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Report

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Desk Study on the transport of larval herring in the southern North Sea (Downs herring).

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Summary

Current understanding about the drift and behaviour of larval herring is reviewed with particular emphasis on the Downs herring and the development of a model for larval transport. Downs herring are the component of North Sea herring that spawn in the southern North Sea and English Channel. Generally the larvae of the Downs herring drift east towards the German Bight and Skagerrak, but this is dependent on the meteorological forcing of local hydrography. Whilst it has been possible to model the broad trajectory of the larvae, modelling the yearly variability in drift patterns has proved difficult. The drift of the larvae and post-larvae does take them close to the Dutch coast in some years (as shown by survey results). It is during this phase of their life cycle (from larvae to metamorphosis) that the strength of the recruiting year class is determined. The larvae show vertical migration as they grow and also begin to aggregate after metamorphosis. There is no evidence in the primary literature for triggers for directional movement (such as salinity or depth of water column). There is no work published to date, on the impact of anthropogenic disruption of larval drift on the productivity of Downs herring or on the fishery.

Samenvatting

De huidige kennis over de driftpatronen en het gedrag van larvale haring is onderzocht, waarbij gekeken is naar kanaalharing (Downs herring) en het ontwikkelen van een model om larvale driftpatronen te beschrijven. Kanaalharing is het deel van Noordzee haringpopulatie dat in het zuidelijk deel van de Noordzee en het Kanaal paait. Over het algemeen driften larvale kanaalharingen oostelijk richting de Duitse Bocht en het Skagerrak, maar dit is afhankelijk van de zeestromen. Het is mogelijk om het algemene traject te modelleren dat larvale kanaalharing afleggen, maar jaarlijkse variaties hierin zijn moeilijk te modelleren. In sommige jaren komen de larven en post-larven dicht bij de Nederlandse kust (gegevens afkomstig van surveys). Gedurende deze levensfase (metamorfose van larve naar jonge haring) wordt de jaarklassterkte bepaald. De larven vertonen verticale migratie gedurende de groei en beginnen na de metamorfose met samenscholen. In de wetenschappelijke literatuur is geen bewijs gevonden dat gerichte bewegingen van larven worden veroorzaakt door bepaald gedrag ten gevolge van omgevingsfactoren als zoutgehalte of diepte. Op dit moment is in de literatuur geen werk beschikbaar over veranderingen in de larvale driftpatronen door menselijk ingrijpen en de gevolgen hiervan op de productiviteit van kanaalharing en op de visserij.

Introduction

Unusual for a commercial fish species in the North Sea, herring (*Clupea harengus* L.) spawn benthic eggs in large mats and clumps that tend to hatch together (Harden Jones, 1968; Burd, 1978; Blaxter & Hunter 1982). This results in high densities of larvae being dispersed from specific points over a short period of time (Boeke, 1906; Wallace, 1924). There has been much debate as to whether herring prefer retention or dispersion as a life history strategy (Iles & Sinclair, 1982; Sinclair & Tremblay, 1984; Cushing, 1986; Heath & Richardson, 1989; Fortier & Gagné, 1990), but in the North Sea herring larvae are dispersed from their spawning sites and drift hundreds of kilometres towards their nursery areas (Munk & Christensen, 1990; Bartsch, 1993; Heath et al., 1997). It is during this drifting period that the year class strength of herring is determined (Cushing, 1967; Anthony & Fogarty, 1985; Nash & Dickey-Collas 2005) and variability in climatic forcing of the larval drift may actually help explain some of the variability in the year class strength in North Sea herring (Bartsch et al., 1989; Bartsch 1993).

Herring in the North Sea

The North Sea herring stock is made up of a number of components (sub-populations) fish that show different physical characteristics, spawning strategies and migration behaviour (Zijlstra, 1958). They were originally called races of herring (Heincke, 1898; Redeke & van Breemen, 1907; Bjerkan, 1917) but are now considered to be parts of the same stock as they are genetically indistinguishable (EU HERGEN project, in prep) and all mix at certain points of their life cycle (ICES, 1965; Cushing & Bridger, 1966; Cushing, 1992). Variability in their environment (particularly temperature) at spawning, hatching and during the first year of life is thought to create the differences between component parts of the stock by influencing growth and physical development (Jennings & Beverton, 1991; Hulme, 1995; McQuinn 1997) and these physical differences are called meristic characteristics (Zijlstra, 1958; Hulme, 1995; Heath et al., 1997).

North sea herring live up to 17-20 years (38-39 cm length; RIVO database) and they spawn once a year (Bowers & Holliday, 1961; Blaxter & Hunter, 1982, referred to as group-synchronous determinate total spawners; Murua & Saborido-Rey 2003) meaning that the ovules in their ovary develop at approximately the same time with no additional ovules appearing during the spawning season, and that the population tends to spawn in unison).

In North Sea herring, the term year class refers to the year of spawning and preparation to spawn. In the southern North Sea, where the herring spawn late in the year from December to January, the term year class then refers to the year leading to this spawning event e.g. the 2000 year class would be spawned from December 2000 to January 2001.

Spawning sites

The spawning sites of herring in the southern North Sea are part of the Downs component of the larger North Sea herring stock. Spawning of the North Sea herring stock begins in the north of the North Sea in September and then progresses southwards with time, ceasing in January in the eastern English Channel with the Downs component (Boeke, 1906; Cushing & Burd, 1957; Zijlstra, 1969; Burd & Howlett, 1974; Figure 1). The number of spawning sites in the North Sea varies with stock size (Burd, 1985; Corten 1999; 2001) with a decline in the number of spawning sites at lower biomasses of North Sea herring. A time series of surveys of herring larvae show that the main centres of spawning have not changed since the 1950s (Figure 1, ICES 2005).

The Downs herring spawn on gravel beds that are generally between 20-40m depth (see Cushing & Burd, 1957; Parrish et al., 1959). The thicker egg mats can suffer high mortalities due to oxygen deficiency (Parrish et al., 1959; Aneer, 1985) and the mats attract predators (spurdog, haddock, mackerel, lemon sole and other herring; Hempel & Schubert, 1969; de Groot, 1980; Skaret et al., 2002; and personal observations). These gravel beds are spread

throughout the southern North Sea and eastern English Channel (Cushing & Burd 1957; Figure 2). Due to the variability in drift, temperature and growth, the recruits from one spawning will not necessarily mature in synchrony (McQuinn, 1997; Brophy & Danilowicz, 2003). Recruitment from each spawning site in the North Sea varies between years and the relative importance of sites to the productivity of the whole stock also varies over time (Cushing, 1968; Corten, 1986; Johannessen & Moksness, 1991). This is due to the complicated multi-component nature of the North Sea herring stock and the different dynamics shown by each component. The larvae produced in the southern North Sea supported the largest herring fishery throughout the 1930s to the early 1950s (Hodgson, 1936; Cushing & Burd, 1957; Cushing & Bridger, 1966), suggesting that recruitment from these areas was strong. Then, once overfishing reduced the biomass in the southern areas, the northern spawning sites, namely off Scotland and Shetland, produced the majority of recruits (Burd, 1985). Larval production and recruitment from the central North Sea increased in the mid 1980s and then declined again (Nichols & Brander, 1989) and increased again in the late 1990s (ICES, 2005). As larval production increased in the southern North Sea (ICES, 2005) the recruitment also improved in the late 1990s (Figure 3). Recent evidence suggests that the very strong 2000 year class comes almost entirely from larvae spawned in the southern North Sea (ICES, 2005). Hence, the strongest recorded year classes from the southern component in the last 100 years were 1921, 1924 and 1929 and now again in 1996, 2000 and 2002 (Cushing & Burd, 1957; ICES, 2005). The 2000 year class is so large that it is the dominant age group in the catch and made up over 60% of the Dutch catch of herring in 2004.

Larval Behaviour

The Downs herring produce bigger eggs and are less fecund than fish of the more northern components (Baxter 1959; 1963; Cushing, 1958; Almaraz & Bailey, 1989), hence the hatched larvae are bigger than their northern counterparts (Heath et al., 1997). Upon hatching, herring larvae rise to the plankton (from the seabed) by increasing their buoyancy by taking on water (85% water content at hatch to 92% water content after hatch, Craik & Harvey, 1984; 1987; Ying & Craik, 1993). The larvae hatch between 7.5 and 9.5 mm in length and have faster escape responses than the smaller northern larvae (Batty et al., 1993). The escape response in herring larvae is not full operational until they are over 20mm in length (Fuiman, 1993). Feeding on microplankton and copepod nauplii begins just before yolk sac absorption, usually within the first week (Checkley, 1982; Munk, 1992) and the larvae feed on a wider range of sizes of prey items as they grow. Herring larvae are predominantly visual feeders (Batty et al., 1990).

As the larvae grow they also begin to express other behaviour such as vertical migration and more active swimming. Small larvae are found in layers near the surface but as they grow they begin to show diel variation with layering during the day but dispersal throughout the top 60m during the night (Heath et al., 1988; Johannessen & Moksness, 1991). Temperature effects the swimming speed of the larvae (Batty et al., 1993) and by 20mm the average swimming speed of the larvae is 2.9 mm per second (Gallego & Heath, 1994). Swimming and shoaling becomes more active after metamorphosis (Heath & Richardson, 1989). This happens in late spring and early summer at about 50mm length (Gallego & Heath, 1994) for herring spawned in the southern North Sea. The presence of already metamorphosed juveniles increases the likelihood of early shoaling in pre-metamorphic herring larvae (Gallego et al., 1995).

It is well documented and understood that any modelling of the transport of herring larvae must account for larval diel behaviour (Bartsch et al., 1989; Lazzari et al., 1993) and also the development and change in larval behaviour with size (Bartsch, 1993; Bryant et al., 1995; Heath et al., 1997).

Although alluded to by Miller (1998), an intensive literature search for further information on the triggers of the behaviour of larvae and post metamorphic juveniles, resulted in no further evidence being found for triggers of directional movement. Personal communication with Dr Mike Heath (Fisheries Research Services Aberdeen), Dr Richard Nash (Marine Institute, Bergen), Dr Peter Munk (Danish Fisheries Institute) and Dr Øyvind Fiksen (University of Bergen)

supported this finding of the paucity of information particularly in relation to directional movement and salinity triggers.

It has been suggested that apparent tidal transport may be caused by the negative buoyancy of the larvae. With the larvae sinking at slack tide and being resuspended by turbulence from tidal flows (Henri et al., 1985) but again the evidence for this is weak. However it is clear that starvation has an effect on buoyancy and hence vertical distribution of the larvae (Blaxter & Ehrlich, 1974; Øyvind Fiksen pers com.). Starvation increases the water content of the larvae and they become more neutrally buoyant and hence stop sinking. The sinking rate of a fed and healthy larvae at 10°C and salinity of 33, are 0.4 cm per second (Blaxter & Ehrlich, 1974; Yin & Blaxter, 1987). The sinking rates decrease at higher salinities. During the early life stages, plaice are more neutrally buoyant than herring larvae (Blaxter & Ehrlich, 1974; Ying & Craik, 1993). As herring larvae grow their sinking rate increases to 1.0 cm per sec at 20mm length. Starving herring larvae also show reduced diel vertical migration (Blaxter & Ehrlich, 1974).

Juvenile nursery areas in the North Sea

The transport and drift of larvae in the southern North Sea is towards the juvenile nursery grounds from the Wadden Sea to the Skagerrak and Kattegat (Wallace, 1924; Burd, 1978; Figure 4). In these nursery areas herring from the North Sea herring stock mix with Western Baltic Spring Spawning herring and local fjord populations from the Norway, Sweden and Denmark (Mosegaard, 1997; ICES, 2005). It is clear that the drifting larvae from the Downs component (Figure 5) are dispersed in high numbers along the Dutch coastline as they are transported towards the German Bight and Skagerrak.

The role of the Waddenzee as a nursery ground for herring is not that clear (Rauck & Zijlstra, 1978), as current surveys of juveniles do not enter Waddenzee thus making comparisons of relative numbers by area difficult and sampling gear used in the Waddenzee are not the best for sampling juvenile herring. The number of post-larvae that enter the Waddenzee differ each year (Corten & Kamp, 1979). There appear to be two waves of larvae: firstly in February and March at approximately 40mm in length (that are assumed to come from the Northern Autumn spawners) and then in April and May at approximately 30mm in length (from the winter spawners in the southern North Sea; Bückman 1950; Bückman & Hempel, 1957). Although Corten & Kamp (1979) suggested that the smaller larvae may arrive at the Waddenzee slightly earlier in late March to April (using data from 1967 to 1978). Corten and Kamp (1979) also commented that catches of post-larvae were extremely variable, both between and within sampling stations suggesting very patching distributions of larvae, and/or the entry of post-larvae into the Waddenzee in waves. They do not mention any tidal component in the abundance time series. Juvenile herring in the Waddenzee stay a few months until early autumn when they head to the main nursery grounds (ICES, 1969). With the use of otolith microchemistry it would be possible to investigate the importance of the Waddenzee to the whole North Sea herring stock.

The dynamic variability in the nursery grounds can be easily seen in the catches of the International Bottom Trawl survey (IBTS, Figure 6). This survey was started in the 1960s and was targeted specifically at herring (Heessen et al., 1997). The distribution of juveniles has not changed and covers the area from the north of the Netherlands, across the German Bight and into the Skagerrak (Figure 6 compared to Figure 4). Importantly, apart from a very few unusual year classes, the abundance of 1 year olds reflects the year class strength of the fish in the adult fishery (Nash & Dickey-Collas, 2005), i.e. recruitment strength is determined prior to arrival at the nursery grounds. It has also been reported that a small but proportionate numbers of juveniles of Downs origin also use the eastern English coast as a nursery area (Wood, 1983) but this is not apparent in recent years (Figure 6).

Fish leave the nursery grounds between ages 1 and 3, depending on their growth and condition and join the adults in their migrations from feeding grounds to spawning grounds (McQuinn, 1997; Brophy & Danilowicz, 2003).

Drift and dispersion

Many studies on larval drift and transport of herring have occurred in European waters:

North Sea

Most of the studies on the drift of herring larvae in the North Sea have been associated with the ACE (Autumn Circulation Experiment) project in the 1980s. The project's findings are summarised in Bartsch et al. (1989), Bartsch (1993), Nichols & Brander (1989) and Heath et al. (1991). They coupled larval drift inferred from field observations with drift determined by a three dimensional circulation and transport model. The broad characteristics in the transport of larvae could be reproduced but the between year variability was difficult to model. The studies did highlight the influence of variability in hydrographic and meteorological conditions in the variability in drift of herring larvae and the successful delivery of fresh juveniles to the nursery grounds. However one problem with these studies was that the production of Downs larvae was very low in the 1980s and the project concentrated on production from the northern and central North Sea. It also did not consider the possibility of anthropogenic disruption of the transport mechanisms.

Norwegian spring spawning herring

The best and most current description of the transport of Norwegian spring spawning herring is given by Holst et al (2004). This stock can be huge in terms of biomass and is characterised by large variability in spawning behaviour and recruitment strengths. At high population biomass the spawning sites are fairly consistent, but like in the North Sea, spawning sites become restricted at low biomasses. The spawning sites are along the Norwegian coast and generally the larvae drift in a north easterly direction towards the Barents Sea following major hydrographic features (Sætre et al., 2002a). Large between year variability exists in the success of larvae reaching the nursery grounds, depending on spawning site and local hydrography (Sætre et al., 2002b). Some herring juveniles do not reach the Barents Sea and nursery in the Norwegian fjords. Large year classes are associated with years when most of the juveniles come from the Barents Sea.

West coast of Scotland

The dispersal of larvae on the Scottish west coast appears to be determined by the Scottish Coastal Current (Saville & Morrison, 1973; Heath et al., 1987; Heath & Rankine, 1988; Heath, 1989). Hatched larvae from the west coast of Scotland drift north towards the Orkneys and northern North Sea. The juveniles are thought to either remain near Scotland on the east coast or drift towards the eastern North Sea and German Bight (Heath & Walker, 1987). Further evidence from genetic studies (EU projects HERGEN and WESTHER, in prep) suggest that there is widescale mixing between the west coast of Scotland stock and the northern North Sea, as larvae and juveniles.

Clyde

The herring larvae spawned in the Clyde show a highly variable dispersal pattern which seems largely determined by the prevailing winds (Parrish et al., 1959; Saville et al., 1966). Often the larvae are held within the Clyde and nursery in the upper regions, but in some years they are carried out from Ballantrae Bank into the North Channel and Irish Sea. Parrish et al. (1959) describe this as an oscillation between the Clyde and Irish Sea caused by certain meteorological conditions.

Irish Sea

Historically there have been two main spawning areas in the Irish Sea (Dickey-Collas et al., 2001); those in the east, the Manx component and those in the west, the Mourne component. Few dedicated studies of drift have occurred in the Irish Sea and most conclusions have been inferred from meristic and growth data of the larvae and juveniles. Bowers (1980) concluded that the larvae from the Manx spawning ground drift towards the English and Scottish coasts, under the effects of meteorologically determined hydrography. The importance of the

prevailing south westerlies in determining the drift of Manx larvae was also highlighted by Özcan (1974). Wood & Howlett (1976) suggested that the Mourne larvae either drift east or north dependent on hydrography. The only study on hatching and growth of Mourne larvae, highlighted the variability in drift along the Irish coast (Anon 1979) and linked it to the prevailing wind direction. Drift of Irish Sea spawned larvae into the Clyde has been mentioned by some authors (Marshall et al., 1939; Özcan, 1974) but no conclusive evidence has been found (Wood & Howlett, 1976).

Celtic Sea

The dispersal of larval herring from the Celtic Sea is even less clear. Some oceanographers describe the residual flows moving in a south westerly direction, away from the Irish Sea, (Monahan, 1977; Grainger, 1980) and others suggest that a flow into the Irish Sea exists (Edwards, 1968; Ramster & Hill, 1969). Most of these studies are based on very small data sets from a few fixed point current meters. Some studies on the drift of larvae have indicated a drift into the southern Irish Sea (Özcan, 1974). Özcan (1974) showed a correlation between wind velocity and the occurrence of Dunmore East larvae and juveniles in the Irish Sea. Recent work by Brophy & Danilowicz (2002) shows large numbers of Celtic Sea juveniles using the Irish Sea as a nursery ground, suggesting large numbers of Celtic Sea herring larvae drift into the Irish Sea.

West coast of Ireland

Data on drift of larvae from the west coast of Ireland are limited. It has been suggested that Donegal herring larvae drift north towards the Scottish west coast (Özcan, 1974; Molloy & Barnwall, 1988) and larvae from Galway disperse south along the Irish coast (Rankine, 1988). However other evidence does not support this (Grainger, 1976), and whilst hatching larvae distributions for north west Ireland are well known (Wood, 1972; Molloy & Barnswell, 1988; Hopkins, 1990), there is little indication of the mechanism controlling larval drift.

Drifting larvae in general

It is clear that the interaction of choice of spawning site and local hydrographic conditions plays an important role in the determination of larval drift or transport. Virtually all stocks in western Europe drift in an easterly direction. In most areas, particularly on the shelf, the local hydrography is highly influence by meteorological forcing through wind, with additional far field effects. Nearer the shelf edge, e.g. west of Ireland and perhaps west of Scotland, the hydrography may well be influenced by more large scale basin effects and oceanographic currents. As most of the studies of herring larval drift occurred prior to the use of geostrophic (density-driven), real-time models with far field forcing it is not surprising that investigators found it difficult to replicate between year variability. Few oceanographic circulation models of the type used in these studies account for, or describe well, the influence of fresh water runoff on the transport of larvae. This may well have important implications particularly in the southern North Sea and Irish Sea.

Anthropogenic impact

There is little work published on anthropogenic effects on larval production, drift and transport. Groot (1980) suggests that gravel extraction in the English Channel would have a detrimental effect on the production of Downs herring, but produced little analysis. In 2003 the ICES herring working group considered the impact of gravel extraction and recommended:

All decisions about the granting of licenses for gravel extraction in the deeper waters of the eastern English Channel should be carried out within the precautionary principle (UNCED, 1992). This principle (no.15) states that "where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason ... to prevent environmental degradation". The working group recommends that no gravel extraction occurs

in rectangle 29F0 for the four month period of November to February, as this coincides with herring spawning in the area. Licenses should not be granted for the remainder of the year unless it can be proven unequivocally that gravel extraction does not have a deleterious impact on herring spawning and larval production in 29F0 and VIIId. (ICES 2003).

The impact of the closing of the Afsluitdijk in 1932 was catastrophic on the spring spawning Zuiderzee herring which became extinct and the fishery closed by 1939 (Groot, 1980).

However no studies to date have investigated the role of large-scale changes to coast lines on the productivity of herring, or the potential impact of changes to drift on the production of Downs herring.

Glossary and acronyms

ACE	Autumn Circulation Experiment, a large project on North Sea circulation and herring larvae.
Component	Part of a stock, that may express different behavioural or physical characteristics
Downs herring	The component of North Sea herring that spawns in the southern North Sea and English Channel.
EU	European Union (europa.eu.int)
Geostrophic	density driven flow (used in hydrography and oceanography)
HERGEN	An EU funded project into herring genetics in the North Sea (www.hull.ac.uk/hergen)
IBTS	International Bottom Trawl Survey (www.ices.dk/datacentre/ibts.asp)
ICES	International Council for the Exploration of the Sea (www.ices.dk)
Recruitment	The new year classes of young fish that join the adult population each year
Stock	A population of fish that are thought to act independently of others around them, hence are managed separately.
UN	United Nations (www.un.org)
UNCED	Declaration of the UN conference on Environment and Development
WESTHER	An EU funded project into the determination of herring stock identities in western waters (www.clupea.net/westher)

References

- Anon, (1979). Final Report of the Cross Border Herring Study. Fisheries Development Limited, December 1979. London and Belfast 160pp
- Almatar, SM & Bailey, RS (1989). Variation in the fecundity and egg weight of herring (*Clupea harengus* L.). Part I. Studies in the firth of Clyde and northern North Sea. J. Cons. Perm. Int. Explor. Mer 45:113-124.
- Aneer G (1985). Some speculations about the Baltic Herring (*Clupea harengus* membras) in connection with the eutrophication of the Baltic Sea. Can J Fish Aquatic Sci 42 (suppl. 1): 83-90
- Anthony, VC Fogarty, MJ (1985). Environmental effects on recruitment, growth and vulnerability of Atlantic herring (*Clupea harengus* harengus) in the Gulf of Maine Region. Can J Fish Aquatic Sci, 42: 158-173
- Bartsch, J. (1993). Application of a circulation and transport model system to the dispersal of herring larvae in the North Sea. Continental Shelf Research, 13: 1335-1361.

- Bartsch, J, Brander, K, Heath M, Munk, P, Richardson, K & Svendsen, E (1989). Modelling the advection of herring larvae in the North Sea. *Nature*, 340: 632-663
- Batty, RS, Blaxter, JHS & Fretwell, K (1993). Effect of temperature on the escape responses of larval herring *Clupea harengus*. *Marine Biology* 115: 523-528.
- Batty, R.S., Blaxter, J.H.S. and Richard, J.M. 1990. Light intensity and the feeding of herring, *Clupea harengus*. *Marine Biology*, 107: 383-388.
- Baxter, AC (1963). A comparison of fecundities of early and late maturity stages of herring in the Northwestern North Sea. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*, 154:170-174.
- Baxter, IG (1959). Fecundities of winter-spring and summer autumn herring spawners. *J. Cons. Perm. Int. Explor. Mer* 25: 73-80
- Bjerkkan P. (1917). Age, maturity and quality of North Sea herrings during the years 1910-13. *Rep. Norw. Fish. Mar. Invest.* III no 1.
- Blaxter, JHS & Ehrlich, KF (1974) Changes in behaviour during starvation of herring and plaice larvae. The early life history of fish. The Proceedings of an International Symposium held at the Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association at Oban, Scotland, from May 17-23, 1973. pp. 575-588.
- Blaxter JHS & Hunter JR. (1982). The Biology of Clupeoid Fishes. In: Blaxter, JHS, Russell, FS & Yonge, M. *Advances in Marine Biology*, vol 20. 1-223
- Boeke, J (1906). Eier und Jugendformen von Fischen der südlichen Nordsee. *Verhandelingen u.h. Rijksinstituut v.h. Onderzoek der Zee. Deel 1 no4* pp3-35.
- Bowers, AB (1980). The Manx Herring Stock, 1948-1976. *Rapp. P. v. Réun. Cons. int. Explor. Mer*, 177: 166-174
- Bowers AB & Holliday FGT (1961). Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). *Marine research (Edinburgh)* 5: 1-15.
- Brophy, D & Danilowicz BS (2002). Tracing populations of Atlantic herring (*Clupea harengus* L.) in the Irish and Celtic Seas using otolith microstructure. *ICES J Mar Sci* 59: 1305-1313.
- Brophy, D & Danilowicz BS (2003). The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (*Clupea harengus* L.). *ICES J Mar Sci* 60: 1103-1113
- Bryant, AD, Heath, MR, Broekhuizen, N, Ollason, JG, Gurney, WSC, Greenstreet, SPR. (1995). Modelling the predation, growth and population dynamics of fish within a spatially-resolved shelf-seas ecosystem model. *Netherlands Journal of Sea Research*. 33: 407-421.
- Bückman, A (1950). Die Untersuchungen der Biologischen Anstalt über die Ökologie der Heringsbrut in der Südliche Nordsee. *Helgol. Wiss. Meeresunters.* 3 (1): 1-205
- Bückman A & Hempel G (1957). Untersuchungen an der Heringslarven Bevölkerung der Innenjade. *Helgol. Wiss. Meeresunters.* 6 (1): 1-150
- Burd, AC (1978). Long term changes in North Sea herring stocks. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*, 172: 137-153
- Burd, AC (1985) Recent changes in the central and southern North Sea herring stocks. *Can. J. Fish. Aquatic Sci.*, 42 (Suppl 1): 192-206
- Burd AC & Howlett, GJ (1974). Fecundity studies on North Sea herring. *J. Cons. Perm. Int. Explor. Mer* 35 (2): 107-120
- Burd AC & Hulme TJ (1984). Prediction of herring recruitment from IYFS data. *ICES CM* 1984/H:5
- Checkley DM, (1982). Selective feeding by Atlantic Herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. *Marine Ecol Progress Series* 9: 245-253.

- Corten, A (1986). On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972-1978. J. Cons. Int. Explor. Mer, 42: 281-294.
- Corten, A (1999). The reappearance of spawning herring on Aberdeen Bank in 1983 and its relationship to environmental conditions. Can J Fish Aquat Sci, 56: 2051-2061
- Corten, A (2001). Herring and Climate. PhD Thesis, Rijksuniversiteit Groningen, The Netherlands. 228pp.
- Corten, A & van de Kamp, G (1979). Abundance of herring larvae in the Dutch Wadden Sea as a possible indication of recruitment strength. ICES CM 1979/H:26.
- Craik JCA & Harvey SM (1984). Biochemical changes occurring during final maturation of eggs of some marine and freshwater teleosts. Journal of Fish Biology, 24: 599-610.
- Craik JCA & Harvey, SM (1987). The causes of buoyancy in eggs of marine teleosts. Journal of the Marine Biological association of the UK 67: 169-182
- Cushing DH (1958). Some changes in Vertebral counts of herrings. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 143 part 1: 126-129.
- Cushing DH (1967) The grouping of herring populations. J. mar. Biol Ass. UK 47: 193-208
- Cushing, DH (1968). The Downs stock of herring during the period 1955-1966. J. Cons. Perm. Int. Explor. Mer 32 (2):262-269
- Cushing, DH (1992). A short history of the Downs stock of herring. ICES J. mar. Sci., 49: 437-443.
- Cushing, DH & Bridger, JP (1966). The stock of herring in the North Sea, and changes due to fishing. Fishery Investigations London, Ser II, 25 (1): 1-123
- Cushing DH & Burd AC (1957). On the herring of the southern North Sea. Fishery Investigations, London, Ser II, 20 (11): 1-31
- Dickey-Collas, M, Nash, RDM & Brown, J (2001). The location of spawning of Irish Sea Herring (*Clupea harengus*). J Mar Biol Ass UK., 81: 713-714
- Groot, SJ de (1980). The consequences of marine gravel extraction on the spawning of herring, *Clupea harengus* Linné. J. Fish Biol. 16: 605-611.
- Edwards, C (1968). Water movements and the distribution of hydromedusae in British and adjacent waters. Sarsia 34:331-346
- Fortier L & Gagné, JA (1990). Larval herring (*Clupea harengus*) dispersion, growth and survival in the St Lawrence estuary: Match/Mismatch or membership/vagrancy? Can. J. Fish. Aquat. Sci. 47: 1898-1912
- Fuiman, LA (1993). Development of predator evasion in Atlantic herring *Clupea harengus* L. Anim. Behav. 45: 1101-1116.
- Gallego, A & Heath, MR (1994). The development of schooling behaviour in Atlantic herring *Clupea harengus*. Journal of Fish Biology 45: 569-588,
- Gallego, A, Heath, MR & Fryer, RJ, (1995). Premature schooling of larval herring in the presence of more advanced conspecifics. Animal Behaviour 50: 333-341,
- Grainger, R (1976). The inter-relationships of populations of autumn spawning herring off the west coast of Ireland. Irish Sea Fisheries Board, Resource paper 32. 21pp
- Grainger, R (1980). Current meter measurements near the Coningbeg LV. Report to Mr Griffith, Department of the Marine, Dublin, January 1980
- Groot, SJ de (1980). The consequences of marine gravel extraction on the spawning of herring, *Clupea harengus* Linné. J. Fish Biol. 16: 605-611.
- Harden Jones, FR (1968). Fish Migration. Edward Arnold Ltd London. 325pp.

- Heath, MR (1989). Transport of larval herring (*Clupea harengus* L.) by the Scottish Coastal Current. Rapp. P. v. Réunion. Cons. int. Explor. Mer, 191: 85-91
- Heath, MR & Rankine, P (1988). Growth and advection of larval herring (*Clupea harengus* L.) in the vicinity of the Orkney Isles. Estuarine, Coastal and Shelf Science, 27:547-565
- Heath, M. & Richardson, K (1989). Comparative study of early life survival variability of herring, *Clupea harengus*, in the North-Eastern Atlantic. J Fish Biol 35 (Supp A): 49-57.
- Heath, MR & Walker, J (1987). A preliminary study of the drift of larval herring (*Clupea harengus* L.) using gene-frequency data. J. Cons. int. Explor. Mer 43:139-145
- Heath, MR; MacLachlan, PM; Martin, JHA, (1987). Inshore circulation and transport of herring larvae off the north coast of Scotland. Marine ecology progress series, 40: 11-23,
- Heath, M.R., Henderson, E.W. & Baird, D.L., (1988). Vertical distribution of herring larvae in relation to physical mixing and illumination. Marine Ecology Progress Series, 47, 211-228.
- Heath, M, Brander, K, Munk, P & Rankine, P, (1991). Vertical distributions of autumn spawned larval herring (*Clupea harengus* L.) in the North Sea. Continental shelf research. 11 :1425-1452.
- Heath, M., Scott, B. & Bryant, AD (1997). Modelling the growth of herring from four different stocks in the North Sea. J Sea Research 38: 413-436.
- Heessen, HJL, Dalskov J & Cook RM (1997). The International Bottom Trawl Survey in the North Sea, the Skagerrak and Kattegat. ICES CM 1997/Y:31. 23pp.
- Heincke F, (1898). Naturgeschichte des Herings. Abhandl. Deutschen Seefisch Ver II
- Hempel, G, & K Schubert. (1969). Sterblichkeitsbestimmungen an einem Eiklumpen des Nordsee-Herings (*Clupea harengus* L.) Ber. Dt. Wiss. Komm. Meeresforsch, 20: 79-83
- Henri, M; Dodson, JJ; Powles, H, (1985). Spatial configurations of young herring (*Clupea harengus harengus*) larvae in the St. Lawrence Estuary: Importance of biological and physical factors. Proceedings of the Symposium on the biological characteristics of herring and their implication for management. CAN. J. AQUAT. SCI. 42 (suppl. 1): 91-104,
- HERGEN. EU project. Conservation of diversity in an exploited species: spatio-temporal variation in the genetics of herring (*Clupea harengus*) in the North Sea and adjacent areas. QLRT 2000-01370. (Final report in prep).
- Hodgson, WC (1936). The recent state of knowledge concerning the origin and distribution of herring populations in western European waters. The Southern Bight. Rapp. Et Proc. – Verb., 100 (2):19
- Holst, JC; Roettingen, I; Melle, W (2004). The Herring. In: Skjoldal, HR (Ed). The Norwegian Sea Ecosystem. Tapir Academic Press, Trondheimpp. 203-226.
- Hopkins, PJ (1990). Report on the ICES herring larvae surveys in the North Sea and adjacent waters. ICES CM 1990/H:40
- Hulme, TJ (1995). The use of vertebral counts to discriminate between North Sea herring stocks. ICES J. mar. Sci., 52: 775-779
- ICES (1965). The North Sea Herring. ICES Cooperative report 4. 57pp.
- ICES (1969). The Report of the North Sea Young Herring working Group. ICES Cooperative report 14. 87pp.
- ICES (2003). Report of Herring Assessment Working Group for the Area South of 62° N. CM 2003/ACFM:17
- ICES (2005). Report of Herring Assessment Working Group for the Area South of 62° N. CM 2005/ACFM:16

- Iles, TD, Sinclair, M, (1982). Atlantic herring: Stock discreteness and abundance. *Science* 215: 627-633
- Jennings, S. & Beverton, RJH (1991). Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) *ICES J. mar. Sci.*, 48: 117-125
- Johannessen A & Moksness E (1991). Herring larvae (*Clupea harengus*) in the Skagerrak area from December 1987 to April 1988. *Fisheries Research* 11: 155-170.
- Lazzari, MA, Stevenson, DK & Shaw, RF (1993). Influence of residual circulation and vertical distribution on the abundance and horizontal transport of larval Atlantic herring (*Clupea harengus*) in a Maine Estuary. *Can. J. Fish. Aquatic Sci.*, 50: 1879-1890.
- Marshall, SM, Nicholls, AG & Orr, AP (1939). On the growth and feeding of young herring in the Clyde. *Journal Marine Biological Association of UK*, 23: 427-455
- Miller, JM, (1988). Physical processes and the mechanisms of coastal migrations of immature marine fishes. Larval fish and shellfish transport through inlets. PROCEEDINGS OF A WORKSHOP HELD IN OCEAN SPRINGS, MISSISSIPPI, USA, August 19-20 1985. *American Fisheries Society Symposium* 3: 68-76
- McQuinn, IH (1997). Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries* 7: 297-329.
- Molloy, J, & Barnwall, E (1988). Herring larval surveys off the west and north west coast 1984-1986. *Fishery Leaflet, Department of the Marine, Dublin* 142
- Monahan, EC (1977). Physical oceanography of the Irish coastal zone. Report for NSC workshop on Management of the Irish Coastal Zone, March 1977
- Mosegaard, H, (1997) Identification of spawning type in adult North Sea herring using otolith increment pattern formed during the larval period. *J Fish Biol suppl* 51a pp33.
- Munk, P (1992). Foraging behaviour and prey size spectra of larval herring *Clupea harengus*. *Marine ecology progress series*, 80: 149-158,
- Munk, P. & Christensen, V (1990). Larval growth and drift pattern and the separation of herring spawning groups in the North Sea. *Journal of Fish Biology*, 37, 135-148.
- Murua, H. & Saborido-Rey, F. (2003). Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science* 33:23-31
- Nash, RDM & Dickey-Collas M (2005). The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.). *Fisheries Oceanography* in press.
- Nichols JH & Brander, KM (1989). Herring larval studies in the west-central North Sea. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*, 191: 160-168.
- Özcan, A (1974). A Review of the Herring Stocks to the West of the British Isles. Phd thesis, University of East Anglia.
- Parrish, BB, Saville, A, Craig, RE, Baxter, IG & Priestley, R (1959). Observations on herring spawning and larval distribution in the Firth of Clyde in 1958. *J mar Biol Ass UK*, 38: 445-453
- Ramster, JW & Hill, HW (1969). Current system in the Northern Irish Sea. *Nature* 224: 59-61
- Rauck, G.; Zijlstra, J.J., (1978). On the nursery-aspects of the Waddensea for some commercial fish species and possible long-term changes. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, 172, 266-275,
- Redeke, HC & van Breemen, PJ (1907). Die Verbreitung der planktonischen Eier und Larven einiger Nützfische in der südlichen Nordsee. *Verhandelingen u.h. Rijksinstituut v.h. Onderzoek der Zee. Deel II no2* pp3-37.

- Saville, A & Morrison, JA, (1973). A reassessment of the herring stock to the west of Scotland. ICES CM 1973/H:24
- Saville, A, Parrish, BB & Baxter, IG (1966). Review of Herring Fisheries and stocks off the west coast of Scotland. ICES CM 1966/H:1
- Sætre, R, Toresen, R, Soeliland, H & Fossum, P (2002a). The Norwegian spring-spawning herring - spawning, larval drift and larval retention. Sarsia. 87: 167-178.
- Sætre, R, Toresen, R & Anker-Nilssen, T (2002b) Factors affecting the recruitment variability of the Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science 59: 725-736.
- Sinclair, M and Tremblay, MJ (1984). Timing of spawning of Atlantic herring (*Clupea harengus* *harengus*) populations and the match-mismatch theory. Can J Fish Aquatic sci 41: 1055-1065
- Skaret, G, Axelsen, BE, Nøttestad, L, Fernö, A and Johannessen, A (2002). Herring as cannibals. J Fish Biol. 61: 1050-1052.
- UNCED (1992). Declaration of the UN conference on Environment and Development. Rio de Janeiro, 1992.
- Wallace, W (1924). First report on the young herring in the southern North Sea and English Channel. Part I- Distribution and growth of larval and post-larval stages. Fish. Invest. Lond. Ser 2, 7(4):1-73
- WESTHER. EU project. A multidisciplinary approach to the identification of herring (*Clupea harengus* L.) stock components west of the British Isles using biological tags and genetic markers.Q5RS-2002-01056. (In prep).
- Wood, RJ (1972). Herring larvae to the west of Scotland in the Autumn of 1971. ICES CM 1972/H:6
- Wood, RJ (1983). Estimating recruitment to the Downs Herring stock from indices of 0-group abundance on the English east coast. ICES CM 1983/H:10 8pp.
- Wood, RJ & Howlett, GJ (1976). On the distribution and abundance of larval and juvenile herring in the north Irish Sea. ICES, CM 1976/H7
- Yin, MC & Blaxter, JHS (1987). Temperature, salinity tolerance and buoyancy during early development and starvation of Clyde and North Sea herring, cod and flounder larvae. Journal of Experimental Marine Biology and Ecology, 107: 279-290
- Ying, MC & Craik, JCA, (1993). Biochemical changes during development of eggs and yolk-sac larvae of herring and plaice.. Oceanologia et limnologia sinica/Haiyang Yu Huzhao. Qingdao 24, (2): 157-165.
- Zijlstra, JJ (1958). On the herring races spawning in the southern North sea and English Channel. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 143 (2):134-145
- Zijlstra, JJ, (1969). On the racial structure of North Sea Autumn spawning herring. J. Cons. Perm. Int. Explor. Mer, 33 (1): 67-80

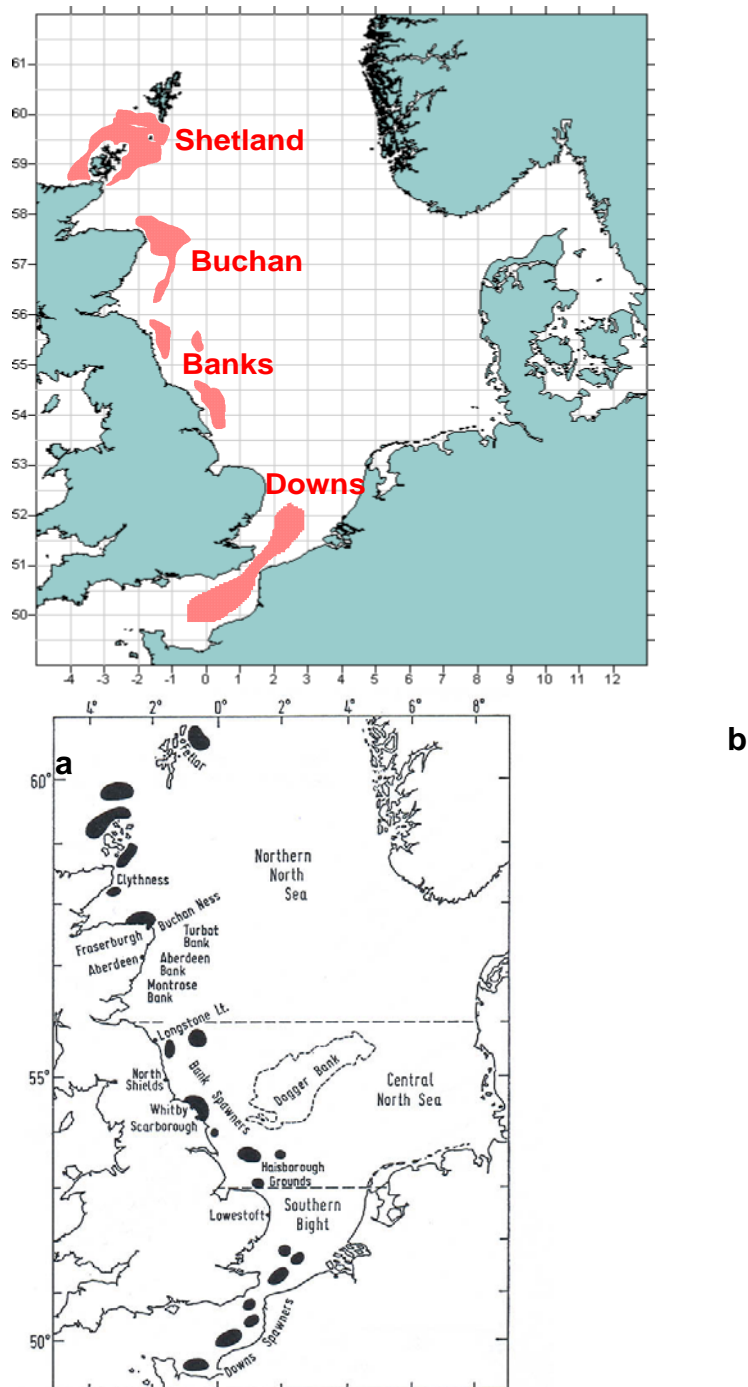


Figure 1. Generalised major spawning grounds of North Sea herring.

- a) inferred from the presence of newly hatched larvae in the ICES herring larval survey (1996 to 2003) and labelled by stock components
- b) from Burd & Howlett (1974).

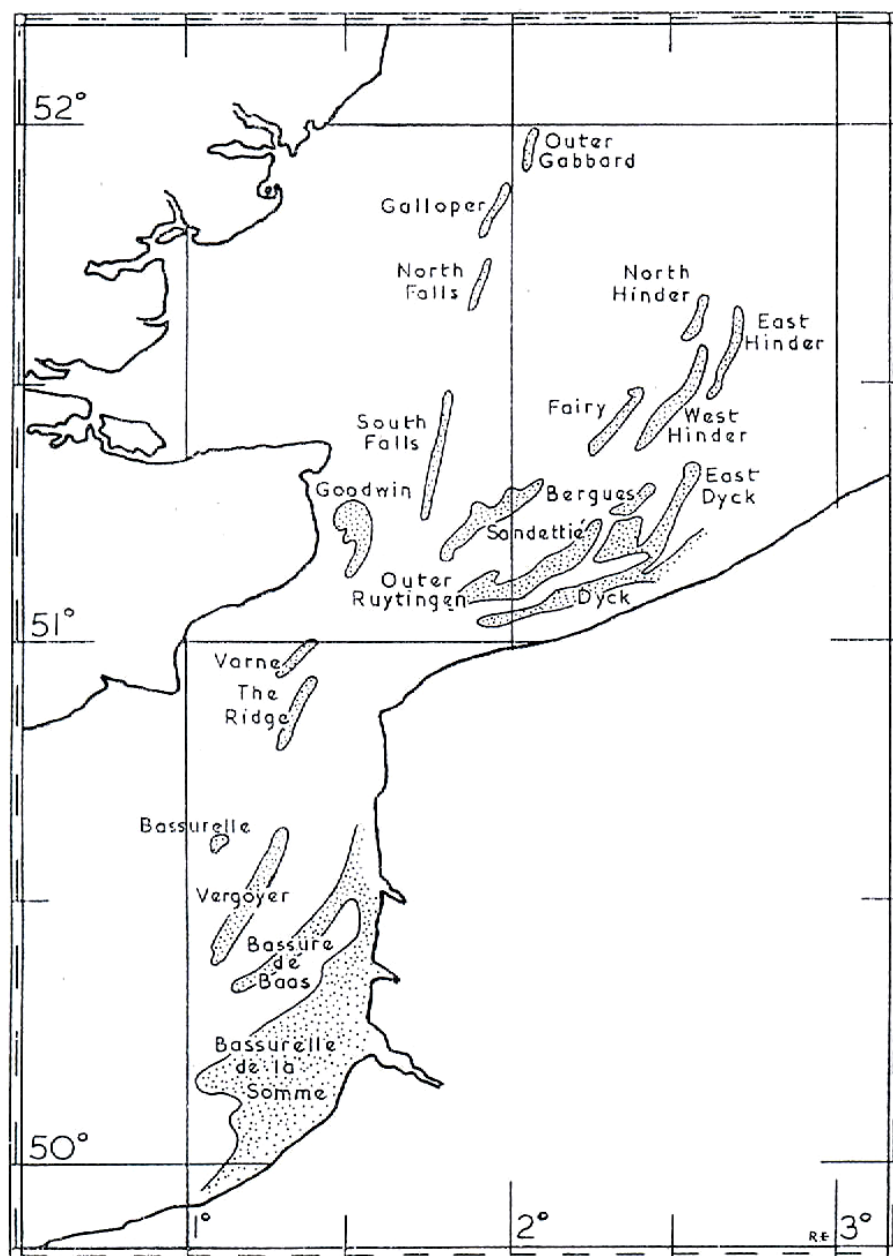


Figure 2. North Sea herring. Specific spawning grounds of Downs component of the North Sea herring stock (from Cushing & Burd, 1957).

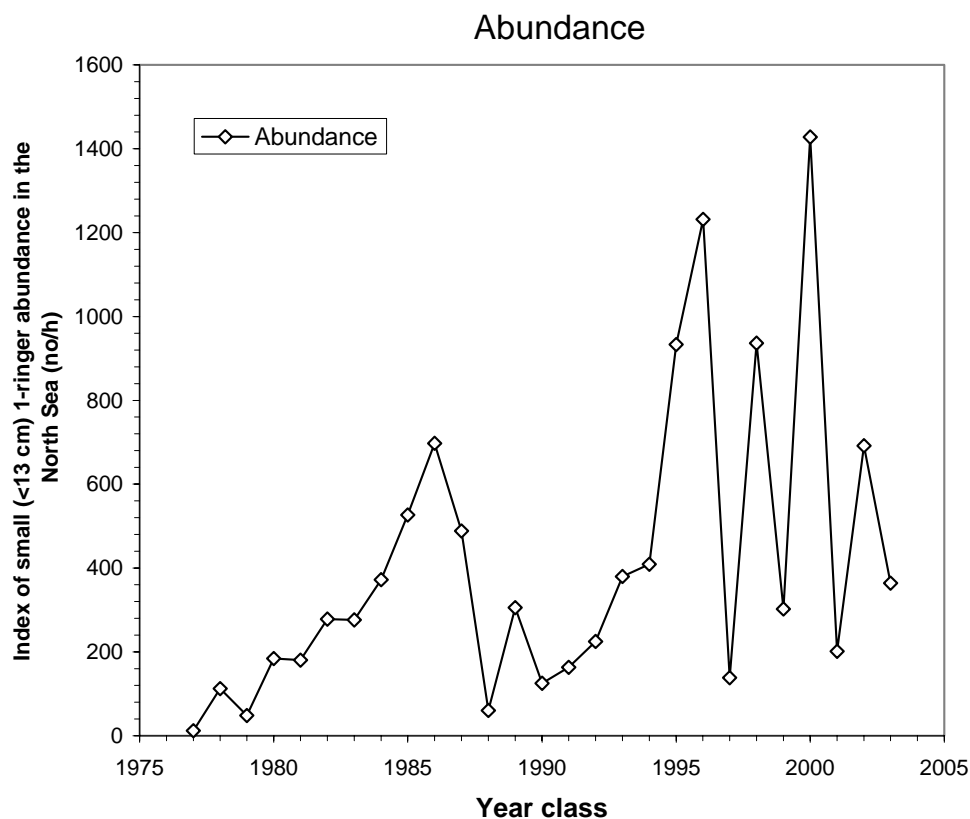


Figure 3. Time series of the abundance of juvenile (age 1) herring assumed to be from the Downs component in the IBTS survey, by year class (from ICES 2005). This series acts as a proxy for recruitment. Downs fish are smaller (<13cm) than the other components at age 1 (see Burd & Hulme, 1984).

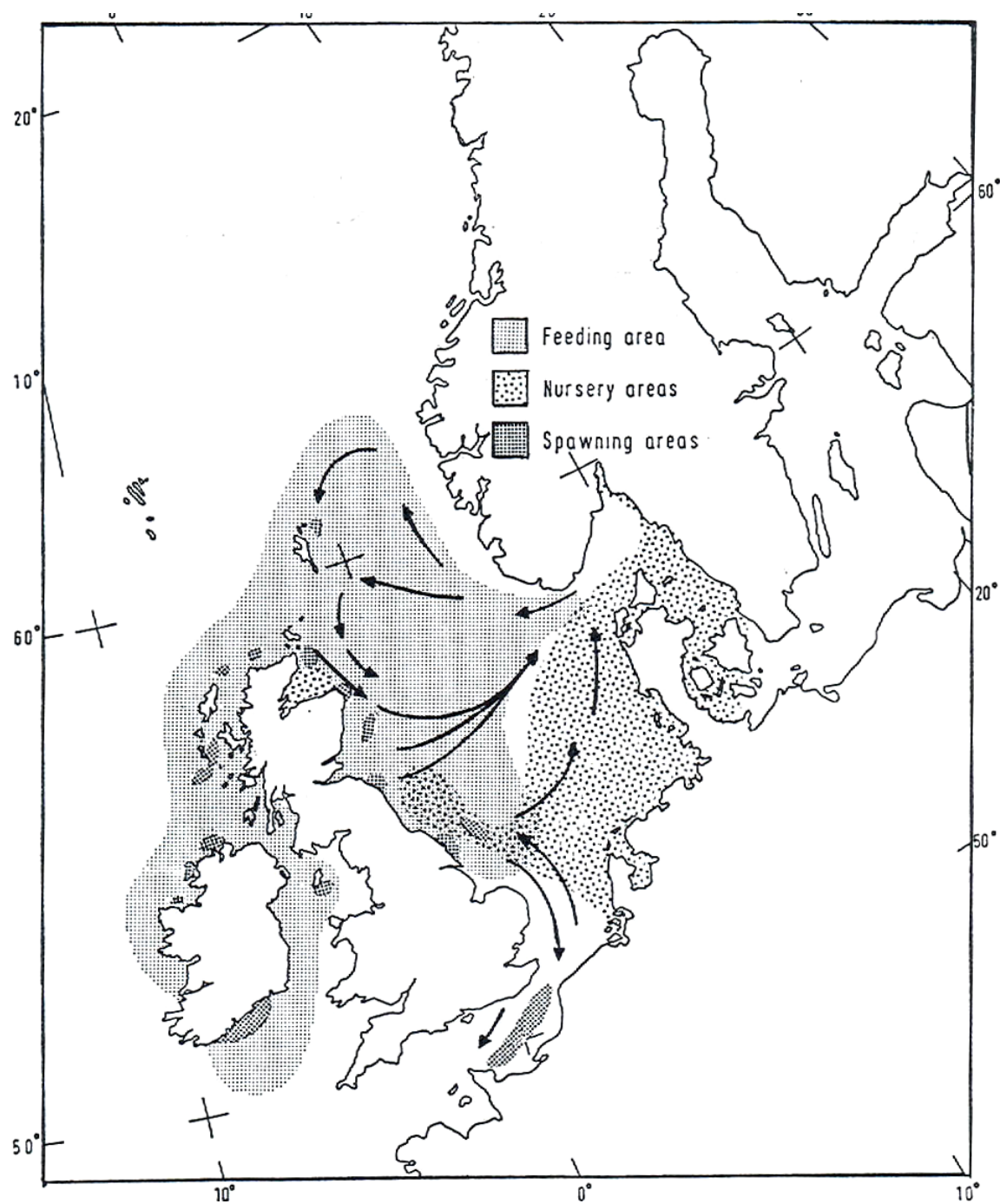


Figure 4. Schematic summary of locations of herring in NW Europe, showing nursery areas for juveniles, from Burd (1978)

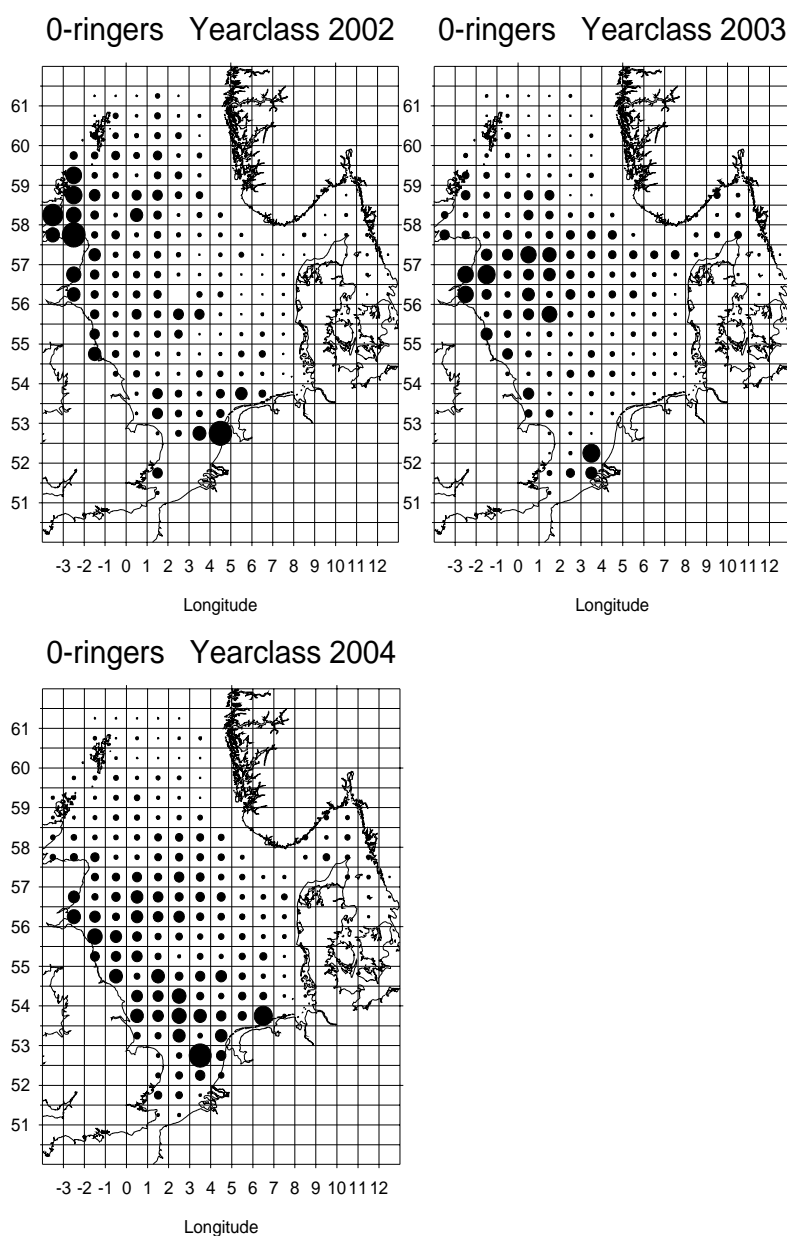


Figure 5. DRIFTING LARVAE AND POST LARVAE. North Sea herring. Distribution of age 0 herring, year classes 2002-2004. Abundance estimates of 0-ringers within each statistical rectangle are based on MIK catches during IBTS in February 2003-2005. Areas of filled circles illustrate densities in no m^2 , the area of a circle extending to the border of a rectangle represents 1 m^2 . (ICES, 2005). Empty rectangles= no sample taken.

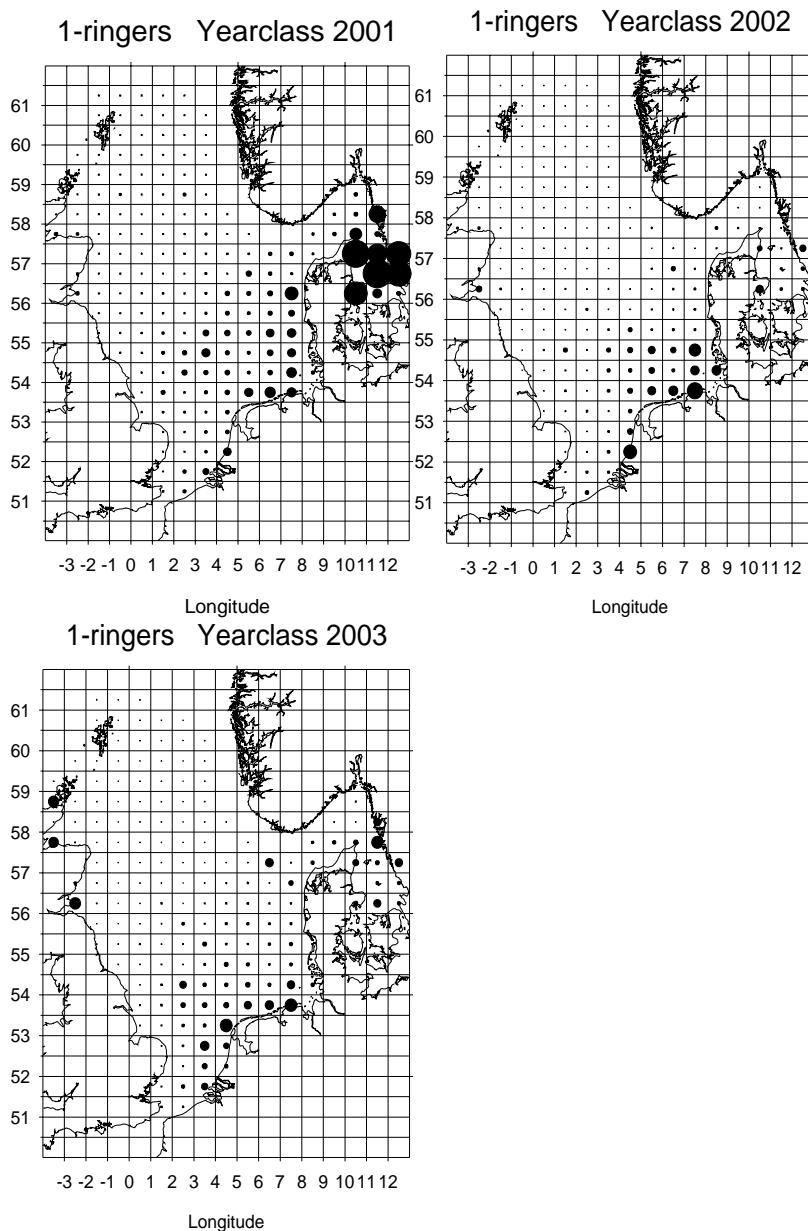


Figure 6. The distribution of juveniles of north Sea herring as determined by survey at age 1 in February 2003-2005. Areas of filled circles illustrate numbers per hour, the area of a circle extending to the border of a rectangle represents 45000 h⁻¹. Empty rectangles= no sample taken.