch per unit effort of horse mackerel is in a decreasing phase since the mid-1990s (ICES 2011a,b). Cod is currently at low abundance levels (ICES, 2012) but as it is a piscivore (Floeter & Temming 2003), removes biomass of several important small pelagic fish species (Engelhard et al in press) and interacts with herring both as prey and predator (Daan 1973, 1985, Fauchald 2010, Minto & Worm 2012), a possible future recovery of cod would probably be important in affecting anchovy too. Thus the combination of changing other pelagic fish species and predatory fish species would probably result in intraguild predation intensity to change as predatory fish also can be involved in this process when one takes ontogenetic trophic changes

into account (Irigoien & de Roos 2011) e.g. if their juvenile stages are zooplanktivores competing with anchovy for food.

It is thus clear that while focusing on a single species as we did in this study may reveal a general pattern, single species models are a not a very good representation of reality so this work shouldn't be interpreted as more than just an illustration of the importance of the mechanism in determining population dynamics. One possible way to address the inherent complexity of processes and trophic interactions in marine food webs has been to use end-to-end models of ecosystems (e.g. Travers et al. 2007, Rose et al. 2010). These often include the abiotic influences on productivity and lower trophic levels and include the effects on higher trophic levels. They have been suggested to be a useful tool in fisheries management e.g. by increasing understanding of the connectivity between different life stages between stocks (Hinrichsen et al 20 While progress in coupling different models of different ecosystem components is underway which accelerates the development of such 'complete' ecosystem models, many challenges remain (see Rose et al. 2010). Particularly relevant issues to our case of possible depensatory dynamics are that feedbacks in end-to-end models need to be two-way allowing for dynamic interactions rather than one model component outputting to another without the other subcomponent being able to influence the first (Rose et al. 2010), and the existence and scale of different data sources for parameterisation is still problematic (Travers et al. 2007) which will certainly remain an issue surrounding the North Sea anchovy too.

The limited knowledge of ecology of North Sea anchovy means that relating our results to empirical situation remains tricky. Probably North Sea anchovy cannot be well represented by homogeneous environment otherwise the empirical local population present in the southern North sea (Boddeke & Vingerhoed 1996, Petitgas et al. 2012) would not stably exist in space. There must have been a reason why the population did not spread further out of that residual distribution area and a gradient or threshold of population abundance high to low existed in that area. So an environmental threshold probably existed in heterogeneous environment either due to population dynamic factors or environmental barriers to movement. The spatial scale of sampling and type of information we have on anchovy however precludes knowledge of whether this was rather gradual or steep gradient.

Indeed if a discontinuous abundance distribution is observed in a population, this need not be caused by depensation dynamics in a patchy or continuous environment. It can also come about through other mechanisms, e.g. simply a

barrier to movement or a discontinuous environment. That is to say that a discontinuous environmental gradient under warming (rather than continuous gradient we simulated) would lead to a discontinuous range expansion also under logistic growth. Therefore caution is needed to deduce processes from the empirical anchovy pattern observed or apply our results to the anchovy situation. The question what may have changed to allow the increase was probably answered by (Petitgas et al. 2012) by thermal windows and life cycle closure of additional population components in the North Sea. This is equivalent to a change in r growth rate in our model (rather than a change in A for instance).

Since depensation creates hysteresis in a system where two alternative abundance states can occur under a same set of environmental conditions, a resulting property is that once a change of state has occurred, it may be disproportionately difficult to return to the original state again (Scheffer et al. 2001, Scheffer & Carpenter 2003). So if North Sea temperature decreases again (as may be the case if AMO decline, suggested in ICES 2013, continues), anchovy may not retract to smaller area of distribution again which makes it interesting to speculate on possible impacts if other reduced populations (retracted to the North) do increase again because they themselves are not subject to density dependence. Then maybe food scarcity could ensue as too many fish in the sea.

In situations in other systems where exploitation plays a role for the species, it would be important to distinguish between the causes of depensation as management may be able to influence that particular cause more easily than the other depensation mechanisms if necessary.

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CHAPTER 7

Synthesis and General Discussion

The work carried out in the context of this thesis focused on elucidating mechanisms surrounding the European anchovy (*Engraulis encrasicolus*) increase in the North Sea. This species was previously found in high numbers in more southern European waters (Bay of Biscay, Mediterranean and Black Sea (Barange et al. 2009) and in low abundance along the Dutch coast (Boddeke & Vingerhoed 1996), but in the mid-1990s an increase all the way to Scotland was reported (Armstrong et al. 1999, Beare et al. 2004). Populations of small pelagic fish, such as anchovy, are known to fluctuate strongly in abundance and distribution in many different systems of the world, but the mechanisms for large-scale fluctuations are not understood (Lluch-Belda et al. 1989, Schwartzlose et al. 1999, Chavez et al. 2003). The origin of the North Sea anchovy population and the cause for its increase were unknown at the start of this study. Rising temperatures were suspected by some to be implicated in the increase, but as the North Sea plankton environment had been undergoing changes in composition, food requirements were another very likely candidate for causing for the anchovy increase.

Below is a synthesis schematic of the contents of this thesis outlining what knowledge has been gained about the North Sea anchovy increase.
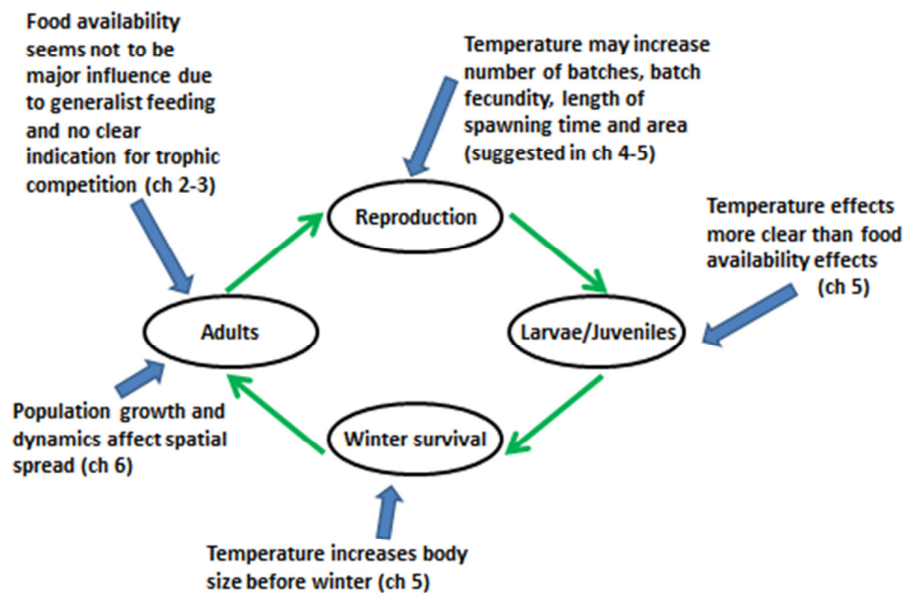
The origin of the North Sea population was addressed in much detail in **chapter 4** using a combination of methods and hypothesis 2 of the introduction (the North Sea anchovy increase is a result of the local anchovy population

increase in the North Sea) was supported clearly, including by genetic work using multiple markers that showed the North Sea anchovy population to be sufficiently homogeneous and distant from Bay of Biscay populations to be considered genetically distinct. The schematic shown above is represented as a closed life cycle within the North Sea since the population is no longer thought to be a possible result of migration or drift by other populations outside the North Sea.

In the following sections, the role of trophic interactions, temperature, and depensation in the anchovy increase are outlined, and finally an extension to possible management implications is made.

The role of food and trophic interactions in the anchovy increase (chapters 2-3, 5)

In combination, information from **chapters 2, 3 and 5** suggests a rather low importance of trophic interactions with zooplankton prey or other pelagic fish in having caused the anchovy increase in the North Sea.

Anchovy was found to be a zooplanktivore like in other systems, with copepods and other small crustaceans constituting a large part of its diet in several areas of the North Sea (**chapter 2**). Comparing the stomach contents of anchovies to those of sprat and herring, it appeared that while the consumed prey items were taxonomically similar, anchovy has a more general diet than the other two species. Dietary overlap between anchovy and herring was lower than for other species pairs (**chapter 3**).

Regarding hypothesis 1 (anchovy abundance in the North Sea has changed due to changes in food availability), the work presented in this thesis does not indicate that food availability was a main driver in the increase of anchovy in the North Sea. The increase of specific plankton species (as suggested for e.g. *Calanus helgolandicus,* Reid et al 2003) is unlikely to have been a mechanism for increased food availability since anchovy seems to be a generalist feeder and does not depend on particular prey species. Overall North Sea zooplankton biomass decreased (Pitois & Fox 2006) so that is also unlikely to have increased food availability to the a generalist feeder. Diet overlap with sprat and herring were not particularly high so the populations of these other small pelagics would probably not have a strong enough effect on anchovy populations either. Below I present several issues regarding the results and conclusions of the thesis that relate to food and trophic interactions and have not necessarily been mentioned in the chapters.

Surprisingly little up-to-date information was available on the diets of North Sea herring and sprat in the field, especially given herring's commercial importance and therefore crucial ecology in the management of the North Sea

system as a whole. There are, however, some existing data sets which may still offer additional information to existing literature on the topic. The DAPSTOM database, for instance (Pinnegar & Platts 2011), includes some anchovy, and "year of the stomach" data (from large scale sampling in 1981 and 1991 organised by the International Council for the Exploration of the Sea) for predatory fish might be analysed in more detail. The trophic linkages with anchovy, if any, and with potential competitors such as herring and sprat before the anchovy abundance increase could be identified (although see Daan et al. 1985 for an existing study of herring predation on cod eggs before anchovy increase). Multispecies models based on year of the stomach data were constructed but include herring and sprat as prey species and not anchovy. So several possible future tasks exist related to identifying more precisely and quantifying trophic linkages around anchovy, and this may give insight on anchovy trophic impacts before and during the observed plankton changes. The diet comparison in **chapter 3** revealed that anchovy consume fish eggs and larvae; there is thus a possibility of cannibalism and/or intraguild predation happening in the North Sea for this species and sprat and herring, as has been observed previously between anchovy and other clupeids in other systems (Szeinfeld 1991, Plounevez & Champalbert 2000, Takasuka et al. 2004). To reliably estimate the possible intraguild predation interactions, however, it is also crucial to identify which predators consume anchovy and possible competitors' eggs and larvae and this remains a challenge (Irigoien & de Roos 2011).

On the issue of spatial overlap between the potential competitors, it can be said that sprat, anchovy and juvenile herring do overlap in space in the southern North Sea (Engelhard et al. in press) but in a large-scale sampling program organised by GLOBEC Germany, they were only rarely found together at a smaller spatial scale (at the haul level, e.g. Raab et al 2012 **chapter 3**). This may be a coincidence, due to the timing of sampling, or it may be a result of spatial displacement between these species. As in any ecological question, causality is a difficult issue when observing a pattern. Are these species not found together because they don't require the same habitat, don't occupy the same niche, or are they not found together because they *do* have the same requirements and therefore must spread spatially in order to reduce resource competition? Ideally, a detailed analysis would be undertaken in the same geographical region on the same population at the same time of year of the three species' diets where they do overlap, and then again where they do not overlap spatially, followed by a comparison of the two situations. If dietary overlap is different between the two situations, this may be an indication of competitive displacement (Sturdevant et al. 2001).

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In the anchovy diet study, the grouping into categories used for the prey item identification affected the later result of which prey items drive the variability in stomach contents. This suggests that caution is necessary when choosing these categories. Without prior knowledge of the species ecology, the categories used are likely to be different taxonomic levels, in some way related to the identifiability of different prey items, or to the observer's scientific question. It would be best to know what criteria forms the basis for what the fish species feeds on (e.g. some may select large prey, or prey with fewer defence mechanisms), and then use categories related to that in comparison between species to assess possible trophic interference. The ingested prey items are limited by the anatomy of the fish species in question, by its gape size, for instance, and the gaps between the gill rakers which it uses to feed, and active selection plays a role when particulate feeding. Morphometric measurements of the feeding apparatus of anchovy, sprat and herring may help to elucidate differences in feeding between the species; these are underway. Moreover, our analysis did not account for differential evacuation rates related to species membership or environmental temperature conditions which may bias our results. Ideally one would have to use these to estimate the speed of digestion to see how representative the observed contents are.

Using a longer time span to study the importance of food in the anchovy increase in the spatio-temporal statistical modelling part of this thesis (**chapter 5**), we found that food did not covary well with the distribution and abundance of anchovy in the North Sea. First, the best representative measure of food was carefully selected by testing different zooplankton variables against each other in the generalised additive model of the anchovy catch per unit effort of the International Bottom Trawl Survey. This turned out to be total zooplankton biomass, which makes sense in light of the result that anchovy is a generalist planktivore. Then this measure was used in a model representing food and compared with a model for an alternative explanation, temperature, for the anchovy increase. The temperature model better explained the pattern of abundance and distribution of anchovy than the food model, suggesting temperature may be more important than food.

The generalised additive modelling study uses survey data from quarter 1 and food data from the previous year's quarter 3; we considered this to be most representative of when feeding occurs, since winter is the low zooplankton season and may not give a clear signal. However, it is possible that there is a crucial period in anchovy life when food plays an even more important role, and we have missed it by using this timing. Food-caused mortality may also occur before the size at which the IBTS gear starts catching anchovy. Young stages are very sensitive in fish, and small changes in growth or mortality may cause large changes in

recruitment of populations (Houde 1989). This can occur by match or mismatch in timing with food resources (Cushing 1990), or losses to the population by lack of spatial overlap with suitable environmental conditions or member vagrancy (Sinclair & Iles 1989) for example. Little data is available on young anchovy and their diet at the North Sea scale, although some local surveys catch them (Kanstinger & Peck 2009), and if diet composition is established for the young stages, the continuous plankton recorder (Warner & Hays 1994, Richardson et al. 2006) would provide relatively good spatio-temporally resolved information on small copepod stages probably consumed by young stages of anchovy.

Another major issue is that the food type may have stayed the same through the decades we used in the model, but the quality of the food may have changed, and our analysis does not take this into account. Indeed, since the dominance of dinoflagellates relative to diatoms in North Sea phytoplankton appears to have increased during the 1980s (McQuatters-Gollop et al. 2007a), and diatoms are considered to be a better food source than dinoflagellates. It is therefore possible that the food quality for grazing zooplankton may have decreased (in terms of energetic content for instance). Overall phytoplankton biomass appears to have increased in the same period however (Reid et al. 1998, McQuatters-Gollop et al. 2007b), which may make up for the relative decrease of diatoms.

The measure for food used in **chapter 5** represents zooplankton biomass but not zooplankton production, which would be a better indication of food availability. Indeed, using this biomass measure always leaves uncertainty about whether the measure represents production (availability) or what is left over, perhaps precisely because it *cannot* be used (i.e. unavailability). This is a complicating factor, but we assume for this time that biomass represents production. Production measures are usually based on model studies, and these also have their weak points, such as interpolation across large distances.

Based on the diet studies undertaken and the conclusion that anchovy is a rather generalist species, one mechanism for the importance of food in the anchovy increase, namely the increase of few prey species that anchovy preferentially targets, can be ruled out. This observation also supports the general hypothesis made about generalist species' responses to climate change, that they are expected to increase more than specialist species (Rijnsdorp et al. 2009).

Trophic interactions with higher trophic levels were not taken into account explicitly in this thesis although predators can have strong impacts on species abundances by predatory release (noted in other systems, e.g. Pace et al. 1999, Jackson et al. 2001, Frank et al. 2005, Myers et al. 2007). Predators are considered only very indirectly in **chapter 6** as providing a possible mechanism for depensatory population dynamics.

Food is clearly important for survival, including in anchovy (Zenitani et al. 2007). Small changes in growth and mortality at young fish stages can cause large population changes via recruitment (Houde 1989), and food is likely to affect growth along with temperature and thus be involved in population dynamics and hence the anchovy increase. So while food probably plays a role in the anchovy increase, its effect in our statistical model is simply overridden by the effect of temperature.

The role of temperature in the anchovy increase (chapters 4,5,6)

The combined information from **chapters 4, 5 and 6** suggests that the importance of temperature in the anchovy increase is high.

The idea that expanded thermal habitats were the reason for a localised resident anchovy population in the North Sea to increase and spread was put forward by Petitgas et al. (2012, **chapter 4**). Indeed, the thermal windows were estimated for the North Sea based on comparison with the Bay of Biscay, and it appears that through time, more days per year exceeded the spawning thresholds of 14°C and 16°C, and winter severity declined (Petitgas et al. 2012). Also, positive temperature anomalies and summer heat content of the southern North Sea increased (Alheit et al. 2012). Warmer temperatures may allow for early life to be more conducive to fish growth, as larger fish likely do better at withstanding both major mortality causes in winter: thermal stress and starvation.

The importance of the early life period of anchovy was then studied in **chapter 5**. If only an empirical study on spatio-temporal statistics of environmental variables versus anchovy abundance had been carried out, then we would not really know what exactly temperature stands for in the result that temperature is more important than food. Temperature affects many processes in biology, including metabolism and behaviour, e.g. reproduction or swimming speed. So it is important to get a more detailed picture of what exactly might be important about temperature. This is where knowledge from other systems and the literature comes in, and modelling studies can be useful. The dynamic energy budget approach with temperature and food model data input was used to simulate the growth of young anchovy in the first 6 months of life. An estimate was computed for each year between 1985 and 2007 of the proportion of the North Sea suitable for their growth to a given size. This habitat suitability index was found to be positively correlated to the catches of anchovy in the following year's IBTS survey (quarter 1), supporting the idea that early life growth may be one of the mechanisms that allowed for the increase. Thus hypothesis 3 (influence of temperature or food during early life allowed for the anchovy to increase) is supported in the sense that

early life appears to be crucial and may have determined the increase. The respective influence of temperature and food was addressed by generalised additive modelling in **chapter 5** and showed temperature to be a better explanation for anchovy dynamics. Moreover, temperature can affect winter survival and reproduction too, so it affects several life cycle processes, but disentangling food and temperature effects remains difficult when one considers all life stages and processes involved.

For the dynamic energy budget (DEB) model used to simulate young North Sea anchovy growth, we used physiological parameter estimates from the Bay of Biscay anchovy (Pecquerie et al. 2009, Freitas et al. 2010), but since parameter values in DEB are partly under genetic control (Kooijman 2010), and Bay of Biscay and North Sea anchovy form distinct populations (Zarraonaindia et al. 2012), this may be an oversimplification. Estimating parameters for North Sea anchovy would be a useful step to take if further DEB modelling is to be carried out on the North Sea population, e.g. for the reproduction of adults in this area.

Increased reproduction, rather than growth, is another mechanism that could possibly increase the anchovy population size. Anchovy is an indeterminate spawner, producing batches of eggs from the onset of warming rather than absolute temperature (Motos 1996). The length of the warm period is therefore influential in the total amount of batches produced. Moreover, batch fecundity increases with temperature. The window of suitable spawning temperatures for anchovy is thought to be about 3-4 months in the North Sea, representing an increase of ca. 2-6 weeks between 1989 and 2007 (Petitgas et al. 2012). This therefore makes for several possible ways to result in increased reproduction when temperatures increase: prolonged spawning period and increased number of eggs per reproductive event, and possibly a larger spawning area as well. When an expanded DEB model, including the reproductive module developed for the Bay of Biscay anchovy (Pecquerie et al. 2009), is parameterised for North Sea anchovy this question can be explored using the DEB coupled to biophysical environmental ERSEM data, again similar to work carried out in **chapter 5**. If the population is limited by having overfilled spawning areas, an increase in temperature that allows new areas of shallow water to attain the spawning temperature threshold is an additional pathway for higher reproduction.

The large-scale species alternations sometimes observed in other locations of the world between anchovy and sardine have been suggested to be a product of temperature's influence (Lluch-Belda et al. 1989, Chavez et al. 2003). Anchovy and co-occurring sardine in these systems experience the same temperature, so it may seem strange that such similar species have a very high population growth rate and the other very low, leading to the observed species alternations but if optimum

temperature for growth is different between the species (as suggested by Takasuka et al. 2007), large differences in population abundance may result. The question remains, however, of why anchovy increases in warm lower productivity periods in one area and in cold periods in other areas of the Pacific (Chavez et al. 2003). A short overview of how the scientific community perceived the issues in small pelagic fish management reveals that this, as it is for many scientific questions, is a very dynamic history (MacCall 2009b). The developments can be characterised into different periods, such as the "doubt period" (Fréon et al. 2005) in the last quarter of the 20th century, during which fisheries management, having witnessed a series of serious population collapses and management failures, had to acknowledge that insights into fish dynamics were not as straightforward as expected. As for small pelagic fish, question of what causes the large scale fluctuations was still not solved (Chavez et al. 2003). A recent synthesis framework takes into account physical, biological, and behavioural mechanisms and multispecies interactions (MacCall 2009a). As the author points out, progress in the field of explaining the sardine-anchovy fluctuations observed across the world can be seen in that no single factor is expected anymore to be the explanation for the empirical patterns. A recent study on complex systems' dynamics used the anchovy-sardine example in its exploration of mapping strength and direction of causal linkages between different time series to determine whether these belong to the same dynamic system or not. The conclusion was that anchovy and sardine time series were not causally related but both strongly linked to temperature (Sugihara et al. 2012). But both this and other studies should take into account that no more than two subsequent episodes of high abundance have been observed in any particular system, so basing any conclusion on such a small sample size is difficult (MacCall 2009a).

There is a move towards increasing complexity in modelling the effects of fishing and climate on fish via end-to-end models which incorporate different trophic levels, ecological and physical-chemical processes (Travers et al. 2007, Rose et al. 2010). While acknowledging the complexity of the answer to any one question about a fish species in the sea is a useful step forward, the approach of end-to-end modelling remains with some challenges (Rose et al. 2010). Perhaps this is one response to the "doubt period", to become increasingly modelling oriented during a time when computing power was ever increasing and seemed very promising. But the complexity of these end-to-end models means that calibration and validation need to be very thorough, and at the moment their performance and robustness is too uncertain to be used in a forecasting way in management. Integrating across different spatial (and temporal) scales is also difficult as available data for parameterisation is often at different scales and

different sub-modules are modelled at different spatial (and temporal) scales. Linking models that were developed separately for e.g. higher and lower trophic levels can be done in different ways and often only those parts that must link with the next model are changed, rather than considering the pathways between the different model components and linking them in a way that is not biased towards one component of the model (Shin et al. 2010). Another challenge that is particularly relevant in the context of **chapter 6** of this thesis is that most end-to-end models have only one-way forcing i.e. do not include feedbacks and thus keep a one-way information transfer in the system, non-linearities are not taken into account.

The role of depensation in the anchovy increase (chapter 6)

The role of depensation, also referred to as positive density dependence or demographic Allee effects, in the anchovy increase remains a major unknown, since we have no empirical test for whether depensation does or does not occur in North Sea anchovy populations.

What is clear, however, is that depensation in spatial fish populations can play an important role in determining the course of a range expansion. In **chapter 6** we explore how the strength of depensation, combined with the mobility and growth of the species, affects the expansion of a simulated local population in a spatial system, which could represent anchovy in the North Sea. We find that, compared to logistic growth, spatial spread under depensation results in much sharper transition between high and low abundance areas, so-called "range pinning" (Keitt et al. 2001). The effect of dispersal is very important, especially in patchy environments, as it determines whether new patches are reached at all and whether there is enough input of arriving population to overcome the depensation effect. This indicates that depensation leads to more accentuated dynamics in a spatial spread of a local population (hypothesis 4).

These results may help to explain why subtle environmental changes may trigger drastic fish abundance changes as, in situations with positive feedbacks and possible alternative states, local shifts to a new state can spread through space (van de Leemput et al. in review). If depensation occurs, the effect of temperature on growth may be exacerbated by population dynamic processes of depensation to cause sudden discontinuous shifts in population range: a slight increase in growth may be the small amount of extra population needed to colonise an adjacent area where depensation was previously too strong for populations to persist. The situation then approaches metapopulation dynamics (Hanski 1998). In addition to the generally low empirical information on anchovy, depensation is notoriously difficult to measure in fish stocks. And although a large scale meta-analysis

revealed indications for depensation in only few stocks, still the idea was not dismissed by the experienced fisheries scientist author (Myers 1998).

The mechanisms potentially causing depensation in small pelagic fish are likely to be occurring in the North Sea anchovy population. We found that anchovy consumes fish eggs and larvae thus cannibalism and/or intraguild predation occurs in this species and in sprat and herring. On the predator pit, little information is available since anchovy is a relatively new population in the North Sea and it is uncertain which species consume anchovy, However, saithe, mackerel and horse mackerel seem likely candidates as these are main predators for herring and sprat. As for the school trap mechanisms (Bakun & Cury 1999), a first step to find out whether this occurs is to analyse in detail acoustic records in the North Sea and/or survey areas with anchovy. Influential factors in determining the strength of the school trap, such as optimal swimming speed, temperature or depth of the school, may vary but this would be rather complex to ascertain empirically. Perhaps a comparison of anchovy condition from mixed schools and pure anchovy schools can provide an indirect way to estimate impact of school mixing on survival.

The anchovy range expansion is one in a series of expansions and contractions throughout the last century: anchovy had increased its abundance in the North Sea in earlier times (Aurich 1950, 1953), and at least the current increase is a North Sea population exhibiting dynamic abundance changes (Petitgas et al. 2012). Nowadays, range changes related to climate change (Perry et al. 2005) as well as dramatic population collapses (Myers & Worm 2003) are reported in high profile journals and thus receive much attention. In contrast, a possible future decrease in abundance may not be reported as prominently if the species is not highly commercialized and economically important - which does not yet seem to be the case for North Sea anchovy, although some fisheries do target anchovy (Cheung et al. 2012).

Mechanisms underlying the North Sea anchovy increase may or may not be involved in causing a subsequent future range decrease. If depensation is occurring, then decreasing growth rates would not lead to a linear range contraction again due to the hysteresis involved. While we do not expect climate change to be a temporary phenomenon, it is possible that the Atlantic Multidecadal Oscillation phases lead to temporary cooling again (as suggested by ICES 2013), and it will be interesting to see what will happen under such circumstances.

Generally speaking, in fish stocks where depensation is thought to play a role, hysteresis may lead to non-linear and therefore possibly unexpected behaviour, since mostly linearity is still assumed in the minds of people, including fisheries managers and assessors—though it is doubtful that nonlinear behaviour would be recorded or identified as such, due to the vast number of other factors likely to be

affecting the stock anyway. So where a temperature increase above a certain threshold may lead to range expansion, decreasing temperatures may not necessarily lead to contraction again. In stocks where exploitation creates a demographic Allee effect, on the other hand, i.e. keeps the population at low levels when low, because it only targets the species above a certain abundance, reducing the exploitation may remove this Allee effect.

North Sea anchovies, regime shifts and management

One limitation of North Sea anchovy studies is the availability of empirical data in general, because the survey that regularly catches anchovy (the International Bottom Trawl Survey) uses sub-optimal gear for catching pelagic fish. Its representativeness may thus be questioned, as it was by several reviewers of papers contained in this thesis. The survey type more suited to assessing distribution and abundance of pelagic schooling fish (acoustic surveys), however, due to it having initially been designed for herring, is employed by ICES in the North Sea only during summertime, when anchovies are known to be inshore and spawning (Ré 1996, Alheit et al. 2007). It is not uncommon for surveys to target only certain pelagic species, despite many others being present in the same area (Iglesias et al. 2003).

These data limitations are a reason for employing ecological models in the study of this species in the North Sea. And while models are sometimes received with hostility by pure empiricists, if there is a balance between use of theoretical and empirical evidence to address a scientific question, the result is likely to be more robust. Accepted terms like intraguild predation or ecosystems are also models, and are helpful in conceptualising the world.

If warming continues, it will likely have further climate change effects, on plankton; on summer growth of early life anchovy due to the warmth of German Bight spawning area; on reproductive output by mature adults, since anchovy is an indeterminate patch spawner; and on overwinter survival, assuming winters get warmer too. Increasing growth rates would affect the spatial area of distribution of anchovy (**chapter 6**) although it appears that by now anchovy has reached much of the North Sea anyway (Cheung et al. 2012, Petitgas et al. 2012). While in early years commercial fishing vessels didn't know what to do with anchovy by-catches, a commercial fishery is now establishing itself, with fisheries targeting anchovies directly since around 2007 (MCCIP, Cheung et al. 2012). It might be time, then, to include anchovy in multispecies models and fisheries advice.

In this thesis we almost exclusively consider adult anchovy data; it would have been helpful to know more about the life cycle earlier in the process. In paper 4 we

address early life stages, but though this is starting to change, little is known empirically on young anchovy in the North Sea (Kanstinger & Peck 2009, Alheit et al. 2012). With a more complete picture of the biology of various life stages of anchovy in the North Sea, maybe one could address in more detail its life cycle closure and limiting effects, if any, on current population growth, e.g. by analysing recruitment variability and environmental variables, since species at the edge of their range seem to be good candidates for such correlations (Myers 1998). The years 2002-3 seem to have been very good for anchovy recruitment, at least in Meldorf Bight, Germany, for example (Alheit et al. 2012). If climate warming continues and temperature increases growth rate as we suspect, the increase in population will continue, maybe to a level where fisheries switch to targeting the species. This is already the case to some extent, and the anchovy fishery is unregulated; perhaps when fishery limitations are put in place, some balance can be achieved between productivity and harvest.

Generally, one can say that using several different approaches in this thesis has the strength of giving a more complete overview, but the resulting weakness is that everything appears to remain a bit superficial. This is a common problem for interdisciplinary studies at a larger scale. So we did not clearly answer the question of whether the anchovy increase reflected a 'regime shift' in the North Sea, for instance. However, if we use the definition of abundance regimes, then for sure 'yes' is the answer, the mid 1990s increase was probably a relatively stable 'anchovy regime' of the North Sea. However, since the amplitude of population fluctuations in this system are so much lower than other anchovy abundance regimes, e.g. in the Benguela, using this terminology may be misleading.

A review of different uses of the term in the marine realm (de Young et al 2004) shows that interpretations vary between authors and the focus can be on driving variables (e.g. climate), the ecological characteristics of phases or the stability properties of the system, and concludes that compared to freshwater systems, definitions of marine regime shifts remain broad and ecologically imprecise. Marine fish recruitment 'phase shifts' have also been described as being distinct from other uses of the term in marine systems which usually refer to "ecosystem-wide changes that occur in response to meteorological forcing" (Duffy-Anderson et al 2005). These authors consider that phases refer to the state of the system (or one of the attributes of the system) while regimes refer to the driving factors mediating the changes in system state and emphasize that for fish recruitment, these would be more than just climatic factors. The dynamics of regime shifts can further be classified into smooth, abrupt/non-linear and discontinuous (with hysteresis; see Lees et al 2006).

Regime shifts probably happen all the time at some level of the considered system and 'identifying' regime shifts is just a nomenclature exercise, an arbitrary choice of when to call which observation of change a 'regime shift'. Different definitions of the term alone make that possible, and when one starts looking at different scales of resolution this is even more so. Scientists/academics are trained in categorising and analytical skills, so if previous studies laid out their points or story in a convincing way, e.g. about the plankton regime shift in the North Sea, then it is likely that more colleagues will take on a similar opinion and, out of scientific curiosity, begin searching for more evidence or possible causal mechanisms for that particular regime shift and time period. Thus they may miss potential changes at other times purely as a result of limited analysis time and attention by any particular individual. This will probably go on until the next overhaul of opinion occurs, possibly when enough inconsistencies or voices of doubt or alternative scenarios have been raised, much as described by Kuhn (2012) but on a smaller scale - a mini scientific revolution per North Sea regime shift that unravels. In a way it then doesn't really matter whether this observed and highly studied regime shift (such as the North Sea regime shift of the late 1980s) did or did not happen, or whether it was more or less influential in other components of the ecosystem than a similar or weaker observed change, or simply a less investigated change in the plankton. Moreover, the expectation that the environment is stable, which is a prerequisite for the big sudden regime shift idea (implying that things are quite stable and then a regime shift disturbs this stability), or the assumption that a relationship between a species and its environment or other species is static, is out of date. But the current paradigm still seems to be that if one could understand a relationship and then base oneself on that forever, that would be best. This is of course a *de facto* necessity due to the impossibility of measuring and studying everything in real time in ecosystems, especially marine. So we might base ourselves on herring diet studies in the North Sea from 20 years ago to infer what they eat now. However, the only sure thing is change—both ecology and evolution can operate at relatively rapid levels in the perception scale (whether that may be days or years) of humans, since that's what we observers are. The hope at both small (e.g. individual) and large (e.g. population) scale is that an organism can keep up with the changes in its environment. Anchovy has apparently managed to maintain a remnant population in the North Sea and is in a phase of expansion. This may be great for the population for now, but who knows what will come next and whether a contraction will happen again in the near future.

Managing changing systems

The regime shift concept (I intend abrupt, discontinuous changes in system state) can be useful, for instance when anthropocentrically viewing ecosystems as providing services which are necessary to humans (Millennium Ecosystem Assessment, 2005) such as food, including fish. Indeed some resources and resulting services are more critical to humans' survival and well-being than others, so reflection on their precarious nature can promote a focus on which variables to monitor and try to keep relatively stable via management.

Detecting pending or ongoing regime shifts is a popular topic at the moment (Dakos et al 2009, Guttal & Jayaprakash 2008, Scheffer et al 2009) as regime shifts can cause switches between ecosystem states which are sometimes perceived by the society exploiting the ecosystem resources or services as 'desirable' or 'undesirable' (e.g. Baltic cod, urchin kelp forests, coral reefs, anchoveta). When a shift to what is perceived as a less 'desirable' state has been detected in an area and is considered likely to propagate then assuming society deems intervention necessary and appropriate, two approaches can be taken: prevention and mitigation/adaptation.

Despite the fact that already decades ago, the maximum sustainable yield (MSY) concept was considered obsolete (Larkin 1977), it is still a prominent concept in fisheries management. The World Summit on Sustainable Development (2002) called for rebuilding stocks to MSY level and the Common Fisheries Policy of the European Union bases itself on it. Many fisheries in the North Sea aim for staying below a given fishing effort (F_{msy}) at MSY. Management proceeds by estimating the spawning stock biomass, i.e. the current adult population biomass. Then the estimated amount of offspring is calculated based on a stock-recruitment relationship and survey information. A proportion of the total biomass can then be culled/fished so as to keep a certain amount of biomass in the sea that would allow for maximum sustainable yield. Measures in place to regulate the amount of fishing that happens are usually total allowable catch (TAC) levels which have to be negotiated once per year at the EU level, along with technical measures and spatial regulations. In current fisheries management, often steady state methodologies from mid last century are still being used (as pointed out by Bakun & Broad 2003). Moreover, species are mostly managed in a single-species context, although ecosystem based fisheries management is now the approach that should be implemented according to European policies. European policies like the Common Fisheries Policy and Marine Strategy Framework Directive (MSFD, EU Commission, 2008) rely on MSY as part of their strategy. Although the MFSD also includes good environmental status (GES, see criteria in EU Commission, 2010) as an aim to be achieved by 2020 and which includes more general targets like

maintaining biological diversity (descriptor 1), keeping the stock within safe biological limits as shown by age and size distribution (descriptor 3) and maintaining food web structure (descriptor 4).

Ecological understanding of fish populations can benefit management by giving insight into processes that regulate population biomass or location; which thus also influence other stocks and food web components too.

The question of how the mobility of organisms affects the spatial spread of a regime shift is of particular relevance when considering small pelagics as these are the first actively mobile level in the marine trophic web (as pointed out by Bakun 2006). They are thus the first element that can pass environmental information between spatial areas, probably making them important agents in spreading or limiting local regime shifts. In terrestrial systems, patterns of organisms' distribution resulting from positive feedback mechanisms on growth have been found to provide recognizable build-up sequences leading to the regime shift, actually representing a good indicator that a system is on its way to change (Rietkerk et al. 2004). The studied system exhibits a sequence of different levels of vegetation patchiness, and this recognisable build-up of self-organised patchiness can thus help in predicting regime shifts. But in marine systems, organisms' distribution is difficult to monitor, because they are much less visually accessible. To our knowledge, no such attempt at detecting self-organised patterns for predicting regime shifts has yet been made for marine organisms or processes. If it is recognized that a system is on its way to or nearing change, it may be possible to modify certain stressors to prevent the shift from happening. Small pelagics may be possible indicator species to aid detection of biological regime shifts that are underway but undetected (e.g. recruitment failure but high enough standing stock biomass, Payne et al. 2009). They respond closely to changes in zooplankton and phytoplankton which are highly influenced by climatic variability, but are much more easily monitored than plankton because of regular surveys and large fishing fleets in contact with them. Therefore small pelagics can be indicators of a past climatic regime shift that has propagated through the whole community, from the primary producers up to zooplankton and other secondary consumers. A strong change in pelagic populations may or may not be the result of a climatic regime shift, but nevertheless it tells of a highly increased risk that other community components, such as the commercially valuable higher trophic levels, will be affected in the near future.

If the regime shift cannot be prevented or delayed, early detection is crucial in providing time to consider how to adjust to the new regime thus making for a smoother and faster socio-economic and exploitation response to the new state. This is a process we have little experience with so far as most management

strategies implicitly assume the stability of ecosystems, as does fisheries management for example (as pointed out by Hughes et al. 2005). Even if we had perfect insight into small pelagics' abundance dynamics and could predict population collapses before they happen, due to the reactivity of the management systems, it would not be possible to keep their biomass at the desired high levels. Hence the suggestion by Bakun & Broad (2003) for a more flexible management structure. Indeed, if considering regime shifts as an integral part of ecological systems, a different kind of ecosystem management that takes this into account may be needed. First steps in this direction showed that regime-specific harvesting strategies, which follow the regimes' relative productivity, have the better balance of benefits and trade-offs when considering time scales longer than the duration of only one regime (King & McFarlane 2006). Other mitigation effects can be made by restoration programmes but these can often be too little too late (i.e. there is a mismatch between restoration efforts and scale of disturbance; Hughes et al. 2005).

Generally speaking, managing human impacts in order to maintain the ecosystem in a desired state is the goal of current fisheries management. If the system is regulated by wasp-waist control it is important to prevent too strong stressing impacts on these species since these may have a disproportionate effect on the rest of the ecosystem. If the main stressor, e.g. climate, cannot be influenced (or influence is not considered sufficient), other factors can be managed as well, such as exploitation or pollution, so that overall resilience is maintained.

Resilience can be defined as the capacity of a system to absorb disturbances and reorganize while undergoing change so as to retain essentially the same function, structure and feedbacks (Folke et al. 2004; see also Holling 1973). Four characteristics make up a system's resilience: the width of the domains of attraction of different ecosystem states (latitude), their depth (resistance), how close the current state is to a switching threshold (precariousness) and the level of cross-scale relationships (panarchy). Reductions in biological diversity can lower this resilience through lowering diversity in populations, in functional groups and in responses to environmental conditions (Elmqvist et al. 2003, Folke et al. 2004) and it has been suggested that maintaining resilience should be the focus of sustainable management strategies (Scheffer et al. 2001). Small pelagic species experience highly variable environments and boom and bust abundance cycles are the norm. Such highly variable stocks are already at high risk of local extinctions due to stochastic processes (thus decreasing the diversity within species and populations), but fishing also increases the risk that traits necessary to a population's response diversity are lost from the population. Fishing populations also inherently increases variability in abundance (Hsieh et al. 2006). The age-truncation of populations that results from fishing (which is highly selective on large and hence old individuals)

leads to more unstable population dynamics, i.e. the population dynamical processes involved become more non-linear, possibly because of increased growth rates (Andersen et al. 2009). Increased growth rates can originate from fisheries-induced competitive release, lowered cannibalism or evolution. Fisheries-induced evolution has been demonstrated in several stocks (Jørgensen et al. 2007), and makes the changed growth rates more difficult to reverse (Stenseth & Rouyer 2008). Another possibility however is that replacements within guilds or functional groups to species of higher growth rates occur, which could be the case with anchovy in the North Sea replacing slightly slower growing planktivores such as herring or sprat. By virtue of its high growth rate, anchovy might therefore increase non-linear behaviour and hence the risk of regime shifts in the North Sea ecosystem.

I think now is an interesting time when it appears that the notion of rapid changes, transitions, tipping points is trickling down into the awareness of the general public (at least media is full of it). I am curious what and whether this will change anything in the daily lives and actions of people with regard to human behaviour towards the environment in general since we appear to be living in an era of overuse of natural environment (Rockstrom et al. 2009).

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SUMMARY

Small pelagic fish populations are of high socio-economic importance in several marine systems of the world. They are known for their strong fluctuations in abundance, for which the mechanisms are not always understood. European anchovy (*Engraulis encrasicolus*) increased its population in the North Sea starting in the mid-1990s while previously it was found in more southern waters in Europe. The reasons for this increase were unknown. A few years earlier, major changes in the plankton community had been reported, and climate change was warming North Sea waters at the same time. Therefore changed food availability (resulting from plankton changes) or changed habitat availability (due to warmer waters) seemed likely candidate explanations for the increase and expansion into more northern areas by a European planktivorous fish species with southern affiliations (**chapter 1**).

Due to its relative novelty in the North Sea, little was known about the ecology of the species in this system. Therefore basic information on diet composition and life cycle information had to be collected to complement the survey data which documented the population increase. In this thesis, the anchovy increase in the North Sea was investigated with, at first, an emphasis on trophic mechanisms but expanding into other areas as it advanced.

In chapter 2, we first describe the food of North Sea anchovy, since it had not been previously analysed in this system. Although there was some spatial variation in stomach contents, the species consumed zooplankton just like in other parts of its range, and copepods formed a major part of the observed diet. **In chapter 3**, the stomach contents of anchovy were compared to its likely competitors sprat and herring, both small pelagic planktivorous species like anchovy. Previous diet information on herring and sprat was sparse in time and space so this study which first described the stomach contents of co-occurring individuals (i.e. from the same haul) of these three species is likely the most recently appropriate accurate estimate of dietary overlap. Anchovy was found to be more general in its diet than sprat than herring, as the latter focused on fewer prey items to form most of its observed diet. The dietary overlap of each species pair indicated that anchovy and herring had low dietary overlap, suggesting they are not the most likely trophic competitors. It

nevertheless remains possible that under changing plankton communities anchovy has a competitive advantage purely because of its generalist diet.

The anchovy increase was then approached by an interdisciplinary group of marine scientists including myself who **in chapter 4** considered three possible pathways to the anchovy increase: expansion of a local population, or invasion by an external population via larval drift or by active adult migration. Information from the North Sea (empirical survey data and physical oceanographic model data) and the Bay of Biscay (larval drift models and more in depth ecological understanding) indicated that the former explanation was the most likely and that an expansion of thermal habitats allowed the North Sea anchovy to expand its population from a residual area of distribution located in the southern North Sea. This may have been due to increased overwinter survival, reproduction, or early life growth.

This latter idea was further built upon **in chapter 5**, in which the focus lay on the first growing season of anchovy. Early life growth was modelled using an ecophysiological modelling approach and ecosystem model data on food availability and temperature, two major determinants of fish early life growth. Temporal development of the growth potential of young anchovy was found to correspond well to the abundance increase in surveys, i.e. the better the modelled early life growth, the higher the abundance in survey catches in the next following season. Adult distribution as documented by the international bottom trawl survey was related to environmental variables representing food availability and temperature. Temperature seemed to better explain the occurrence and abundance of anchovy throughout the North Sea in past decades than various measures of food availability chosen based on insights from earlier chapters.

The spatial spread of anchovy was further investigated **in chapter 6** using a theoretical model that included so-called 'depensation', or positive density-dependence. Several mechanisms in small schooling fish may cause such a characteristic in its population dynamics and although none of these were empirically investigated in anchovy, we wanted to represent the consequences of using this assumption rather than the more commonly used assumption of logistic growth (where population growth is always positive and becomes null when maximum carrying capacity of the system is reached). We found that the spread of a localized anchovy population depended on the intensity of depensation and dispersal characteristics of the population. Therefore an investigation of the possible depensation-causing mechanisms for North Sea anchovy or in other small

schooling fish populations would be highly relevant to understand the range changes in these populations.

In conclusion, the North Sea anchovy expansion is likely to have been made possible through a combination of its generalist feeding behaviour, which may avoid limitation due to food scarcity, and by increased temperatures, making for improved population growth conditions for young fish, and possibly through positively influencing overwinter survival and reproduction. The possibility for depensatory dynamics in the population exists and remains a further topic of investigation. This and other topics of broader interest are discussed **in chapter 7.**

This doctoral thesis thus contributes to an increased understanding of the ecology of anchovy in the North Sea, its diet (**chapter 2**) and potential trophic interactions (**chapter 3**), but also the likely origin of the expanded population (**chapter 4**), important environmental variables in the increase (**chapter 5**) and the population dynamic properties affecting this type of range expansion (**chapter 6**).

These insights can support studies of small pelagic fish in other systems of the world and may support fisheries scientists who wish to integrate more ecology into their assessments and management practice.

SAMENVATTING (DUTCH SUMMARY)

Kleine pelagische vispopulaties zijn wereldwijd van groot sociaal-economisch belang voor mariene systemen. Ze staan bekend om hun sterke schommelingen in aantallen, een verschijnsel waarvan het achterliggende mechanisme niet altijd duidelijk is. Sinds het midden van de jaren 90 stijgt de populatie van Europese ansjovis (*Engraulis encrasicolus*), een verschijnsel wat al eerder werd waargenomen in de meer zuidelijke Europese wateren. De redenen voor deze stijging waren onbekend. Wel werden grote veranderingen in de plankton levensgemeenschappen waargenomen en tegelijkertijd resulteerde klimaatverandering in de opwarming van de Noordzee. Het daardoor veranderde voedselaanbod (als gevolg van veranderingen in het aanwezige plankton) en het veranderde beschikbare leefgebied (door de warmere wateren) leken waarschijnlijke verklaringen voor de toename en uitbreiding van deze normaalgesproken in zuidelijke wateren voorkomende Europese planktonetende vissoort naar meer noordelijke gebieden (**hoofdstuk 1**).

Als relatieve nieuwkomer was er weinig bekend over de ecologie van Europese ansjovis in de Noordzee. Daarom was het voor het onderzoek naar de toename van de populatie nodig basisinformatie over voedselsamenstelling en levenscyclus te verzamelen. In dit proefschrift is daarom de toename van ansjovis in de Noordzee onderzocht, aanvankelijk met de nadruk op trofische mechanismen, maar later is dit uitgebreid met andere onderzoeksthema's.

In **hoofdstuk 2** beschrijven we eerst het voedsel van ansjovis in de Noordzee omdat dit voor dit ecosysteem nog niet eerder was geanalyseerd. Alhoewel er enige geografische variatie was in de maaginhoud, consumeerde de soort zoöplankton, net als in zijn andere verspreidingsgebieden. Copepoden waren een belangrijk onderdeel van het waargenomen dieet. In **hoofdstuk 3** werd de maaginhoud van ansjovis vergeleken met die van haar meest waarschijnlijke concurrenten: sprot en haring, beide net als ansjovis kleine, pelagische, planktonetende soorten. Informatie over het dieet van haring en sprot en hoe deze varieërt in ruimte en tijd was schaars. Deze studie beschrijft als eerste de maaginhoud van tegelijkertijd voorkomende individuen (bijvoorbeeld uit dezelfde school) van deze soorten en is daarmee waarschijnlijk de meest recente en acurate schatting van de overlap in hun dieet. Hierbij bleek dat ansjovis minder kieskeurig (en dus meer generalistisch) is

in zijn dieet dan sprot en haring, waarbij minder prooitypen de hoofdmoot van hun dieet uitmaken. De overlap in dieet van elke soortcombinatie geeft aan dat ansjovis en haring weinig overlap in dieet hebben, wat suggereert dat ze waarschijnlijke geen trofische concurrenten zijn. Het blijft echter mogelijk dat met de veranderende planktongemeenschap ansjovis in het voordeel is, puur vanwege zijn generalistische dieet.

De toename van ansjovis werd vervolgens onderzocht door een interdiscipinaire groep mariene wetenschappers, waaronder mijzelf, die in **hoofdstuk 4** drie verschillende scenarios voor de toename van ansjovis bekeek: 1) uitbreiding van een lokale gemeenschap, 2) invasie door een externe populatie via larvale drift, of 3) door actieve migratie van volwassen exemplaren. Informatie vanuit de Noordzee (empirische onderzoeksgegevens en fysisch-oceanografische modelresultaten) en de Golf van Biskaje (larvale drift modellen en een meer diepgaande kennis over het ecologisch functioneren van dit systeem) geeft aan dat de eerste verklaring de meest waarschijnlijke is, en dat een toename van thermische habitats de ansjovis de mogelijkheid heeft gegeven haar populatie uit te breiden vanuit een overgebleven verspreidingsgebied in de zuidelijke Noordzee. Dit kan gekomen zijn door een verhoogde overlevingskans na de winter, door verhoogde reproductie, of door een toename van de jonge aanwas.

Dit laatste idee is verder onderzocht in **hoofdstuk 5**, waarin de nadruk ligt op het eerste groeiseizoen van ansjovis. De groei van jonge ansjovis is gemodelleerd met behulp van een ecofysiologische modelbenadering en ecosysteem modelgegevens van de twee belangrijkste determinanten van vroege groei: voedselbeschikbaarheid en temperatuur. De ontwikkeling van het groeipotentieel van jonge ansjovis in de tijd kwam goed overeen met de toename die is waargenomen in veldonderzoeken. Dat wil zeggen, hoe sterker de vroege groei in de modellen, hoe hoger de aantallen in onderzoeksvangsten in het seizoen daarop. De verspreiding van volwassen exemplaren zoals gedocumenteerd in veldgegevens van het internationale bodemtrawlnettenonderzoek liet een relatie zien met omgevingsvariabelen die voedselbeschikbaarheid en temperatuur weergeven. Temperatuur lijkt de aanwezigheid en abundantie van ansjovis in de Noordzee over de laatste decennia beter te verklaren dan verscheidene maatstaven van voedselbeschikbaarheid die gekozen waren op basis van in eerdere hoofdstukken opgedane inzichten.

De ruimtelijke verspreiding van ansjovis was verder onderzocht in **hoofdstuk 6** met een theoretisch model dat gebruik maakt van zogenaamde 'depensatie', of

positieve populatie afhankelijkheid. Verscheidene mechanismen in kleine scholende vissen kunnen een dergelijke eigenschap in de populatiedynamiek veroorzaken en alhoewel geen van deze empirisch zijn onderzocht voor ansjovis, willen we laten zien wat de consequenties van deze aanname zijn in plaats van de meer algemeen gebruikte aanname van logistische groei (waarbij populatiegroei altijd positief is en stabiliseert wanneer de maximale draagkracht van het systeem is bereikt). We vonden dat de verspreiding van een lokale ansjovispopulatie afhangt van de intensiteit van depensatie en verspreidingskenmerken van de populatie. Het zou daarom zeer relevant zijn om te onderzoeken wat de mogelijke depensatie veroorzakende mechanismen zijn voor de Noordzee ansjovis en andere kleine scholende vispopulaties om de veranderingen in verspreidingsgebied van deze populaties te begrijpen.

Concluderend, de toename van de Noordzee ansjovis is zeer waarschijnlijk mogelijk gemaakt door een combinatie van zijn generalistische fourageergedrag, waardoor populatiekrimp door voedselschaarse vermeden kan worden, en door hogere temperaturen, die populatiegroei van jonge vis bevorderen, en mogelijk door het positief beinvloeden van overwinteringsoverleving en voortplanting. De mogelijkheid voor depensatiedynamiek in de populatie bestaat en blijft een verder onderzoeksonderwerp. Dit en andere onderwerpen van breder belang worden besproken in **hoofdstuk 7**.

Dit proefschrift draagt bij aan een beter begrip van ansjovisecologie in de Noordzee, het voedsel van de ansjovis (**hoofdstuk 2**) en mogelijke trofische interacties (**hoofdstuk 3**), maar ook de waarschijnlijke oorzaak van de uitbreiding van het leefgebied van de populatie (**hoofdstuk 4**), belangrijke omgevingsvariabelen voor deze uitbreiding (**hoofdstuk 5**) en populatiedynamica die dit type van leefgebiedsuitbreiding bepalen (**hoofdstuk 6**). Deze inzichten kunnen studies naar de ecologie van kleine pelagische vis in andere systemen van de wereld ondersteunen en kan visserijwetenschappers ondersteunen die meer ecologie willen integreren in hun beoordelingen en beleidsmaatregelen.

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ABOUT THE AUTHOR

Kristina is a citizen of several countries (CDN, DE, USA) and completed high school in Strasbourg, France, before initiating her studies at the University of St Andrews, Scotland. She went to Trieste, Italy, on an Erasmus exchange year as part of her first degree, in Marine and Environmental Biology (BSc, 2004). After a summer of guiding whale watching tourists in Norway, she moved to York, England where she worked on projects related to benthic ecology and marine protected areas as part of her MRes in Ecology and Environmental Management (MRes, 2005). Its last component, a project on jellyfish trophic ecology, was completed at Shannon Point Marine Centre in Washington State. A short stay at the Marine Conservation Biology Institute in Washington DC allowed her to work on policy topics, such as trawling legislation. She then spent some time in Iceland as part of an EU project on fisheries-induced evolution, which led her to Lund University, Sweden, and later on this PhD position at the University of Wageningen and IMARES. Along with the work reported in this thesis, Kristina has been involved in various activities related to biodiversity and ecosystems including a summer school (ALTER-Net, Peyresq, France), science-society (Positive Visions for Biodiversity, Brussels, Belgium) and science-policy meetings (stakeholder at the Intergovernmental Platform on Biodiversity and Ecosystem Services' first plenary, Bonn, Germany), which she hopes to carry on combining with her marine ecology interests in the future.

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