ICES COOPERATIVE RESEARCH REPORT

RAPPORT DES RECHERCHES COLLECTIVES

NO. 306

OCTOBER 2010

Life-cycle spatial patterns of small pelagic fish in the Northeast Atlantic

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Recommended format for purposes of citation:

Petitgas, P. (Ed.) 2010. Life cycle spatial patterns of small pelagic fish in the Northeast Atlantic. ICES Cooperative Research Report No. 306. 93 pp.

Series Editor: Emory D. Anderson

ISBN 978-87-7482-081-9

ISSN 1017–6195

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1 Introduction

The spatial organization of fish populations is expected to play a key role in population dynamics and its response to environmental forcing. It has been argued (Sinclair, 1988) that the size of populations and the spatial organization of their life cycles match key oceanographic physical features in space and time. The characterization of a functional linkage between key physical features and fish habitats was recognized as a first and important step towards understanding the variability of spatial patterns and population dynamics. Therefore, the 2004–2006 reports of the ICES Study Group on Regional Scale Ecology of Small Pelagic Fish (SGRESP; ICES, 2004a, 2005, 2006a) attempted to characterize patterns in the life-cycle organization of fish stocks in the Northeast Atlantic and cross-map these with physical features. Results were consistent with previous findings.

In Sinclair's (1988) perspective, physical retention explained maintenance of the life-cycle pattern, and vagrancy out of the pattern corresponded to losses to the population. However, in this case, the maintenance of these patterns is explained by biological behavioural processes and population substructure. This led to the recognition that habitats are not necessarily occupied, even if they are potentially suitable, because of the history of the population.

In this report, we document life-cycle patterns and how they match physical features for small pelagic fish stocks in the Northeast Atlantic. Species considered include herring (*Clupea harengus*), sardine (*Sardina pilchardus*), sprat (*Sprattus sprattus*), anchovy (*Engraulis encrasicolus*), mackerel (*Scomber scombrus*), and blue whiting (*Micromesistius poutassou*). For each case study of a stock, a similar template was followed, and the knowledge compiled of the stock's biology, life-cycle pattern, and past history, served as an "identity card" for the populations. The template documents life history traits; habitats for all life stages (spawning, feeding, wintering, and nurseries); migration patterns, including larvae drift; long-term trends in the population; potential environmental influences; and observed changes (e.g. spawning, migration, and behaviour) in relation to climate or ecosystem change (e.g. Baltic Sea). The proposed schematic representation of life-cycle patterns allowed the differentiation of the roles of different migratory components in structuring life-cycle patterns. It can also serve as a knowledge basis for spatial management. Perspectives on continuing the work relate to habitat modelling, bioenergetics, behaviour, and operational oceanography.

2 Norwegian spring-spawning herring

Aril Slotte and Georg Skaret

Life-history traits

The oldest herring recorded in the Institute of Marine Research (IMR) database was aged 25 years. Where 50% of recorded herring is mature, age varies from 4 to 7 years and 28 to 31 cm, respectively (Engelhard and Heino, 2004). The Norwegian spring-spawning herring (NSS herring) is a determinate one-batch spawner.

Wintering

Wintering has occurred in the open ocean east of Iceland (prior to the stock decline in the late 1960s), off northern Norway, and in fjords along the west and north coasts of Norway (Figure 2.1). Since the late 1980s, wintering has occurred in Vestfjorden in northern Norway, but a large proportion of the stock made up of recruits of the 1998/1999 year classes started to winter in the open ocean off northern Norway in 2002. During wintering, herring occur in enormous schools or layers which are distributed deeper during the day than at night, and which exhibit a swim–sink–glide behaviour during the night and schooling behaviour during the day (I. Huse and Korneliussen, 2000). Two separate layers, an upper layer of recruits and a deeper layer of adults, may occur. Co-occurring species during winter include cod (*Gadus morhua*), saithe (*Pollachius virens*), blue whiting (*Micromesistius poutassou*), and killer whales (*Orcinus orca*).

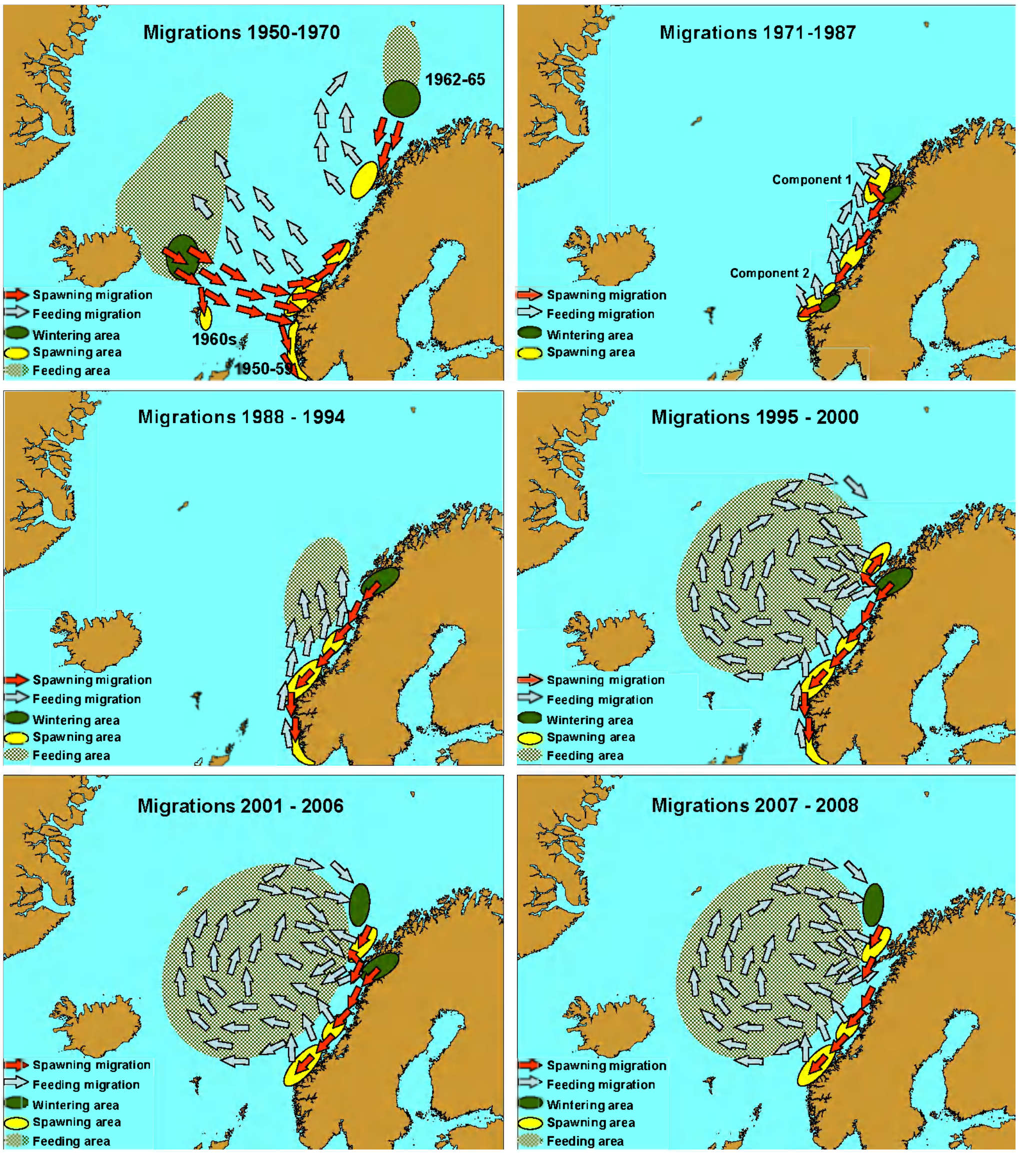

Figure 2.1. Schematic overview of historical changes in the adult NSS herring seasonal migration pattern.

Spawning

Time. Spawning occurs during February–April. There are two major spawning waves: the repeat spawners first and the recruit spawners second (Slotte *et al.*, 2000).

Habitat. Eggs are deposited on hard bottom, coarse sand, gravel, and rocks at depths of 30–250 m. The spawning grounds are located off the Norwegian coast from 58°N to 70°N. The selection of spawning grounds seems to be influenced by the size and structure of the stock (Slotte, 2001) and by the homing tendency of the herring (G. Huse *et al.*, 2002). Expansion of the spawning area increases with stock size (Dragesund *et al.*, 1997), and larger individuals tend to migrate farther to spawn (Slotte and Fiksen, 2000). Johannessen *et al.* (2009) found indications that young mature NSS herring may also join schools of local herring and adopt their traditional spawning grounds.

Schooling behaviour. This changes rapidly around spawning time: from large, dense, and deep-swimming schools during the spawning migration to small, loose schools when feeding is resumed immediately after spawning (Nøttestad *et al.*, 1996). At the spawning location, herring occur either in dispersed layers close to the surface or in dense schools in contact with the bottom during the night, and close to the bottom during the day (Skaret, 2007). The main spawning occurs during the night (Skaret *et al.*, 2003; Skaret, 2007).

Co-occurring species. Gadoids, flatfish, and killer whales.

Feeding

Time. Feeding occurs during April–August, with May–June being the main period. Herring do not feed during the wintering period (September–January) and spawning season (February–April). Feeding starts immediately after spawning.

Habitat. Feeding occurs all over the Norwegian Sea during periods of high stock abundance and closer to the Norwegian coast during periods of low abundance. The feeding migration seems to occur in a clockwise manner, starting in the south, then going west, north, and east, ending up in wintering areas in northern Norway (Misund *et al.*, 1998).

Predation mode. The herring is a snapping or filter feeder.

Prey species. Mainly calanoid copepods, but also euphausiids and amphipods.

Schooling behaviour. During the feeding season, herring schools frequently split and join, with school size generally small, and packing density low.

Co-occurring species. Blue whiting, mackerel (*Scomber scombrus*), various mesopelagic fish, and whales.

Migrations

It is believed that recruits learn the migration route to the wintering, spawning, and feeding grounds from the adults; hence, changes in migration pattern usually take place when the population is unstable, for example, during recruitment of strong year classes (Slotte, 1999a, 2001; G. Huse *et al.*, 2002, 2010). There is a tendency for a year class to spawn farther south as it grows older (Slotte, 1999a, 2001). The migration distance may be reduced if the fish are in poor condition. Modelling the size-specific costs of migration (Slotte, 1999b) and the benefits of larval survival farther south resulting from drift through warmer temperatures, has demonstrated that, with increasing size and condition, spawning is optimal farther south (Slotte and Fiksen, 2000). Similarly, the largest fish have been found to undertake the longest feeding migrations, visiting areas farther south, west, and north (Nøttestad *et al.*, 1999).

Larval drift and nursery areas

Hatched larvae drift northwards along the coast, but the northward displacement may be slowed when they enter retention areas (Figure 2.2). Some larvae drift into fjord nurseries, but most larvae end up in the Barents Sea nursery area (Holst and Slotte, 1998). As the 0–3 group, they occur both in layers and in schools. The main co-occurring species in the Barents Sea nursery area include cod, saithe, haddock (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus*), various whales, and seals. Herring are known to feed on capelin larvae, thus exerting a negative influence on capelin recruitment. The immature herring leave the fjord and Barents Sea nursery areas and join the adults in the Norwegian Sea to feed during summer before the first spawning (at ca. 28 cm length and ages of 2–8, depending on growth).

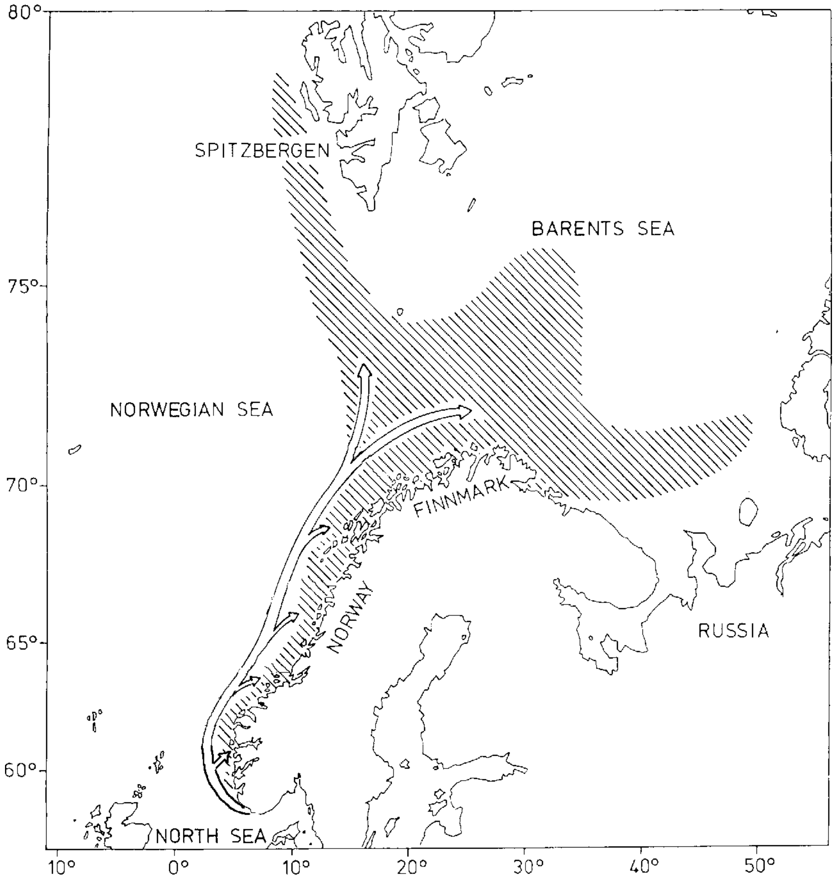

Figure 2.2. Drift routes of Norwegian spring-spawning herring larvae and adjacent nursery areas (hatched areas) for immature herring (0–3 year old).

Long-term trends

Stock size has varied from ca. 20 million t at the beginning of the 1950s to ca. 100 000 t in the late 1960s and then up to more then 10 million t again in the late 1990s (Toresen and Østvedt, 2000). During this time, the use of wintering, spawning, and feeding areas changed, as mentioned above (Dragesund *et al.*, 1997).

Present characteristics

A tendency towards a more northerly distribution in the Norwegian Sea has been observed in recent years. The wintering area has moved from fjords in northern Norway to oceanic areas off the coast following the recruitment of the large 1998–1999 and 2002 year classes. Spawning has also moved farther north.

Potential environmental influences

Inflow of Atlantic water to the Norwegian and Barents seas (the North Atlantic Oscillation, or NAO, index) seems to influence both the condition and fecundity of adult fish, as well as the survival of larvae (Figure 2.3; Holst, 1996; Toresen and Østvedt, 2000; Fiksen and Slotte, 2002; Sætre *et al.*, 2002). There is a very good correlation between local environmental changes in the spawning and nursery areas and large-scale variations in the Atlantic water inflow. Hence, growth in the fjord nurseries follows the interannual changes in temperature, but has also been found to decrease northwards along the coast and with increasing density (Husebø *et al.*, 2007). Environmental conditions also affect the condition of the fish, which again may reduce fecundity (Oskarsson *et al.*, 2002). Strong year classes have occurred during periods of good condition and high temperatures (Oskarsson *et al.*, 2002). However, recent research suggests that the highest survival of larvae occurs when they hatch early in the season, owing to a reduced overlap with predators or favourable conditions during the larval drift northwards (Husebø *et al.*, 2009). Early spawning is linked with high temperatures during wintering; hence, the environmental influence on recruitment may be more indirect through regulation of maturation and spawning time (Husebø *et al.*, 2009).

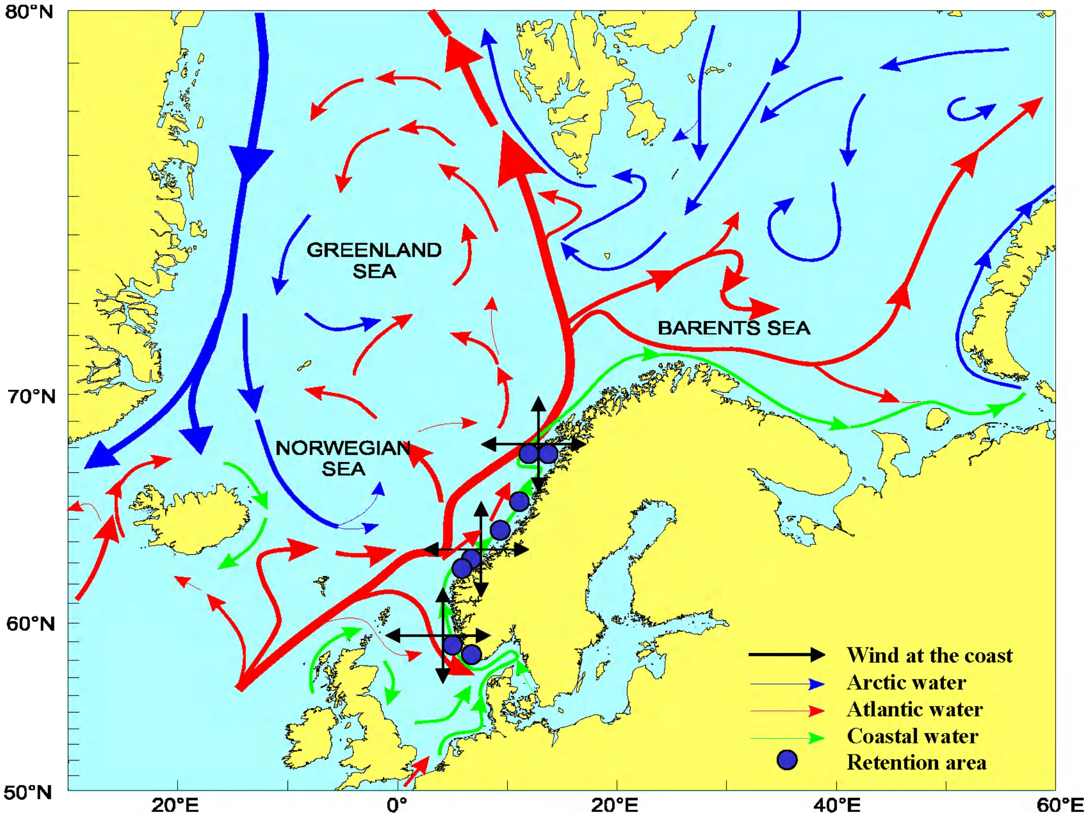

Figure 2.3. Physical forces on Norwegian spring-spawning herring. The survival of eggs at the bottom on the spawning grounds along the Norwegian coast is influenced by the temperature (T) and salinity (S) of the cold and less saline coastal water and mixing with warmer, more saline Atlantic water. Larval survival is also influenced by the T and S of the cold, less saline coastal water and mixing with warmer, more saline Atlantic water, and the northward flow of these currents. Wind force (i.e. direction and speed) may also influence larval drift, retention, and survival. The 0–3-group in the Barents Sea and fjords is influenced by the inflow of warm Atlantic water, having historical fluctuations in growth following temperature changes. Adult herring distribution, growth, and condition during the feeding season, and hence migration and reproductive potential during the spawning season, is also influenced by the flow of Atlantic/Arctic water into the main feeding area in the Norwegian Sea.

3 North Sea herring

Mark Dickey-Collas

The high phenotypic plasticity in Atlantic herring (*Clupea harengus*; McQuinn, 1997; Geffen, 2009; Dickey-Collas *et al.*, 2009a) means that the influence of the environment is fairly strong on most characteristics of the population (Cushing, 1967; Jennings and Beverton, 1991). It also results in many substock components (Figure 3.1; Heincke, 1898; Redeke and van Breemen, 1907; Cushing, 1955; Zijlstra, 1958; Baxter and Hall, 1960; Bridger, 1961) that interact with each other and are influenced in different ways by the environment (Wallace, 1924; Anthony and Fogarty, 1985; Hulme, 1995; Bierman *et al.*, 2010). There are also strong density-dependent effects in the population characteristics (Cushing and Bridger, 1966; Hubold, 1978; Winters and Wheeler, 1996; Melvin and Stephenson, 2007) that are currently very pertinent because the population increased in the late 1990s (Nichols, 2001; Simmonds, 2007; Dickey-Collas *et al.*, 2010).

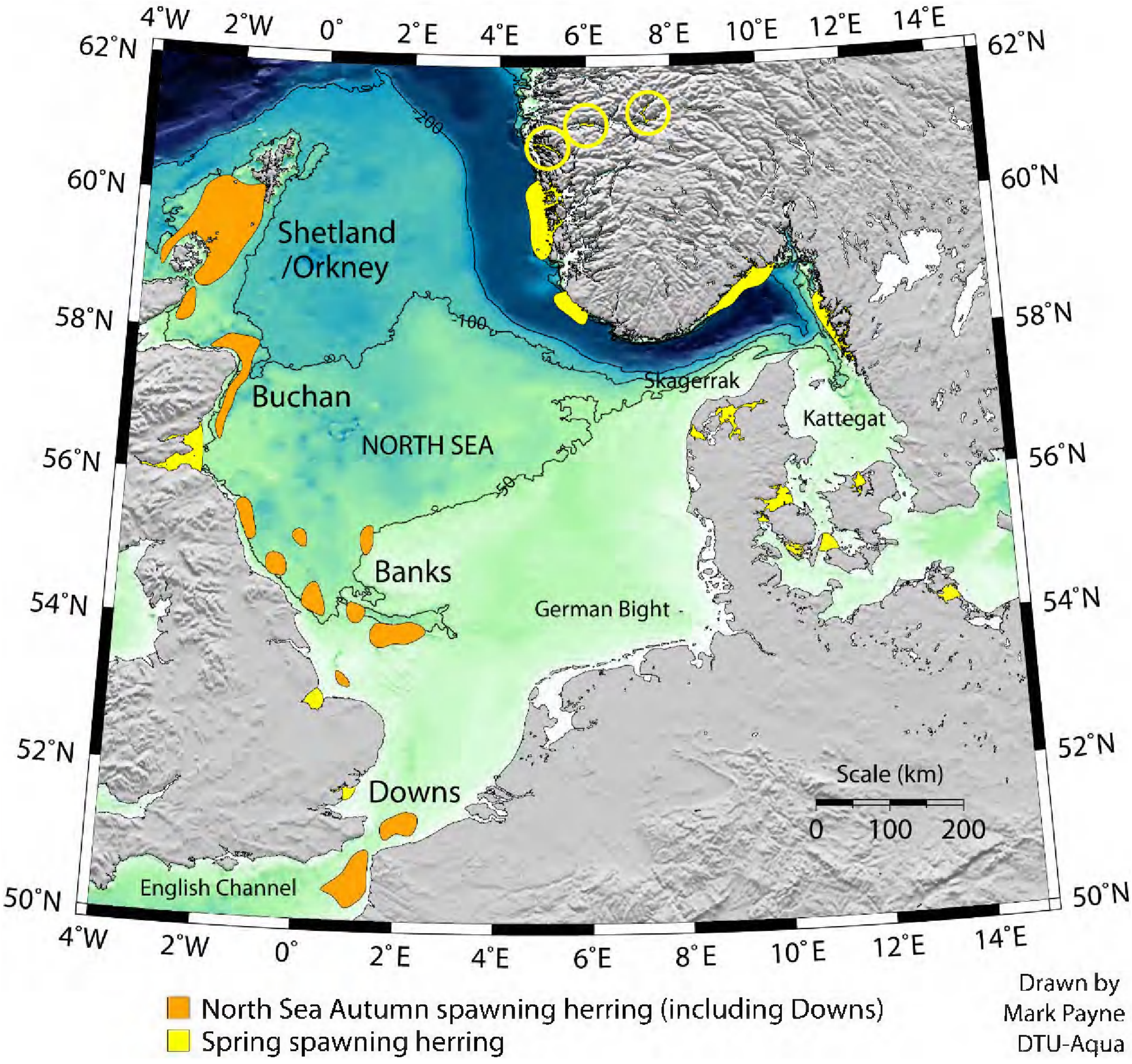

Figure 3.1. The current spawning sites of herring in the North Sea and adjacent waters and the location of the four spawning components of North Sea autumn-spawning herring. From Dickey-Collas *et al.*, 2010.

Life-history traits

The lifespan of the North Sea herring is 17–20 years (38–39 cm length; IMARES data). It currently matures between the ages of 2 and 3 years, although this changes over time (3–5 years from 1950 to the1960s; Cushing, 1967) with population size and individual year-class strength (ICES, 1965, 2009a; Burd, 1978, 1984). Mean length at maturity also exhibited an increasing trend from the 1930s to the 1970s, but then declines (mean length at maturity: 25–27 cm at age 2, 26–28 cm at age 3; Saville, 1978). The sex ratio is usually 50:50 for all ages. There is no sexual dimorphism in growth in length.

Wintering

The location of overwintering in the 20th century is based on knowledge of historical herring catches; however, detailed information, in the form of maps, is lacking. Harden Jones (1968), Burd (1978), and Corten (2000) assumed that overwintering occurs southwest of Norway in most years. This is only applicable to those fish that have already spawned (the Shetland, Buchan, and Banks components), because the Downs component is still spawning at this late stage in the year (Figure 3.2). Corten (2000) suggested that an early onset of *Calanus* production southwest of Norway delays the migration of the fish leaving this area to the normal feeding grounds. There is little in the way of survey data to support the ideas about locations or dynamics of the populations during the overwintering period. In recent years, there has been no fishery data on overwintering fish. Information from the mid-19th century suggests that overwintering may have been to the north (Poulsen, 2008; Figure 3.3). Evidence from other stocks (e.g. Norwegian spring-spawning herring) suggests that the location of overwintering may change over relatively short periods, but the timing or duration of overwintering may also change over longer time-scales (Alheit and Hagen, 1996, 1997; Corten, 1999a and references therein) when the Open Skagerrak periods or Bohuslän herring periods take place. These are periods when some of the overwintering herring enter the Skagerrak in winter.

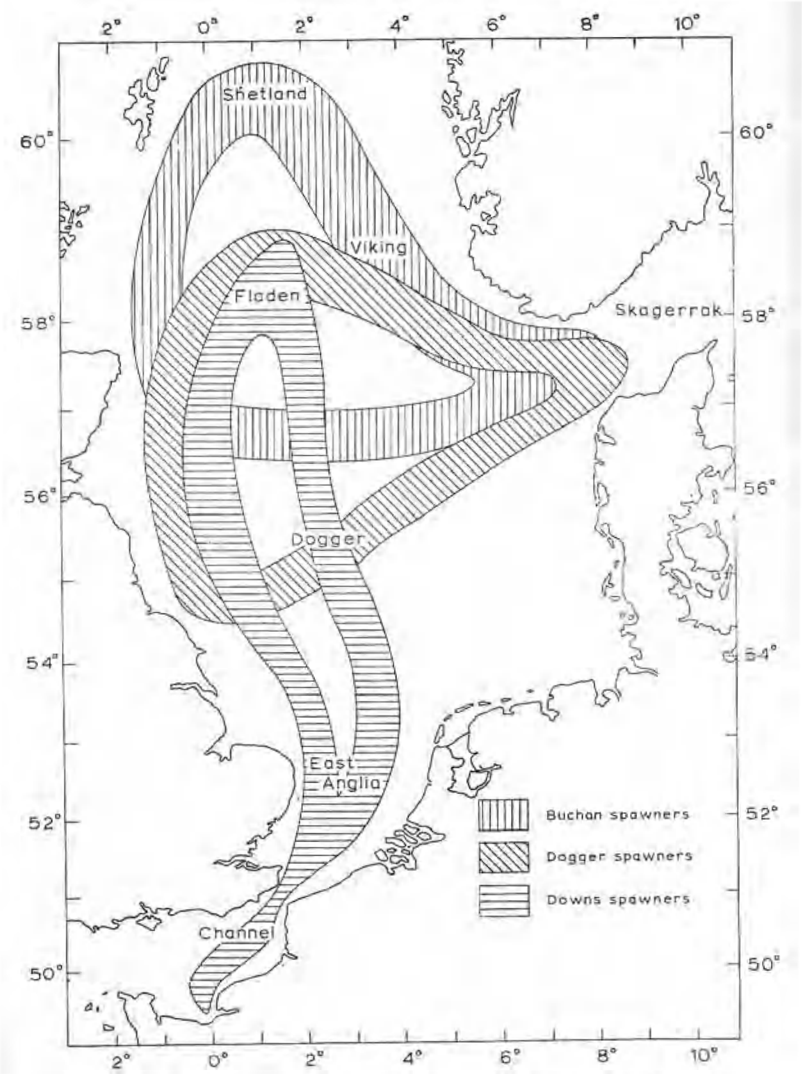

Figure 3.2. Suggested migration routes of three components of the North Sea herring stock. From Cushing and Bridger (1966).

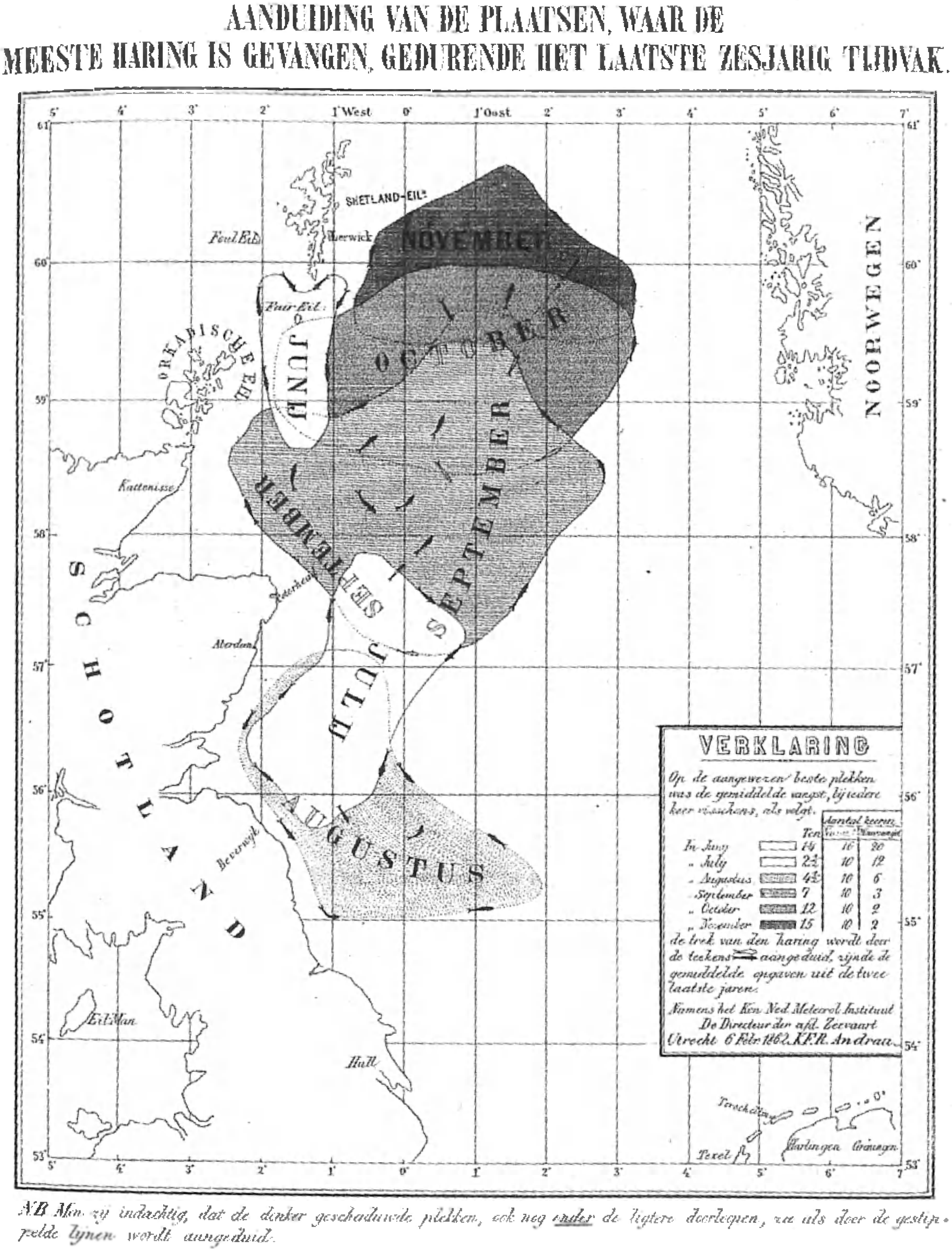

Figure 3.3. Map of the monthly distribution of fishing effort, 1856–1862. Inferred overwintering route of autumn-spawning herring from fleet activity in the mid-19th century. Copied from Poulsen (2008).

Spawning

The Atlantic herring is a synchronous determinate batch spawner (Bowers and Holliday, 1961; Blaxter and Hunter, 1982; van Damme *et al.*, 2009).

Time. Spawning of the main North Sea herring population begins in the northern part of the North Sea in September and then progresses southwards with time, ceasing in January in the eastern English Channel (See Figure 3.4; Boeke, 1906; Cushing and Burd, 1957; Zijlstra, 1969; Burd and Howlett, 1974). Smaller coastal populations tend to spawn in spring (Redeke and van Breemen, 1907; de Groot, 1980; Fox, 2001; Roel *et al.*, 2004).

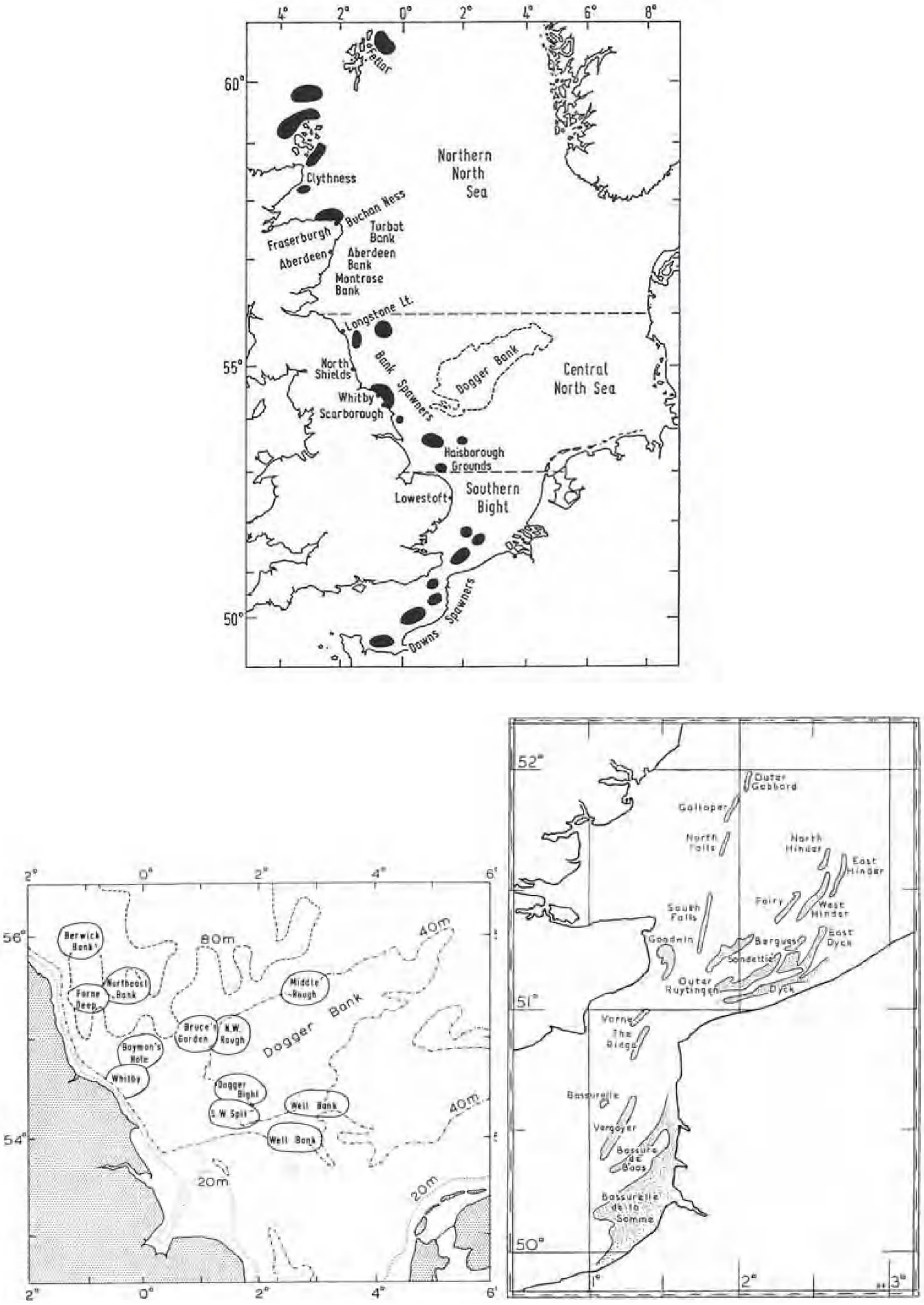

Figure 3.4. Detailed descriptions of North Sea herring spawning grounds in the 20th century. Top: map showing distribution of Dogger and Banks spawners (from Burd and Howlett, 1974). Bottom left: the Banks component (from Cushing and Bridger, 1966). Bottom right: the Downs component (from Cushing and Burd, 1957).

Habitat. Atlantic herring spawn benthic eggs that adhere to the substratum or to each other (Blaxter and Hunter, 1982; McPherson *et al.*, 2003). In the North Sea, herring use gravel beds that are generally at depths of 20–40 m (see Cushing and Burd, 1957; Parrish *et al.*, 1959). This constraint (gravel beds) limits and fixes the spawning location. The presence of the exposed gravel beds suggests that these areas have higher flows over the seabed and higher seabed shear stress. These sites must also be "upstream" of the nursery grounds. The number of spawning sites varies with stock size (Burd, 1985; Corten, 1999b, 2001a), with a decline in the periphery spawning sites at lower biomass of North Sea herring (Schmidt *et al.*, 2009). Atlantic herring are spatial repeat spawners (McQuinn, 1997), which is either a behaviour caused by natal returns to the "home" spawning bed or an adopted behaviour that has been learned or rediscovered by large year classes (Harden Jones, 1968; Wheeler and Winters, 1984; McQuinn, 1997). Like Pacific herring (*Clupea pallasii*), Atlantic herring are assumed to spawn in waves (temporally discrete cohorts; see Ware and Tanasichuck, 1989; McPherson *et al.*, 2003), but evidence to support or reject this hypothesis is weak. In thicker egg mats, mortality caused by oxygen deficiency can be high (Parrish *et al.*, 1959; Aneer, 1985), and the mats attract predators such as spurdog (*Squalus acanthias*), haddock (*Melanogrammus aeglefinus*), mackerel (*Scomber scombrus*), lemon sole (*Microstomus kitt*), and other herring (Hempel and Schubert, 1969; de Groot, 1980; Skaret *et al.*, 2002).

Feeding

Time. The main feeding period for North Sea herring is April–June (Hardy, 1924; Savage, 1937). Feeding intensity reduces in the build-up to spawning, and little feeding occurs over winter (Hardy, 1924). As the majority of North Sea herring are autumn and winter spawners, their energy strategy is different from that of Norwegian spring-spawning herring (Iles, 1984; Winters and Wheeler, 1996; Slotte, 1999b).

Predation mode. Herring mostly feed by foraging and targeting prey items, with perhaps very limited filtering at low light intensities (Hardy, 1924; Batty *et al.*, 1986, 1990).

Prey species. The prey of North Sea herring varies by location (Savage, 1937), season (Hardy, 1924), and year (Last, 1989). Larvae feed on nauplii and microzooplankton (Bowers and Williamson, 1951; Checkley, 1982) and then move on to *Pseudocalanus*, *Paracalanus*, and *Temora* copepodites, and small meroplankton; adults feed on *Calanus*, *Temora*, *Oikopleura*, Schizopoda, Amphipoda, and juvenile *Ammodytes* spp (Hardy, 1924; Savage, 1937; Last, 1989). In the northern part of the North Sea, the gastropod *Limacina* is also prominent in the diet. Seasonality in stomach contents is clear; fish eggs are present in the very early spring (when the feeding rate is low; Daan *et al.*, 1985; Segers *et al.*, 2007) and in June (Savage, 1937). *Calanus* is eaten in large numbers in spring, but the smaller copepods begin to dominate the diet by summer. In years when post-larval and juvenile sandeels are present in the stomachs (ca. 50% in the southern and western North Sea), they are present in substantial biomass in February–April (Hardy, 1924; Savage, 1937; Last, 1989). In some years, there may be a gradient in the feeding locations by component, but this is not true for all years (Harden Jones, 1968; Bierman *et al.*, 2010). Likewise, it appears likely that water depth and body length influence distribution (Guiblin *et al.*, 1996).

Schooling behaviour. It has long been noted that the distribution of feeding shoals correlates to plankton abundance; herring shoals are rarely found near diatom blooms (Savage and Wimpenny, 1936), whereas feeding is invariably associated with zooplankton abundance (Maravelias and Reid, 1997; Maravelias, 2001). Variability in spatial structure of these shoals tends to be at a scale of 6.5–20 nautical miles (Maravelias *et al.*, 1996), ignoring the unresolved small-scale variability. The distribution of feeding herring demonstrates very strong affinity with the southerly incursion of *Calanus* and *Limacina* into the North Sea every year (Bainbridge and Forsyth, 1972); both are influenced by the Atlantic inflow. In years when the *Calanus* peak is farther north, herring catches are also farther north (Corten, 2001b). The ratio between zooplankton production in the Buchan area and in the northeastern North Sea is also thought to influence where the herring feed (Bainbridge and Forsyth, 1972), because years with poor zooplankton production in the Buchan area were also years when the herring moved farther north (as determined by catches).

Migrations

The migrations of North Sea herring have been broadly mentioned in the sections above, and the traditional patterns are summarized in Figures 3.2 and 3.5. As stated above, the characteristics and mechanisms for overwintering are less easily defined than the spawning and feeding processes and locations. The occurrence of different migration patterns based on phenotypic differences of the components is currently thought to adhere to the adopt–migrant hypothesis (McQuinn, 1997), where generally stocks mix in the nursery areas and the summer feeding grounds, but migrate with others of their size as the need to spawn approaches. Isolated migrants (fast-growers or slow-growers) can join other components, and dispersal is more prevalent when established populations become unstable (after collapse or a recruitment boom; McQuinn, 1997; Corten, 2001a). Repeated imprinting of migration intensifies the spatial patterns, making straying less likely with spawning experience. However, evidence from west of the British Isles (Brophy and Danilowicz, 2002, 2003) suggests that, whether or not they are fast or slow growers, or from different nursery grounds, Celtic Sea maturing herring all return to their broader spawning area, suggesting natal homing (see Harden Jones, 1968).

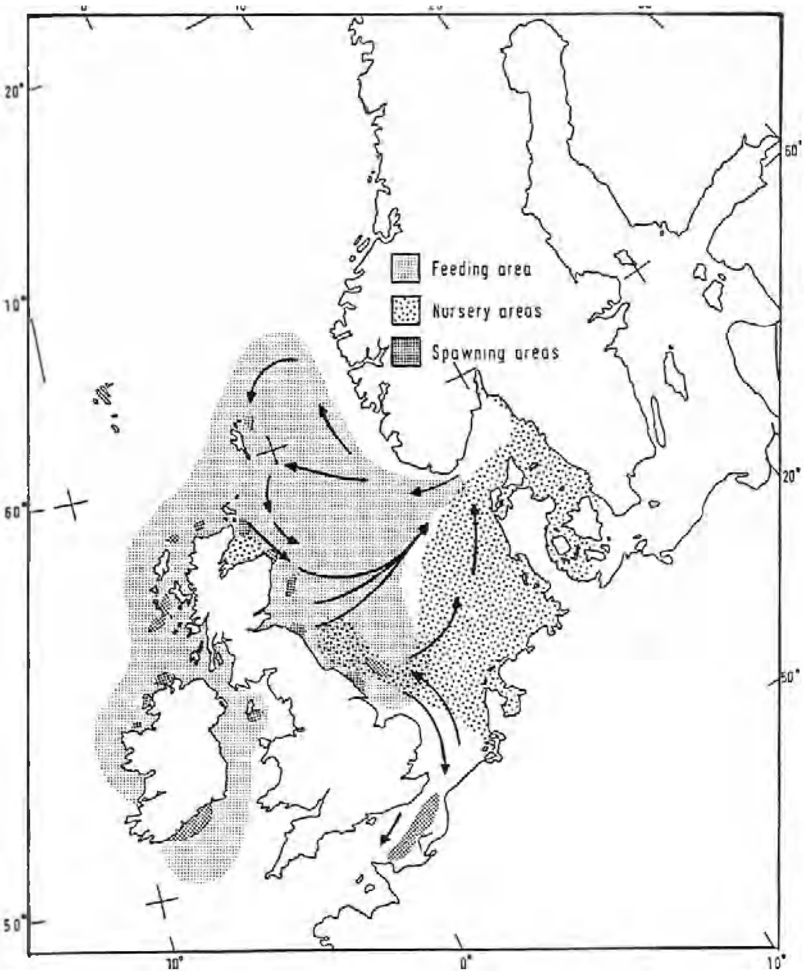

Figure 3.5. Schematic summary of generalized migration patterns of North Sea herring, from Burd (1978).

Larval drift and nursery areas

As a result of herring laying demersal eggs, the newly hatched yolk-sac larvae are closely associated with the spawning grounds (Postuma and Zijlstra, 1974). The abundance of young larvae is clearly linked to spawning potential (e.g. spawning-stock biomass, or SSB), with temperature being a slight influence of at the time of spawning (Postuma and Zijlstra, 1974; Saville, 1978; Schmidt *et al.*, 2009).

Larval drift is thought to be driven by wind-induced flows (Heath and Rankine, 1988; Heath *et al.*, 1997; Dickey-Collas *et al.*, 2009b). Larvae drift up to 9 km d^{-1} (Heath and Rankine, 1988). The Methot Isaacs–Kidd (MIK) net surveys of post-larvae demonstrate a general movement of the larvae in an easterly direction (ICES, 2009a), which is in broad agreement with prevailing winds and flows (Figures 3.6 and 3.7). The abundance of herring post-larvae in the MIK net survey demonstrates a strong relationship with the subsequent associated recruiting year class (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009), suggesting that year-class strength is mostly determined between the larval and post-larval stages (see Anthony and Fogarty, 1985; Oeberst *et al.*, 2009). The different spawning grounds in the North Sea experience different environmental variability (Petitgas *et al.*, 2009) and are affected by different boundary forcing (Hjøllo *et al.*, 2009); thus, searching for one "environmental driver" for recruitment may be naïve if there is no accounting for spatial and temporal differences in the environment. Most post-larvae metamorphose between April and July (Heath and Richardson, 1989). Variability in larval growth is thought to be temperature-dependent, with added variability from prey availability (Heath *et al.*, 1997; Fiksen and Folkvord, 1999; Johannessen *et al.*, 2000). In terms of larval abundance, the North Sea is not isolated, because larvae originating west of Scotland are also introduced by the Scottish coastal current into the northern North Sea (Heath and Rankine, 1988; Heath, 1989). Larvae from spring-spawning herring in the Norwegian fjords and Skagerrak and Kattegat also enter the North Sea.

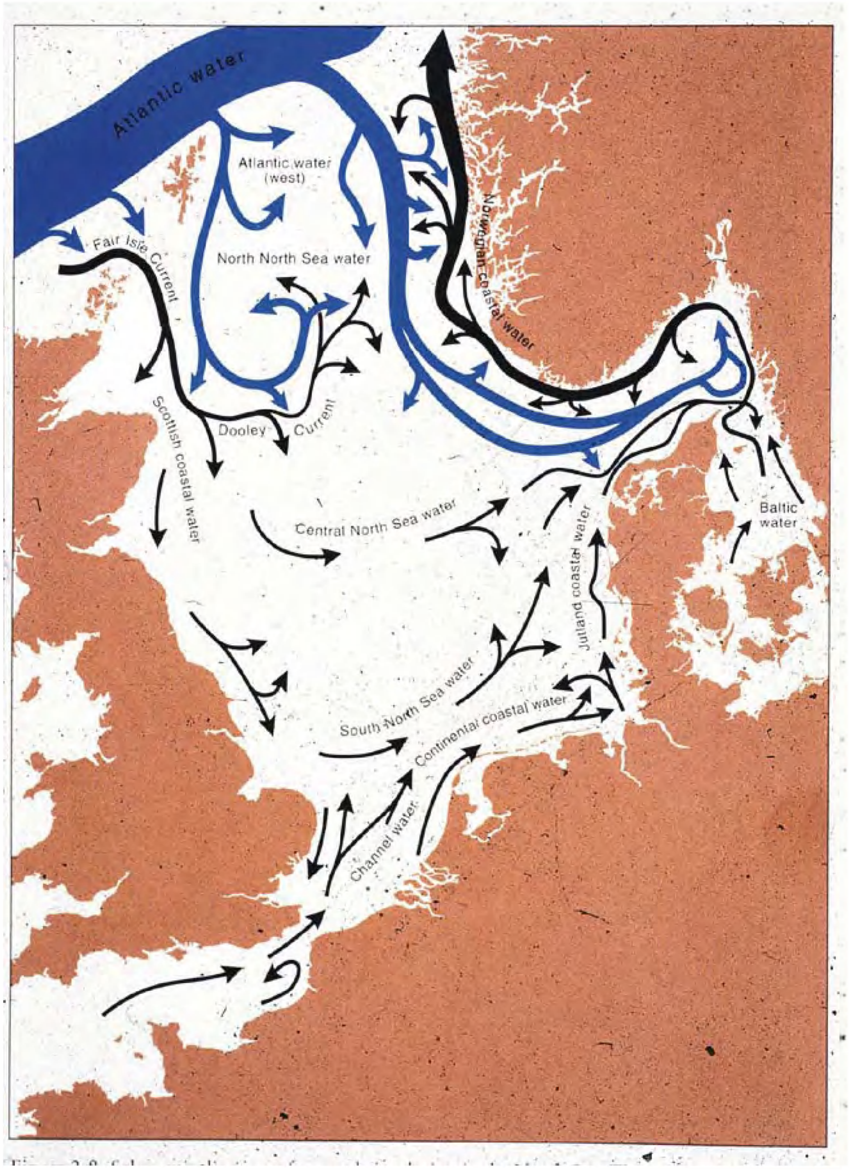

Figure 3.6. Schematic outline of the general circulation in the North Sea, showing the Atlantic inflow in the northwest, the English Channel inflow in the southwest, and the Baltic outflow in northeast, with their associated currents along the coast and across the North Sea.

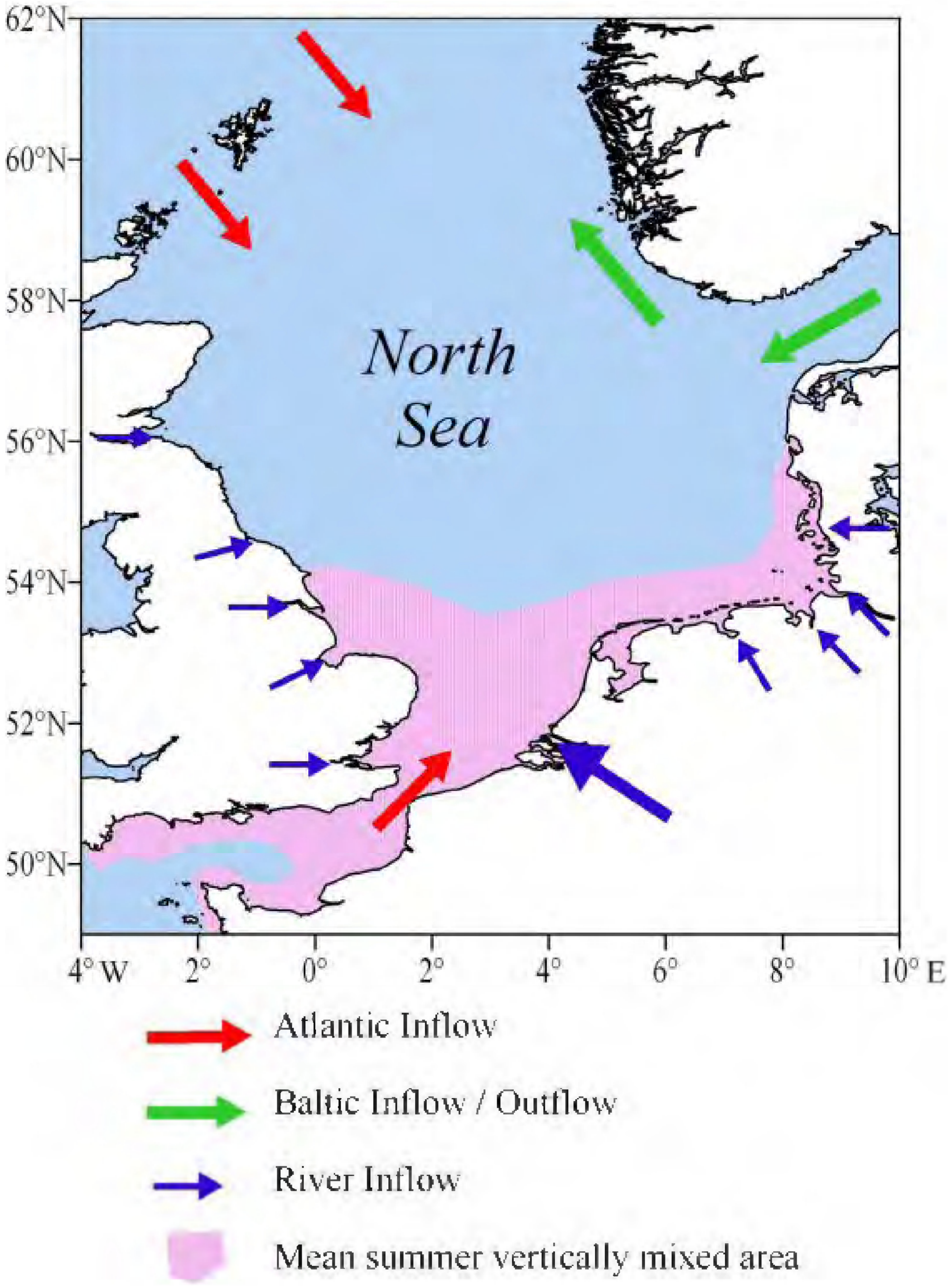

Figure 3.7. Schematic diagram of North Sea physical features. General circulation is that of a gyre, with Atlantic inflow from the northwest and Baltic outflow to the northeast. Tidal mixing fronts are important in the southern part, while summer thermal stratification develops in the central and northern parts. The southern part also shows many river discharges.

The nursery grounds for the metamorphosed juvenile 0-group fish are mostly in the southern and eastern North Sea (German Bight and Skagerrak). The juveniles appear to remain in these generally mixed waters (and to a lesser degree in other coastal areas) until they are 2 years old. Recruiting to the adult population is probably size- and maturity-dependent (Brophy and Danilowicz, 2003). The herring join the feeding adult population through active migration (Wallace, 1924). Burd (1984) suggested that the population is most likely to exhibit density-dependent effects on growth at age 1, but Heath *et al.* (1997)

suggest that these differences in length come from variability in growth during the larval stages. The length of fish at age 1 has a great influence on their length at later ages (Hubold, 1978). Recent year classes of North Sea herring (e.g. 2000) are apparently exhibiting density-induced decreases in growth and maturation rate (ICES, 2009a; Brunel and Dickey-Collas, 2010).

Long-term trends

The North Sea herring fishery has a long history (Poulsen, 2008), with countries going to war over the rights to fish and land their catches (e.g. England and Holland in 1652–1654). The catches between 1600 and 1850 were usually between 40 000 and 100 000 t year^{-1} (Poulsen, 2008). Catching opportunities for the fishery were known to be variable, and the variability of year-class strength led to the 18th century ideas that North Sea herring were part of a "mega-stock" that migrates to the Arctic in winter, and that a variable proportion of the mega stock returned every year to the North Sea (Sinclair, 2009). This was discredited in the late 19th century (Sinclair, 2009).

Variability in recruitment strength in the North Sea is considered to be less than in the Baltic (Cushing, 1996; Myers, 2001). Recruitment patterns from components of the stock also differ (Bjerkan, 1917; Cushing, 1992). Recent estimates suggest that spawning-stock biomass (SSB) between 1880 and 1940 was approximately 5 million t (Mackinson and Daskalov, 2007). In the 20th century, mechanization of the fishery led, for the first time, to a severe human impact on the stock (Hodgson, 1936; Cushing and Burd, 1957; ICES, 1965; Burd, 1978, 1985; Cushing, 1992; Nichols, 2001; Simmonds, 2007), as the stock went from an SSB of over 2 million t to below 50 000 t. Recruitment became highly impaired (Nash *et al.*, 2009). The fishery was closed from February–June 1977 to June 1983 (Burd, 1985; Dickey-Collas *et al.*, 2010). The collapse affected different components of the stock in different ways, with the southern components declining before the northern components (Burd, 1985; Cushing, 1992). As the stock declined, spawning became restricted, and many spawning grounds were abandoned (Schmidt *et al.*, 2009). The stock was considered healthy again by the early 1990s, but a decline in biomass occurred again in the mid-1990s, and only a swift response by management ensured that the stock did not collapse (Simmonds, 2007).

It is widely accepted that the recruit–stock relationship is domed for herring and that productivity per spawner is impaired at high spawning biomasses (Anthony and Fogarty, 1985; Zheng, 1996; Fox, 2001), but overall stock size or area size may influence this density-dependent effect (Winters and Wheeler, 1987). Until 2002, only 20% of the North Sea herring year classes had failed to correspond to a virtually linear relationship between spawning potential and recruitment strength at age 1 (Nash and Dickey-Collas, 2005); however, since 2002, recruitment has been poor despite over 1 million t of herring SSB (Payne *et al.*, 2009). This decline in recruitment has been attributed to a change in the hydrography or zooplankton of the North Sea (bottom–up controls).

Potential environmental influences

Kenny *et al.* (2009) suggested that the North Sea pelagic components of the ecosystem were predominantly controlled by top–down (fishery) mechanisms between 1983 and 1993, which shifted to a state responding mainly to bottom–up (environment) influences from the mid-1990s onwards. However, it is difficult to disentangle the influences of the fishery and the environment during other times of reduced productivity, e.g. the stock collapse of the 1970s. Corten (2001a) suggests that many recent fluctuations in the distribution of North Sea herring are driven by stock increase, changes in zooplankton production, and variability in the Atlantic inflow caused by the Fair Isle Current. The interaction of year-class strength and environmental signals (combined imprinting effects on the individual and, hence, lag effects on the population) may make the interpretation of the influence of environment difficult (Corten, 2001a; Payne *et al.*, 2009). Authors have suggested a relationship between changes in the distribution of overwintering herring and the North Atlantic Oscillation (NAO), as seen in the Open Skagerrak periods (Alheit and Hagen, 1996, 1997; Corten, 1999a), but as highlighted by Hjøllo *et al.*, (2009), the NAO does not influence all areas of the North Sea in the same manner. As mentioned above, the location of the feeding grounds is probably in response to zooplankton abundance. The spatial nature of the life cycle has never been accounted for in a multispecies virtual population analysis (MSVPA) type of approach (ICES, 2009b), hence, realistic multispecies interactions are difficult to assess. An attempt to consider the spatial nature of North Sea herring dynamics was begun relatively successfully by Heath *et al.* (1997). Overall, the evidence suggests that changes in the abundance of horse mackerel (*Trachurus trachurus*), mackerel, and sandeel (*Ammodytes marinus*), as well as in the production of *Calanus*, *Temora*, and *Pseudo*/*Paracalanus* (Beaugrand, 2003; P. C. Reid *et al.*, 2003) will affect herring production and distribution (Bainbridge and Forsyth, 1972), and vice versa. The relative role of herring in the system also varies and can be described as a prey-to-predator loop (P2P; Bakun and Weeks, 2006). The increased abundance of herring, combined with a reduction in zooplankton, will increase the impact of herring on the survival of the eggs of plaice (*Pleuronectes platessa*) and cod (*Gadus morhua;* Ellis and Nash, 1997; Segers *et al.*, 2007). Sprat (*Sprattus sprattus*) and herring appear to have a complex relationship, with some sympatric signals (Torstensen and Gjøsæter, 1995) and divergent signals in other areas (Corten, 2001a).

4 Northwest Irish herring

Leonie Dransfeld, Maurice Clarke, Kieran Lyons, and Clementine Harma

Life-history traits

The oldest reported age for Northwest Irish herring is 16 years (Bracken, 1963). The current assessment pools all fish over 10 years in a plus group. In the assessment, 100% maturity is assumed to be at 3 years of age (2-winter rings), whereas younger ages are considered 100% immature (ICES, 2009a). However, a maturity ogive from the 2007 acoustic survey revealed maturities of 58% at 1-ring, 99% at 2-rings, and 100% at 3-rings. The maturity ogive used in the assessment considers all 1-ringers to be immature and all subsequent age groups as fully mature (ICES, 2007a). *Clupea harengus* is a determinate one-batch spawner (Blaxter and Hunter, 1982). The Northwest Irish stock is composed of autumn-, winter-, and spring-spawning components. Farran (1938) reported that fecundity was 50% lower in spring spawners than in autumn spawners, but that individual ova were larger in spring spawners than in autumn spawners. He also demonstrated that spring-spawning fish reached a much greater maximum length than autumn spawners. Relationships between fecundity and length can be found in Grainger (1976).

Wintering

Spawning occurs during autumn and winter, and shoals congregate and move to inshore spawning grounds (Figure 4.1). After spawning, shoals disperse and move to offshore waters. The distribution of shoals after spawning has changed. Aggregations of overwintering fish were traditionally fished along the west coast of Ireland and in Donegal Bay, but no high concentrations of overwintering fish have been found recently in these areas (ICES, 1994; Molloy and Kelly, 2000). Some occurrences of overwintering fish have still been observed east of Tory Island (ICES Division VIa(S)) for several weeks in January (Molloy and Kelly, 2000).

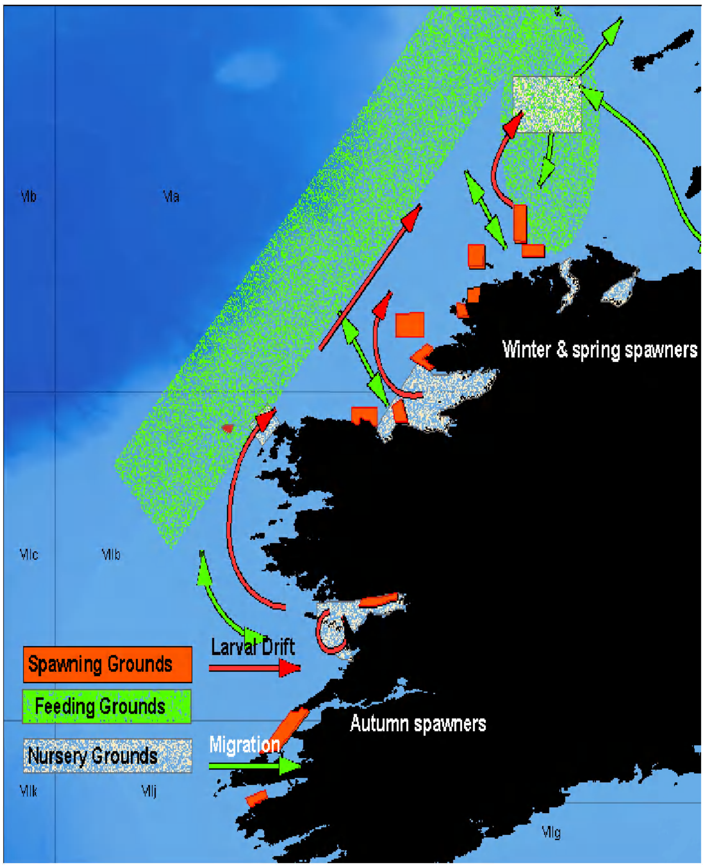

Figure 4.1. **Schematic presentation of the life cycle of herring west and northwest of Ireland.**

Spawning

Time. Spawning has traditionally been between September and October, with a southward progression of spawning (Molloy, 1983; Grainger and McArdle, 1985; Molloy and Barnwall, 1988). Recently, spawning has extended into November (Breslin, 1998; Molloy and Kelly, 2000).

Habitat. Spawning occurs in shallow water close to the west and northwest coasts of Ireland (Molloy, 1983; Molloy and Barnwall, 1988; Breslin, 1998), although recent reports are that spawning also occurs in deeper waters (Molloy and Kelly, 2000). West coast herring are autumn spawners, with spawning grounds off the mouth of the River Shannon, Casla Point, Galway Bay, and along the coast of Sligo and Mayo (ICES, 1994; Breslin, 1998).

In the northwest Irish herring fishery, there are three separate spawning units: autumn spawners during September and October in Donegal Bay, and winter spawners and spring spawners off the north coast (Molloy, 1983; Breslin, 1998). Anecdotal evidence from fishers suggests that the spring-spawning component of the north coast was increasing in the 1990s (Breslin, 1998). Peak spawning times from the autumn component have been inferred by larval surveys and occur in late September and October in water temperatures of 10–12°C (Molloy and Barnwall, 1988).

There is evidence from several stock-identification methods (genetics, morphometrics, parasitology, and micro-otolith structure) that the spawning aggregations west and north of Ireland are distinct from those of other neighbouring herring populations, such as west of Scotland or Celtic Sea herring (Hatfield *et al.*, 2007).

The fishery currently occurs on spawning aggregations. However, until the 1980s, fishing was mostly on recovering spent fish or, especially in the 1920s, on pre-spring-spawning fish.

Feeding

There is little information on the diet of herring in this area. Farran (1944) noted that the stock is distributed west of what is now known as the Islay Front. These waters of salinity >35 are richer in plankton than the fresher, colder water farther east (Farran, 1944).

Time. Feeding times have been inferred from studies of fat content. No feeding occurs throughout winter, and the fat content is at a minimum in March and April. Feeding is resumed in late spring, and fat reserves peak during July and August. Feeding is also interrupted during spawning, and autumn spawners briefly resume feeding in October/November before overwintering (Molloy and Cullen, 1981).

Habitat. Feeding grounds are offshore waters (Figure 4.1) extending from Galway west of Ireland to Stanton Bank and between Tory Island and Malin Head (Molloy, 2006).

Schooling behaviour. Results from stock-discrimination methods suggest that Northwest Ireland herring are mixing with other herring from the west of Scotland and possibly Irish Sea herring at feeding grounds over the Malin shelf (Hatfield *et al.*, 2007). A synchronization of the three herring acoustic surveys in this area (led by the Republic of Ireland, Northern Ireland, and Scotland) has been organized since July 2008 to estimate the biomass more accurately for stock-assessment purposes and to determine whether or not the mixing hypothesis in the feeding grounds can be validated.

Migration

The "triangular" migrations described for many herring stocks, i.e. movements between spawning, feeding, and wintering areas, also characterize herring in this area.

Fish move from offshore towards the well-known spawning grounds. These fish were traditionally fished from December to January along the line of the outer headlands (Farran, 1944) in depths of ca. 40 m as they moved inshore to spawn. Bracken (1964) described how the autumn fishery tracked shoals from north of Aranmore Island to Rathlin O'Beirne Island where they spawned. The fish quickly dispersed northwestwards to waters of ca. 120 m depth. This pattern of post-spawning migration was described for the other west-coast spawning grounds by industry sources (Molloy and Kelly, 2000). These reports suggest that herring overwinter in deeper waters off the west coast, although Molloy (2006) notes that autumn spawners also overwintered in the inshore waters of Donegal Bay.

On the north coast, anecdotal reports from fishers describe migrations toward the spawning grounds from the north and northwest.

Farran (1937) noted that the north-coast spring spawners were fished by pelagic driftnets between 16 and 64 km (10 and 40 miles) off north Donegal (ICES Division VIa(S)) from April to June when they were feeding. The fish then moved northwestwards towards the shelf edge in water ca. 160 m deep, where they were fished by French bottom trawlers. In Division VIIb, herring are located towards the shelf break northwest of Eagle Island in summer, where they were fished by Dutch trawlers at 120–150 m depths (Molloy, 2006; Molloy and Kelly, 2000).

The extent to which these herring migrate into the neighbouring ICES Division VIa north is not known.

Tagging experiments conducted in 1990 off the west coast of Ireland (ICES Division VIIb), have demonstrated that the majority of fish migrated northwards between July and February and were recaptured not far from the release area (Figure 4.1). Some fish also migrated southwards and were captured between October and November in Galway Bay, with a few moving into the neighbouring stock area of Division VIIj. Maturity stages of recaptured fish suggested migration to spawning grounds (Molloy *et al.*, 1993).

Larval drift and nursery areas

Drift patterns in this area are not well documented. It has been suggested that larvae from ICES Division VIa(S) drift towards the Scottish west coast (Grainger and McArdle, 1985; Molloy and Barnwall, 1988), and that larvae hatching farther south follow this northward drift. This is in line with known current directions in this region (Figure 4.2). There is evidence, based on parasite loading, that some juvenile herring from Scottish west-coast sea lochs belong to this stock (McKenzie, 1985). It is likely that larvae from the neighbouring stock in Division VIIj drift into Divisions VIIb and VIa(S) (ICES, 1994).

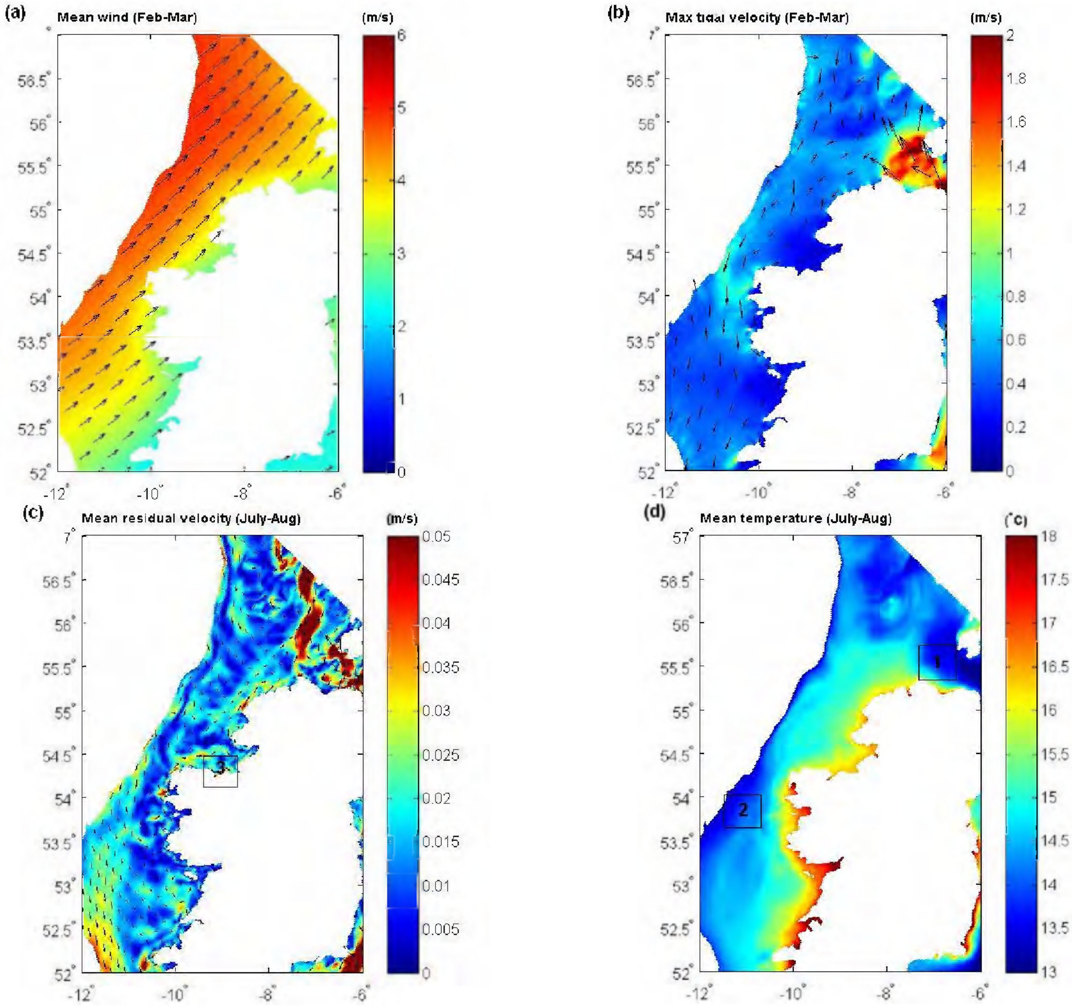

Figure 4.2. Mean model output to illustrate prevailing oceanographic conditions around Ireland. Examples of winter/spring conditions: (a) mean windfields and (b) tidal currents in February–March. Examples of summer conditions during stratification: (c) residual flows and (d) mean surface temperatures in July–August. Fronts include the Islay front northeast of Ireland (1) and the Irish shelf front west of the Celtic Sea (2); both are thermohaline fronts persisting throughout the year, with an additional tidal mixing front developing near Islay during summer stratification. Residual currents are the Irish coastal current (3), a clockwise density current, and the Atlantic shelf edge current (not shown). Circulation is mainly wind driven, prevailing southeasterlies from October to May, and density driven from May to October. Model details are available from http://www.marine.ie.

Studies in Galway Bay indicated that larvae are circulated in a cyclonic gyre in the Bay, with some larvae being advected outwards (Grainger, 1980a). Maximum larval depth below the surface was between 5 and 15 m, and there was no evidence of diel migration or variation in the distribution of different larval size categories (Grainger, 1980a).

Nursery grounds are typically in inshore bays. Among the best-known nurseries are Galway Bay, Broad Haven, Donegal Bay, Sheep Haven, Lough Swilly, and Lough Foyle (ICES, 1994; Molloy and Kelly, 2000). The latter authors also record Stanton Bank as a nursery area. This area is now known to contain juveniles from this stock and also from the Division VIa(N) and VIIa(N) stocks (Hatfield *et al.*, 2007).

Long-term trends

Spawning stock size peaked in 1988 as a result of two extremely large cohorts (1981 and 1985 year classes) entering the stock. Since then, there has been a steady decline. Preliminary assessments are only informative in the converged VPA (until 1998). However, they indicate that the stock has been below B_{lim} for the last decade (Figure 4.3; ICES, 2009a). Landings have fallen drastically since 1999 (ICES, 2009a). Mean weights-at-age display a relatively stable pattern over the available time-series (see Figure 4.4); however, this series is quite short.

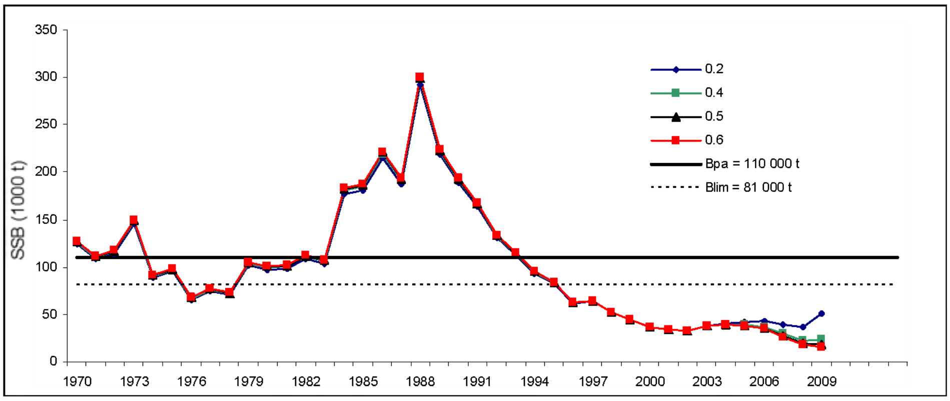

Figure 4.3. Estimation of spawning-stock biomass of herring in ICES Divisions VIa(S) and VIIb and c (see ICES, 2009a) in relation to reference points.

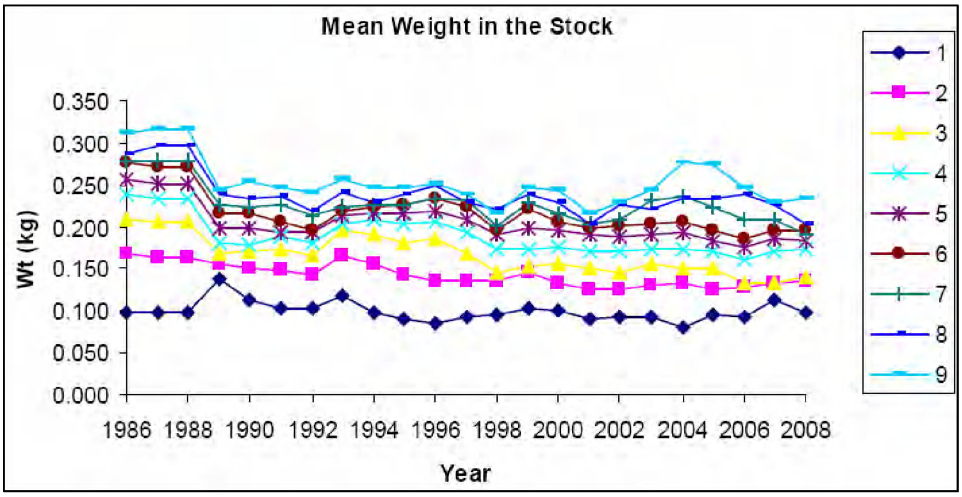

Figure 4.4. ICES Division VIa(S) and Division VIIb and c herring. Mean weights in the stock (kg; ICES, 2009a).

Long-term changes in the spawning components have occurred both in the area and at the time of spawning. The largest fishery from 1908 to the end of the 1920s was the spring-spawning herring located off the north and west coasts of Donegal. Although autumn spawners were present on the northwest and Donegal Bay coasts, they made up a much smaller component of the catches at that time (Farran, 1944). These autumn spawners, because of their inshore migrations in late summer, were fished by artisanal fisheries. In Mayo, Sligo, and Galway, only autumn spawners were fished, and only in small quantities. However, mackerel (*Scomber scombrus*) fishing was much more important in these areas than in Donegal (Farran, 1944). From the 1930s to the 1950s, herring abundance was low throughout Ireland. The revival of large-scale fishing after 1958 was based largely on autumn spawners off west Donegal and, by the late 1960s and early 1970s, off Mayo, Sligo, and Galway (Bracken and Phillips, 1968; Molloy, 2006). This pattern continued into the 1980s. However, by the early 1990s, the winter/spring-spawning component of the north Donegal coast was much more important again (Molloy, 2006; Molloy and Kelly, 2000). There is clear evidence that the stock declined from high levels in the 1920s, and that recruitment in the 1930s was poor. The revival of the fishery in the 1960s was only of the autumn-spawning component, and the spring-spawning component did not become an important part of the catch again until the 1990s.

This stock has had some very high recruitment, interspersed with long periods of fairly poor recruitment. Good year classes were spawned in 1914, 1920, 1924, and 1925 (Farran, 1930), in 1963 (Bracken and Phillips, 1968), and in 1981 and 1985 (ICES, 2009a). There is no evidence of good recruitment since.

Present characteristics

The stock is currently at a low level. Anecdotal evidence from fishers and catch data indicate that, in recent years, spawning has occurred in deeper water, herring have a more northerly distribution, and spawning has occurred later (Molloy and Kelly, 2000).

Potential environmental influences

Studies on the influence of the environment on the life cycle and population dynamics of northwest Irish herring are limited. Prevailing oceanographic conditions in the study area are shown in Figure 4.2, highlighting the main currents and fronts. These can potentially influence larval and juvenile transport routes, act as barriers, and/or provide areas of increased productivity for feeding.

Grainger (1980b) examined 80 years of Irish landings data and considered them to be a reasonable index of abundance. Trend over time varied widely, with a "secular trend" and superimposed shorter-term fluctuations. The secular trend was inversely related to sea surface temperature (SST). Short-term trends were related to SST and salinity anomalies 3–4 years earlier. The environmental factors seem to act at the winter larval stage. These long-term trends in herring catches revealed herring abundance decreasing with a warming of the SST in the 1930s–1940s. Short-term fluctuations in catches are believed to reflect real fluctuations in herring abundance on a cycle of ca. 10 years. These were correlated with:

- salinity in the Western Approaches, especially in the two winter quarters, with a lag period of three years; and
- SST on the shelf and west off the shelf, especially November, December, and January, with a lag period of 3–4 years. Although herring correlated negatively with temperature in the long term, short-term variations were positively correlated.

5 Celtic Sea herring

Leonie Dransfeld, Maurice Clarke, Kieran Lyons, and Clementine Harma

Life-history traits

The lifespan of Celtic Sea herring (*Clupea harengus*) can be up to 12 years (Irish Marine Institute, unpublished data). However, in recent years, fish older than 8 years have rarely been caught, and the plus-group in stock assessment is currently 6-winter rings (ICES, 2009a). The stock assessment considers 0% of 1-year-olds, 50% of 2-year-olds, and 100% of 3-year-olds to be mature. However, this oversimplifies the situation for fish up to 2 years old. Of the fish caught in the adult fishery in the Celtic Sea proper, maturity at 2 years is much greater than 50% (Lynch, 2009). This effect has been demonstrated by maturity studies on acoustic surveys of this stock (ICES, 2009a). A dramatic shift towards earlier maturity has taken place in cohorts spawned since 1971 (Lynch, 2009). Brophy and Danilowicz (2002) demonstrated that late-maturing 1-ringers leave the Irish Sea and appear as 2-ringers in the Celtic Sea catches. New information (Beggs *et al.*, 2009a) indicates that some older fish also stay in the Irish Sea and return as 3-ringers or even 4-ringers, to the Celtic Sea. It is possible that, when stock size was low, the relative proportion of late-maturing fish from the Irish Sea was greater. This may explain why observed maturity in the catches was later in those years.

The herring is a determinate one-batch spawner (Blaxter and Hunter, 1982). The Celtic Sea stock is composed of autumn-, winter-, and spring-spawning components. The relationship between fecundity and length has been calculated for both spawning components of Celtic Sea herring. The regression equations of fecundity vs. fish length can be found in Molloy (1979).

Wintering

The overwintering areas for this stock are poorly understood. Shoals congregate for spawning in inshore waters along the coast and then move to deeper waters after spawning. The fish tend to disperse quickly after spawning (Molloy, 2006). Some shoals of spent fish have been found close to the coast.

Spawning

Time. Celtic Sea herring consist of a mixture of autumn and winter/spring spawners, with spawning occurring between late September and February. The two spawning components are known to exhibit differences in biological parameters in relation to growth, recruitment, and mortality rate. The timing of peak spawning has undergone several changes. Prior to 1974, autumn spawning was not evident (Molloy and Cullen, 1981). Subsequently, spawning off the southeast coast occurred in autumn (October–November) and in winter, with peak spawning in January (Molloy, 1989; Breslin, 1998). Herring on the southwest coast of Ireland were mainly autumn spawners that spawned between September and October, and herring in the southeast were mainly winter spawners. As shown in Figure 5.1, autumn spawning along the south coast is now rare (Harma *et al.*, 2009), and an otolith microstructure study revealed that winter is currently the dominant spawning season in the Celtic Sea (Brophy and Danilowicz, 2002). Larger autumn-spawning fish can still be a relatively important component around the west coast.

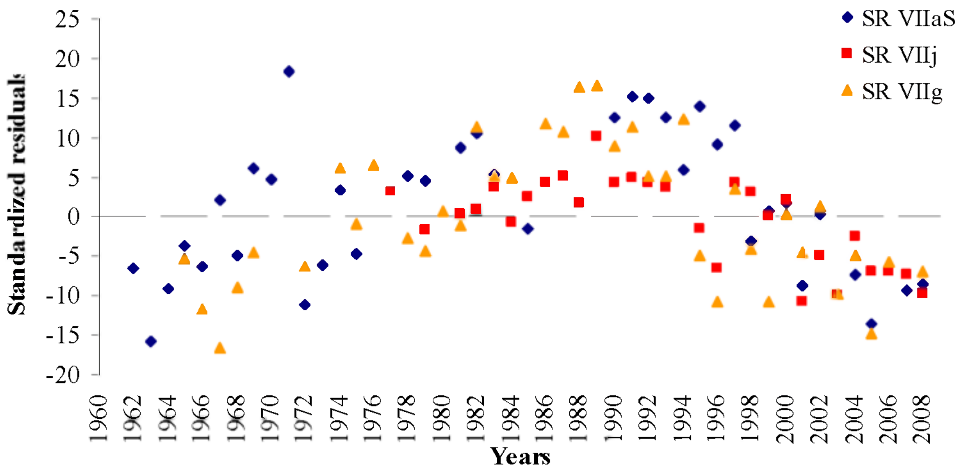

Figure 5.1. Long-term changes in the proportion of autumn-spawning fish (AS) per ICES division in the Celtic Sea. Distribution of standardized residuals extracted from Chi-squared analyses ($p<0.001$); negative values represent a lack of AS compared with what would be expected if the distribution had been random (Chi-squared distribution, without assumption); positive values represent a surplus of AS in the samples compared with the long-term expectation.

Habitat. Spawning grounds are well defined along the south and southwest coasts of Ireland (Molloy, 1980; Breslin, 1998; ICES, 2009a). Location of spawning grounds, derived from the distribution of small herring larvae, ready-to-spawn adult fish, and anecdotal information from fishers overlap and are consistent over years (Breslin, 1998). Individual spawning beds within the spawning grounds have been mapped and consist of either gravel or flat stone (Figure 5.2; Breslin, 1998; C. O'Donnell, pers. comm.).

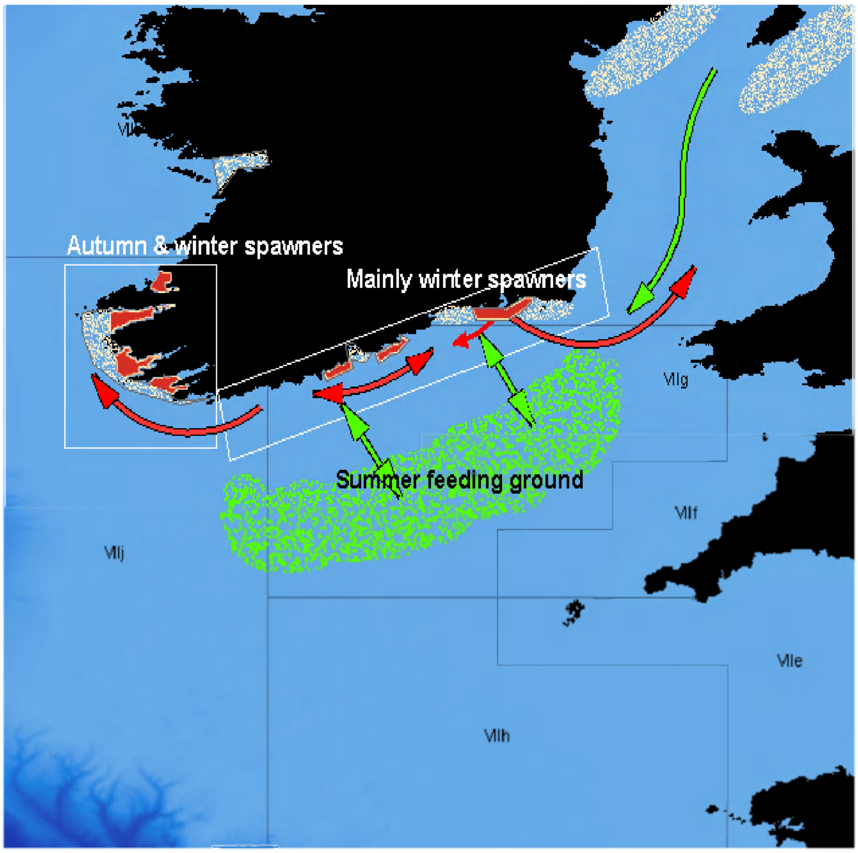

Figure 5.2. Schematic presentation of the life cycle of Celtic Sea and ICES Division VIIj herring.

Feeding

Time. There is little information on the specific diet of this stock. Farran (1927) highlighted the importance of *Calanus* spp. copepods and noted that they peaked in abundance in April/May. Fat reserves peak in June–August (Molloy and Cullen, 1981). Feeding is interrupted during spawning, and autumn spawners, spawning in September, resume feeding briefly in October before stopping again during winter. No feeding occurs throughout winter.

Habitat. Feeding grounds are located in offshore waters in the central Celtic Sea (ICES, 1994). The summer offshore feeding grounds (Figure 5.2) have demonstrated an absence of immature stage-1 fish, indicating that prerecruits do not migrate with the adults to the summer grounds (Burd and Bracken, 1965).

Shoaling behaviour. Summer shoals are dispersed during feeding (Molloy, 1980) and are often located in the upper part of the water column (Breslin, 1999). However, they have been fished by bottom trawls in these areas (Hodgson, 1951).

Migrations

Juveniles migrate from nursery areas to spawning areas for their first spawning. Age distribution of the stock suggests that recruitment in the Celtic Sea occurs first in the eastern part of the Celtic Sea and then moves westwards (ICES, 1994). Analysis of otolith microstructure indicates that herring disperse from the Celtic Sea into the Irish Sea during the larval phase (Figure 5.2; Brophy and Danilowicz, 2002, 2003). Tagging experiments reveal evidence of juvenile migration from the Irish Sea to the Celtic Sea (Molloy *et al.*, 1993). The return of juveniles of Celtic origin from the Irish Sea is attributed to larval imprinting rather than juveniles learning from repeat spawners, because there are no spawning adults migrating with them (Brophy *et al.*, 2006). Recent work by Beggs *et al.* (2009b) demonstrates that some late-developing fish remain in the Irish Sea, returning as 3-, 4-, or 5-year-olds.

The relative proportions of winter-spawned (of Celtic Sea origin) and autumn-spawned herring at nursery grounds in the Irish Sea vary considerably from year to year (Brophy and Danilowicz, 2002, 2003; Burke *et al.*, 2009). In autumn and winter, some of them migrate back to the Celtic Sea for first-time spawning (Molloy *et al.*, 1993; Burke, 2008). In one year class examined, otolith-shape analysis revealed that 42% of adults spawning in the Celtic Sea had spent their juvenile period in the Irish Sea (Burke, 2008; Burke *et al.*, 2008). Adult Celtic Sea herring migrate from spawning grounds to feeding grounds, and vice versa in spring and autumn. Shoals congregate and move into shallow coastal waters for spawning, after which the shoals disperse into deeper offshore waters to feed in the central Celtic Sea (Figure 5.2; Molloy, 1980). Off the southwest coast of Ireland, herring congregate for spawning in autumn, but little is known about where they reside in winter (ICES, 1994).

Larval drift and nursery areas

Herring larvae are found from October to March near the spawning grounds described above. Larvae are transported by currents either into the Irish Sea or westwards along the south coast of Ireland (Figure 5.2; Molloy and Corten, 1975; ICES, 1994).

Nursery areas are located in the bays and estuaries along the south and southwest coasts and in the western and eastern Irish Sea (ICES, 1994). Microstructure analysis of otoliths from juveniles in Irish Sea nursery grounds indicated that a large proportion of individuals caught were winter spawners, originating in the eastern Celtic Sea (Brophy and Danilowicz, 2002). Juveniles originally from the Celtic Sea stock were found to have different growth rates, depending on whether they resided in nursery areas in the Celtic

Sea, or in the western and eastern Irish Sea. The variability in growth-rate patterns occurs mainly in the larval phase and could be attributed to the different temperature regimes of the Celtic and Irish seas, suggesting that larval drift into the Irish Sea could be a factor in Celtic Sea recruitment variability (Brophy and Danilowicz, 2002). Larval dispersal can further influence maturity-at-age. In the Celtic Sea, faster-growing individuals mature in their second year (1 winter ring), whereas slower-growing individuals spawn for the first time in their third year (2 winter rings). Prerecruitment dispersal, such as into the Irish Sea, and subsequent decreases in growth rates could, therefore, determine whether juveniles are recruited to the adult population in the second or third year (Brophy and Danilowicz, 2003). The proportion of winter-spawned Celtic Sea herring in Irish Sea nursery areas has fluctuated widely over the last 10-year period (24–89%; Burke *et al.*, 2009). Herring from the west and southwest coasts spend time close to the south coast as juveniles, but also have been found to migrate up to the west coast (Molloy, 2006).

A recent survey of juvenile areas found large concentrations in the bays of southwest Ireland, Kinsale and Cork harbours, Dunmanus Bay, and the east coast of Ireland from Rockabil to Dundalk Bay (Clarke and Egan, 2008).

Long-term trends

Mean size- and weight-at-age peaked in the mid-1970s and have declined since (Figure 5.3). Condition factor has also declined during this period. Growth rates of cohorts from the 1960s and 1970s were higher than in the 1980s and 1990s (Lynch, 2009). The maturity of the population at age 2 shifted from low (~30%) to very high (~75%) in the early 1970s (Lynch, 2009; Molloy, 1979).

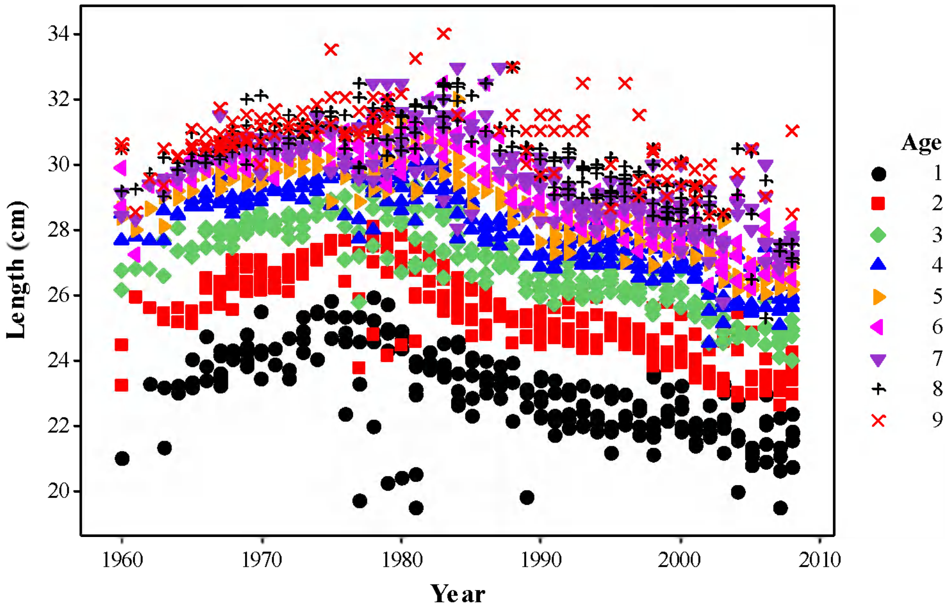

Figure 5.3. Long-term changes in mean lengths-at-age for Celtic Sea herring.

Compared with other stocks, the Celtic Sea herring stock had low productivity, in terms of recruits per spawner, throughout the whole time-series (ICES, 2007a).

From the early part of the 20th century until the 1950s, the fisheries were relatively small, and annual catches remained below 15 000 t (Burd and Bracken, 1965). Sharp increases in the catches in the late 1960s were supported by a period of good recruitment. Low recruitment, in tandem with high fishing mortality, led to collapse, and a closure was implemented in 1977 (Molloy, 1980). The fishery was reopened in 1982 when the first of several good year classes entered the stock. The stock was fairly stable until the mid-1990s when recruitment entered another poor phase. From the mid-1990s, the stock began to decline again, reaching its lowest observed level in 2004. Since then, some recruitments have been well above average, and the stock had rebuilt to well above the target reference level by 2009 (ICES, 2009a).

Changes in biological parameters have yet to be fully explained. Density dependence on its own does not appear to be the cause of the decline in growth and condition (Lynch, 2009; Molloy, 1984). Some of this variability can be explained by changes in the stock composition of Celtic Sea herring. The relative abundance of the faster-growing, autumn-spawning fish has declined in recent years, and slower-growing, winter-spawning fish now dominate the stock. However, the decline in mean length and mean weight-at-age is also apparent within each seasonal spawning group, demonstrating that the observed changes in growth rate are not only attributable to changes in stock structure (Harma *et al.*, 2009). Further work examining long-term fluctuations, such as the North Atlantic Oscillation and Atlantic Multidecadal Oscillation, copepod abundance, and other environmental parameters, is being conducted.

Current characteristics

There was a strong decline in biomass from the mid-1990s to 2004 (Figure 5.4). This trend is now reversed, and biomass has increased to levels above B_{pa} in the last two years (ICES, 2009a). Although demonstrating signs of recovery, the stock is currently composed mainly of young fish (ICES, 2009a).

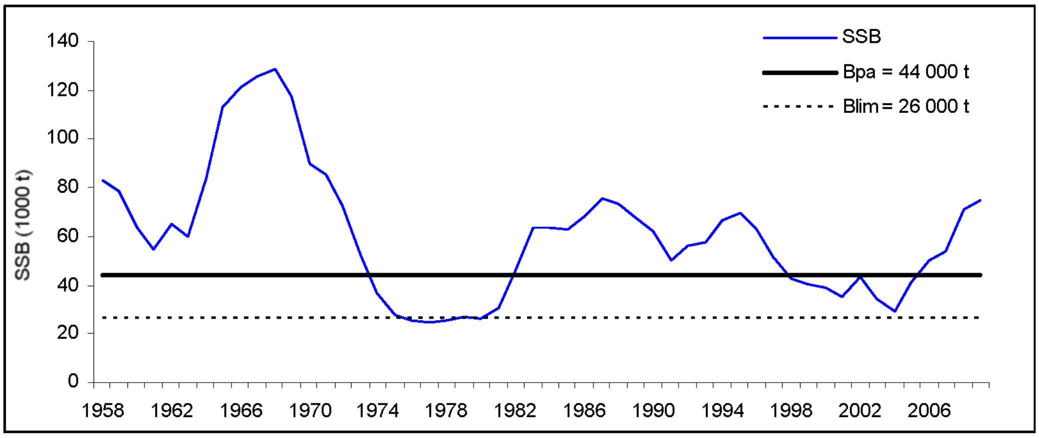

Figure 5.4. Long-term spawning-stock biomass (SSB) changes for herring in the Celtic Sea and ICES Division VIIj.

Potential environmental influences

Physical factors controlling the dispersal of larvae from the Celtic Sea into the Irish Sea, such as wind-driven circulation, tidal currents, and the formation of the Celtic Sea front, influence transport to nursery grounds and can, therefore, affect growth rates and subsequent maturation age (Figure 5.5; Brophy and Danilowicz, 2002, 2003; Brophy *et al.*, 2006). In the Celtic Sea, herring is at its most southerly distribution in the Northeast Atlantic and is, therefore, expected to be vulnerable to environmental fluctuations. Warm sea temperatures result in a fast-growing and fast-maturing stock, but high sea temperatures are expected to have a negative effect on recruitment, as has been demonstrated for other species at the southern limits of their distribution (Brander, 1998). Mean length-at-age for 2- and 3-ringers, as well as condition, have been demonstrated to have a weak but significant negative correlation with SSTs in both the Celtic and Irish seas (Lynch, 2009).

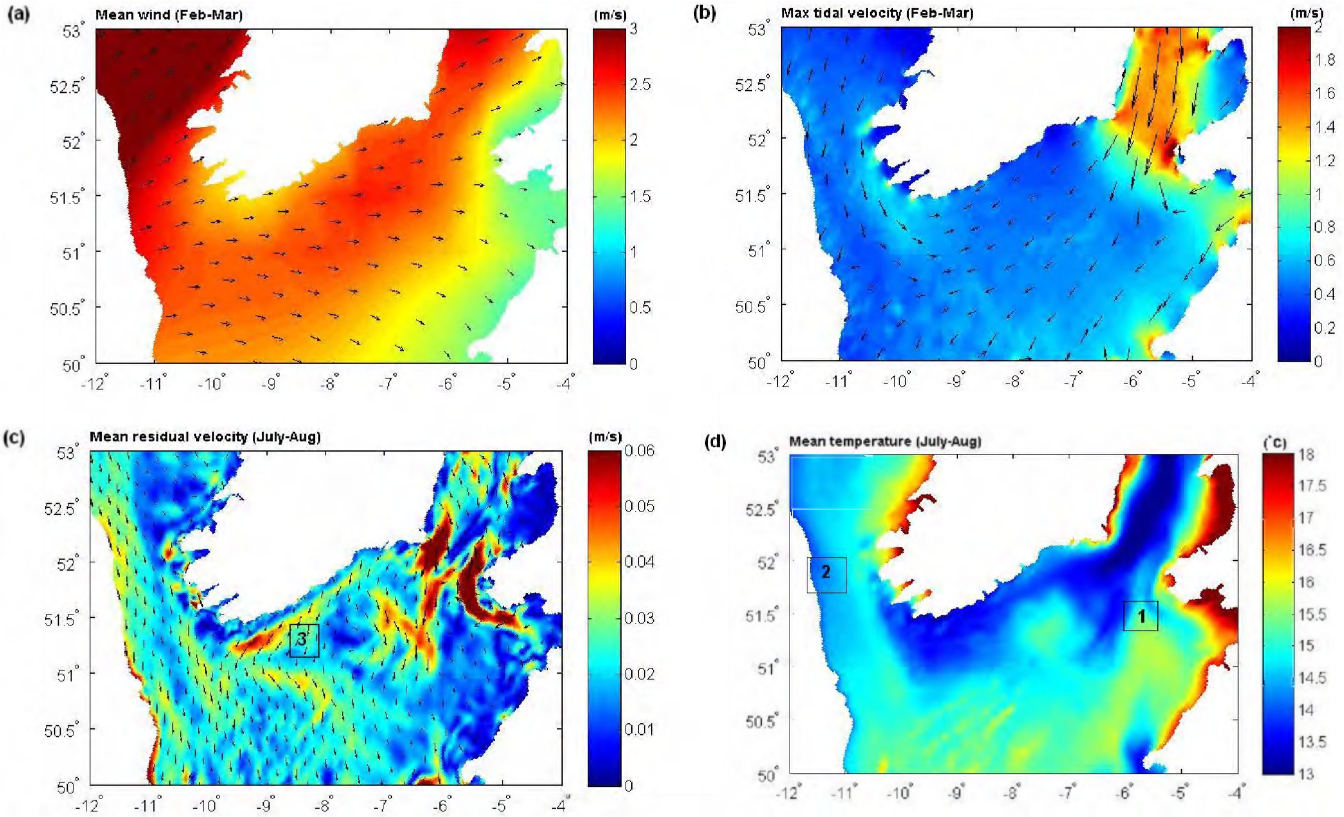

Figure 5.5. Mean model output to illustrate prevailing oceanographic conditions around Ireland. Examples of winter/spring conditions are shown in (a) mean windfields and (b) tidal currents in February–March. Examples of summer conditions during stratification: (c) residual flows and (d) mean surface temperatures in July–August. Fronts include the Celtic Sea front southeast of Ireland (1) and the Irish shelf front to the west of the Celtic Sea (2); both are thermohaline fronts persisting throughout the year, with an additional tidal mixing front developing near Islay during summer stratification. Residual currents include the Irish coastal current (3), a clockwise density current and the Atlantic shelf edge current (not shown). Circulation is mainly wind-driven, with prevailing southeasterlies, from October to May and density-driven from May to October. Model details are available from www.marine.ie.

6 Baltic herring

Michele Casini

The Baltic herring (*Clupea harengus*) stock reviewed here is the spring-spawning, central stock located in ICES Subdivisions 25–29 and 32, and excluding the Gulf of Riga.

Life-history traits

The average lifespan of the Baltic herring is 9–10 years, with a maximum of 20 years. Maturity occurs at 2–3 years of age, with maximum length of 25–30 cm (depending on the area), with a decrease from southwest to northeast. It is a one-batch determinate spawner, with a relative fecundity of ca. 300–500 eggs g^{-1} of body weight of the female fish (Laine and Rajasilta, 1998).

Spawning

Time. Spawning occurs in March–July and typically early in the southern areas and later in northern areas (Aro, 1989).

Habitat. The demersal eggs are commonly laid on vegetation growing on hard bottoms, although bare stones, gravel, sand, and blue mussels can also be used as a substratum (Aneer and Nellbring, 1982; Aneer, 1987; Kääriä *et al*., 1997).

Schooling behaviour. Successive schools appear to enter the inshore area throughout the spawning season, each consisting of mixed size and age classes (Jørgensen *et al*., 2005; Rajasilta *et al*., 1993). Egg deposition proceeds from very shallow (0.5–3 m) to deeper areas during the spawning season, following the seasonal warming of surface waters (Rajasilta *et al*., 1993).

Growth

Time. Most growth takes place in late summer–autumn.

Schooling behaviour. Successive schools form at sunrise and migrate downwards during the day and disperse in surface waters at night. Older and larger herring are found deeper in the water column (Orlowski, 2000; Cardinale *et al*., 2003; Nilsson *et al*., 2003).

Co-occurring species. Sprat and cod (*Gadus morhua*) in offshore areas (Ojaveer and Lehtonen, 2001) and threespine sticklebacks (*Gasterosteus aculeatus*) in more coastal areas (Aro, 1989; Peltonen *et al*., 2004).

Factors affecting growth. Hydro-climatic conditions (mainly salinity), and intraspecific competition, as well interspecific competition with sprat (*Sprattus sprattus*), are both mechanisms affecting prey abundance (Cardinale and Arrhenius, 2000; Rönkkönen *et al*., 2004; Casini *et al*., 2006, 2010).

Feeding

Time. Feeding takes place during daylight hours, with daily vertical migrations linked to feeding (Cardinale *et al*., 2003). The main feeding period is in summer and autumn (Arrhenius and Hansson, 1993; Hansson *et al*., 1990; Möllmann *et al*., 2004a, 2004b; Casini *et al*., 2004).

Predation mode. Baltic herring are particulate- or filter-feeders, depending on the density and size of the prey (Flinkman, 1999).

Prey species. Mostly large copepods (e.g. *Pseudocalanus* spp. and *Temora longicornis*), but also cladocerans in late summer and early autumn. Larger herring also feed on nektobenthos (mysids, amphipods, and polychaetes); particularly during winter, a larger share of the diet is nektobenthos.

Migration

Adult herring migrate to inshore areas during spring for spawning. Feeding migrations take place in summer–autumn to offshore areas (Figure 6.1). Feeding migrations seem to be age-dependent, with older fish undergoing longer feeding migrations than younger fish, whose migrations are more localized and associated with coastal areas. Several subpopulations can be distinguished on the basis of different spawning sites (Parmanne *et al.*, 1997). Migrations can occur to and from the Gulf of Riga and the Bothnian Sea, although the latter is considered insignificant (Otterlind, 1976; Aro, 1989; Parmanne *et al.*, 1994).

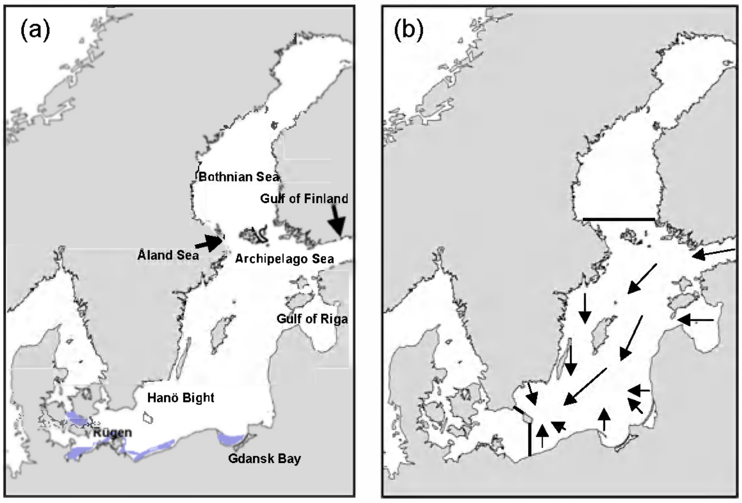

Figure 6.1. Map showing: (a) Spawning locations; and (b) feeding migration of central Baltic herring. The lines in panel (b) define the area of the central Baltic herring stock as defined by ICES (Subdivisions 25–29, and 32, Gulf of Riga excluded).

Nursery areas

Nursery areas for Baltic herring include inshore shallow areas all around the central Baltic Basin (Aro, 1989; Parmanne *et al.*, 1994).

Long-term trends

There was a constant decrease in spawning-stock biomass (SSB) from the 1970s to 2001, with a slight increase thereafter (Figure 6.2). Apart from the impact of high fishing mortality (above F_{pa} for almost three decades) on the stock, the decrease in SSB was also caused by a drop in mean weight-at-age (Figure 6.2). Recruitment has been quite variable, but has undergone a decrease since the mid-1980s and has continued to remain below average (Figure 6.2; ICES, 2009c).

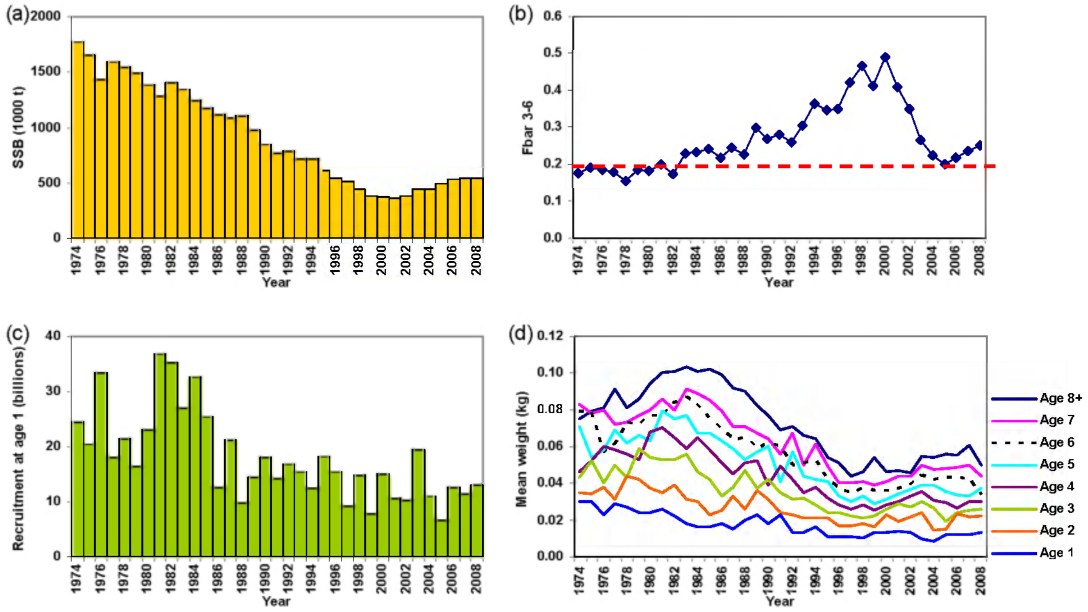

Figure 6.2. Trends in (a) spawning-stock biomass, (b) fishing mortality ages 3–6 (the red dashed line indicates F_{pa}), (c) recruitment, and (d) weight-at-age.

Potential environmental influences

Although recruitment seems to be linked to SSB (a stock–recruitment relationship does exists; ICES, 2009c), environmental factors can affect herring recruitment both directly and indirectly by acting on different phases of its life cycle. For example, oxygen, temperature, and the life cycle of the algae on which the eggs are deposited may directly affect egg survival (Aneer, 1987). Temperature also influences the timing of zooplankton production in the Baltic and, in turn, herring larval feeding and growth (Axenrot and Hansson, 2003). On the other hand, deep-water salinity, mostly influenced by inflows from the North Sea (Figure 6.3), affects the dynamics of the main food species of adult herring and, therefore, adult herring growth and condition (Rönkkönen *et al.*, 2004). However, biotic interactions, such as interspecific competition with sprat, also have a crucial impact on herring growth and condition (Cardinale and Arrhenius, 2000; Casini *et al.*, 2006). Herring condition prior to spawning is important for hatching success and egg survival (Laine and Rajasilta, 1999), thus potentially influencing recruitment success (Cardinale *et al.*, 2009).

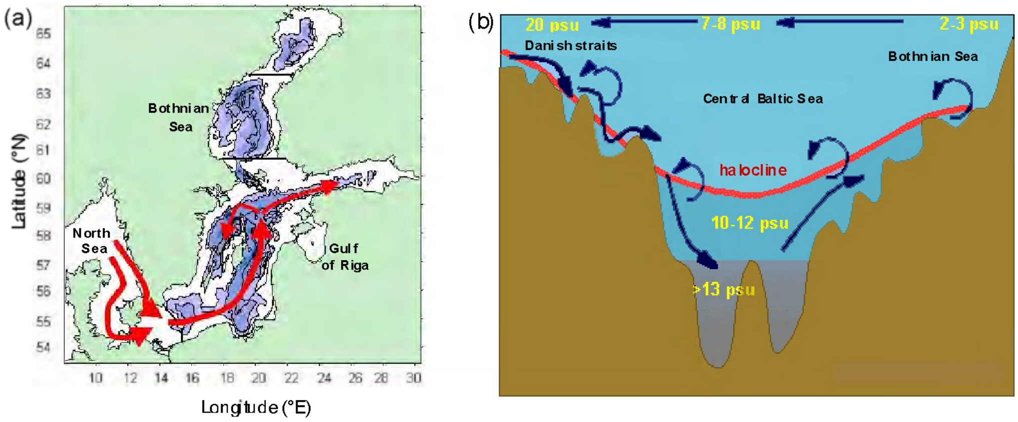

Figure 6.3. (a) Route of saline inflows from the North Sea through the Danish straits to the Baltic Sea (red arrows). (b) The heavy saline water flows along the seabed, and the less-salty surface water flows out of the Baltic Sea. The water becomes stratified, and a halocline separates the layers of varying salinity. Modified from the Baltic Sea Portal.

7 Baltic sprat

Rüdiger Voss, Jörn Schmidt, and Christian Möllmann

Life-history traits

The lifespan of Baltic sprat (*Sprattus sprattus*) is 8 years. Sexual maturity occurs at an age of 1–2 years. Sprat is an indeterminate multiple-batch spawner (ICES, 2009c).

Spawning

Spawning takes place from March to August, depending on temperature (Karasiova and Voss, 2004; Voss *et al.*, 2006). In some recent years, winter spawning in January–February was observed.

Spawning habitat is the deep basins (Bornholm Basin, Gdańsk Deep, and Gotland Basin; Figure 7.1).

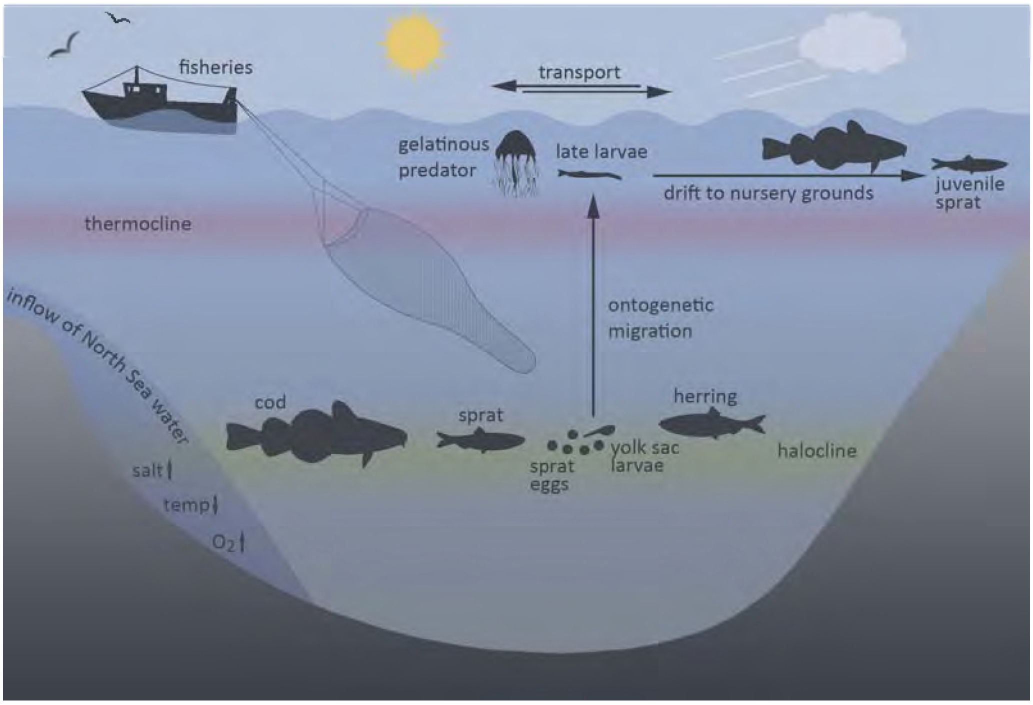

Figure 7.1. Schematic illustration of sprat habitat in Baltic deep basins, including driving forces for population dynamics.

Growth (adult)

Growth of adult sprat takes place in summer/autumn in coastal areas (Aro, 1989). Co-occurring species at this time include juvenile herring (*Clupea harengus*).

Feeding

The predation mode of sprat is either filter-feeding or snapping, depending on the size of the prey. Principal prey species include copepods (*Pseudocalanus* sp., *Acartia* spp., *Temora longicornis*; Möllmann *et al.*, 2004a). Feeding sprat school in the halocline during the day, but are dispersed in surface waters at night (Stepputtis, 2006). Co-occurring species include herring (*Clupea harengus*), and cod (*Gadus morhua*) during the day.

Migration

Adult sprat of the central Baltic Sea migrate for overwintering and prespawning feeding into the deep basins, i.e. Bornholm Basin, Gdańsk Deep, and Gotland Basin (November–December; Figure 7.2; Aro, 1989). Spawning takes place in the deep basins between March and August (Voss, 2002), after which the sprat leave the deep areas for coastal feeding (June–August; Figure 7.2). Based on repeated surveys in the Bornholm Basin, high concentrations of sprat were recorded in early April when sprat egg production started (Figure 7.3; Stepputtis, 2006). Higher abundance occurred in the northern part of the basin during spawning. At the end of peak spawning (May), sprat occupied the northern edge as well as the western parts of the basin. Small numbers of spawning adults, as well as early egg stages, were found all over the investigation area up to July. However, sprat abundance in the basin decreased sharply after peak spawning had ended in May.

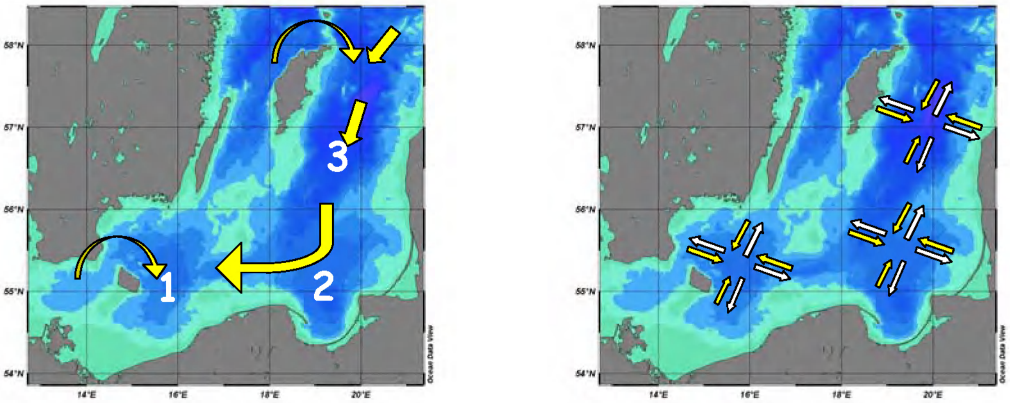

Figure 7.2. Schematic illustration of seasonal adult sprat migration. Left: Winter feeding migrations (among basins). 1 = Bornholm Basin; 2 = Gdansk Deep; 3 = Gotland Basin; blue areas = approximate spawning areas. Adapted from Aro, 1989. Right: Spawning and feeding migration (into and out of deep basins). Yellow = into and out of basin migration (March–July); white = post-spawning coastal feeding (June–August).

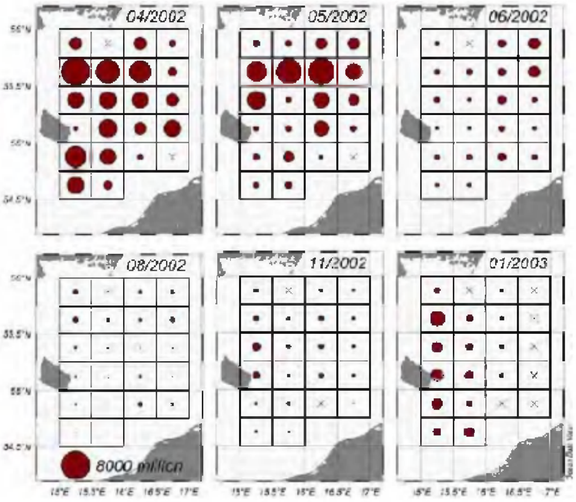

Figure 7.3. Seasonal changes in mesoscale distribution of sprat in the Bornholm Basin.

Larval drift and nursery areas

Eggs and larvae drift out of the deep basins into coastal nursery areas, depending on the wind-driven currents, but mainly in a northeasterly direction (Hinrichsen *et al.*, 2005). Early juveniles are found in coastal areas in April–September (Figure 7.4; Baumann *et al.*, 2007).

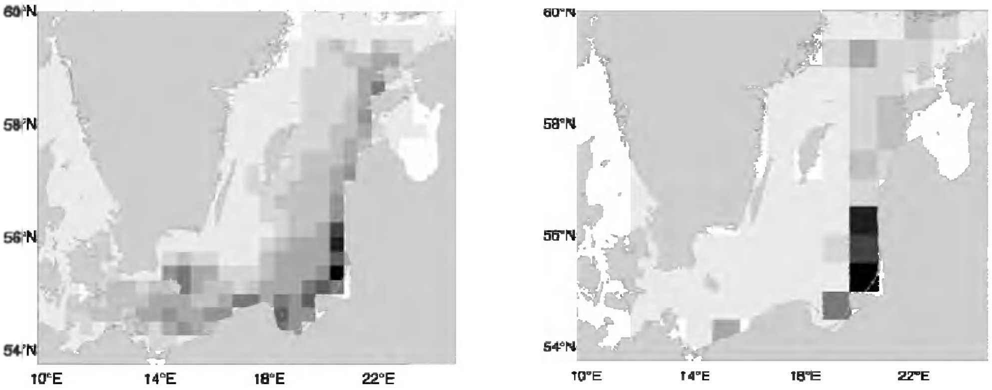

Figure 7.4. Mean observed distribution of sprat juveniles, based on hydroacoustics (left) and coupled hydrodynamic modelling 1979–2002 (right).

Long-term trends

There was a period of extremely high stock sizes in the 1990s (up to 1.8 million t spawning-stock biomass (SSB)) caused by a release in predation pressure from the collapsed cod stock, low fishing pressure, and high (although variable) recruitment (ICES, 2009c). Stock size decreased in the early 2000s owing to an increase in fishing pressure. The stock is currently stabilizing at ~1 million t SSB.

Potential environmental influences

Adult growth has been reduced (potentially affecting recruitment) since the late 1990s (Cardinale *et al.*, 2002; Möllmann *et al.*, 2003a, 2003b) by a decrease in abundance of *Pseudocalanus* sp. (main adult food in winter/spring) and strong competition owing to the high stock size. Overall, recruitment is positively influenced by increased temperatures (high North Atlantic Oscillation index; Alheit *et al.*, 2005; MacKenzie and Köster, 2004) via increased egg survival (Nissling, 2004; Hinrichsen *et al.*, 2007) and faster larval growth (Baumann *et al.*, 2006a), and by an associated increase in *Acartia* spp. abundance (main larval food; Voss *et al.*, 2003; Baumann *et al.*, 2005; Dickmann *et al.*, 2007; Möllmann *et al.*, 2009). However, more precisely, not a single factor could explain recruitment variability.

Larval feeding success and growth, obviously two key processes in Baltic sprat recruitment dynamics, are influenced by a wide range of potentially interacting environmental factors (Voss *et al.*, 2008). Larval feeding success was influenced by bottom depth, cubed windspeed as a proxy for small-scale turbulence rates, degree of cloudiness as a proxy for light conditions, and prey density in combination with a feeding-period–cloudiness-interaction term. A comparable approach was used to define the key factors for larval growth. Remarkably, both model approaches, although based on completely independent data, demonstrated a high similarity in the significant factors identified. Both studies demonstrate that the important recruitment processes of Baltic sprat larvae are controlled by a number of key environmental factors acting simultaneously.

Integrating over all life stages, temperature and larval drift seemed to be the most important variables determining recruitment success (Baumann *et al.*, 2006b, 2008). Given the likelihood of further temperature increases in the Baltic, our current understanding of the recruitment process indicates an enhanced recruitment potential in sprat (Köster *et al.*, 2003a, 2003b; MacKenzie and Köster, 2004; Voss *et al.*, 2006). A temperature increase would positively affect larval growth, shorten egg development (and hence decrease predation mortality; Petereit *et al.*, 2008), and increase abundance of suitable food (Möllmann *et al.*, 2003a). However, there are also potential negative effects, which are currently hard to evaluate. Changes in the windfield will affect larval transport (Hinrichsen *et al.*, 2005). More intensive westerly winds would accelerate larval transport to the coast, which, in turn, would be negative for larval survival (Baumann *et al.*, 2006b, 2007). Climate variability might also change the "environmental envelope", so that new, potential competitors can enter the Baltic Sea (Haslob *et al.*, 2007). One example is anchovy (*Engraulis encrasicolus*), which has been recently recorded in high densities in the western Baltic Sea during hydroacoustic surveys (ICES, 2009d).

Major changes in relation to changes in the Baltic Sea ecosystem

Adult stage

Sprat in the Baltic Sea have demonstrated large interannual oscillations in condition during the last few decades (Cardinale *et al.*, 2002; Möllmann *et al.*, 2004a), with deteriorating adult sprat condition during the 1990s. In the Baltic Sea, clupeid condition is believed to be linked mainly to feeding conditions. For example, variability in clupeid condition has been related to changes in the zooplankton community that are largely driven by oceanographic features, especially the decrease in the copepod *Pseudocalanus* sp. However, inter- as well intraspecific competition could also affect food availability and, in turn, condition. Baltic herring and sprat have different and separate life cycles. However, during the common feeding season (late spring to early summer), the two species meet in the offshore areas of the deep Baltic basins and their food spectrum largely overlaps (Möllmann *et al.*, 2004b). During this period, herring and sprat suffer from high levels of feeding competition, as reflected in their condition. Later in the season, sprat migrate more inshore, whereas herring stay in the offshore areas. At this time, therefore, interspecific competition for food can be assumed to be lower.

Large-scale distribution based on winter habitat definition

In the Bornholm Basin, combined hydroacoustic and hydrographic transects were performed in 2002 and 2003 (Stepputtis, 2006). The combination of hydrographic data with horizontally and vertically resolved acoustic distribution data allowed the definition of threshold values for sprat distribution in winter (Figure 7.5). In winter 2003, sprat appeared to be captured in the water mass defined by a minimum temperature of 4°C from above and a minimum oxygen level of ca. 1.5 ml l^{-1} from below. For typical stagnation years, with oxygen depletion in the deep part of the basin (Fonselius and Valderrama, 2003), sprat is, therefore, restricted to a rather thin, well-defined water body. When applying the defined thresholds of 4°C and 1.5 ml l^{-1} oxygen, a time-series of habitat area in winter could be established for the different subdivisions. Overall, habitat area was highly variable between years as well as between subdivisions. General trends for spring were confirmed by relative distribution patterns derived from (a) spring hydroacoustic surveys, (b) egg abundance data, and (c) area-disaggregated MSVPA analysis for the second quarter. Relative distribution between subdivisions derived from autumn hydroacoustic surveys demonstrated different patterns, indicating a redistribution of the sprat stock between subdivisions over the year.

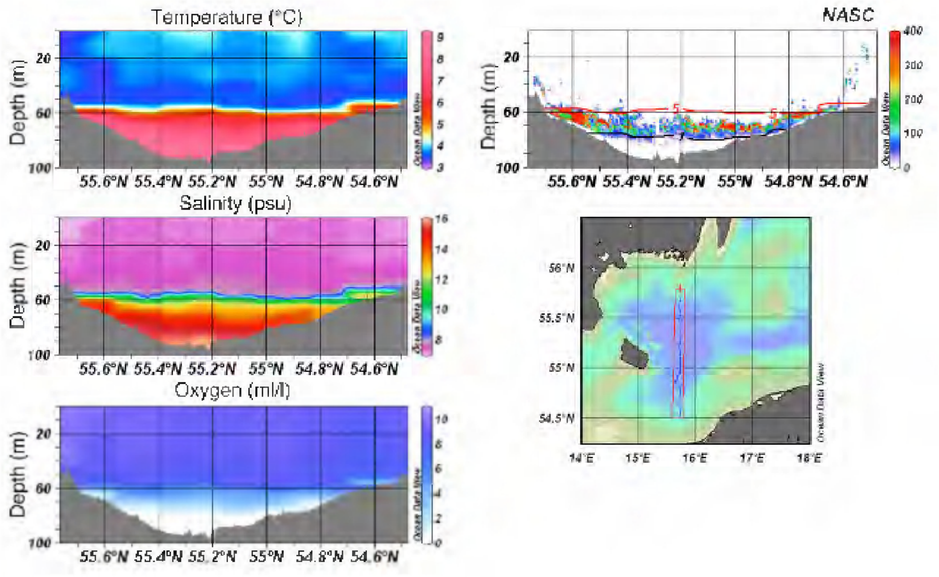

Figure 7.5. Transect through the Bornholm Basin in winter: (left column) hydrographic data; (right column) sprat distribution based on echo-intensity (upper panel) and position of the transect (bottom panel).

Vertical distribution

The vertical distribution of sprat depends on temperature and oxygen content (Stepputtis, 2006). However, with temperatures of the intermediate winter water layer increasing above 5 °C in late spring and summer, sprat start a diurnal vertical migration. This introduces a discontinuity into the sprat distribution pattern that strongly affects the predator overlap during spawning time.

Egg stage

The horizontal distribution of the egg stage closely follows the distribution pattern of adult fish (Voss, 2002). Vertically, the centre of the sprat egg mass usually changes over the season (Figure 7.6). In 2002, at the beginning of the spawning season (March) in the Bornholm Basin, eggs were mostly found at depths between 60 and 70 m, with an increasingly shallower distribution up to 30–40 m depth in July. After a major Baltic inflow in early 2003, sprat eggs were less concentrated vertically. However, again, the centre of mass became shallower over the course of the season.

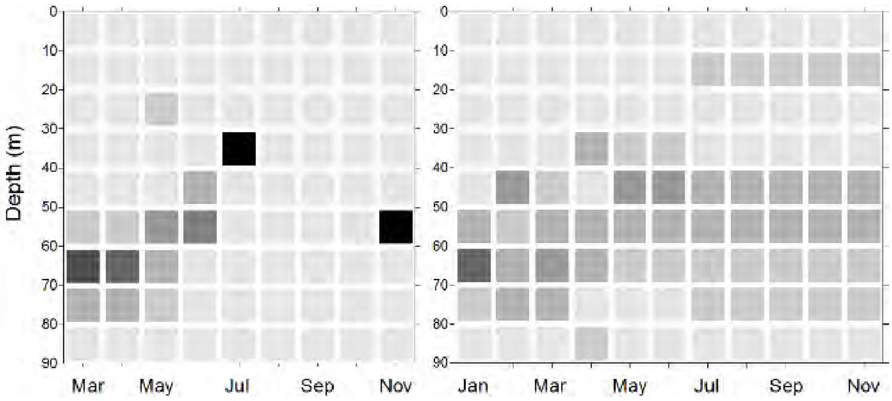

Figure 7.6. Relative vertical distribution of sprat eggs throughout the spawning season; left: stagnation scenario (March–November 2002); right: post-inflow scenario (January–November 2003).

Larval/juvenile stage

The vertical distribution pattern and diel migration behaviour of Baltic sprat larvae changed between 1989–1990 and 1998–2002 (Voss *et al.*, 2007). In 1989 and 1990, the sprat larvae migrated to the surface at night, but remained at 30–50 m depth during daytime. In 1998–2002, sprat larvae demonstrated no signs of diel vertical migration, but remained the entire day in warmer, near-surface waters. This behavioural change happened concurrently with changes in the Baltic ecosystem (Möllmann *et al.*, 2009). The major prey organism (*Acartia* spp.) of Baltic sprat larvae increased in abundance (Möllmann *et al.*, 2003a). In the Bornholm Basin, near-surface temperatures have increased since the 1990s, and *Acartia* spp. have aggregated in this water layer. Therefore, the vertical profile of suitable food for sprat larvae changed, resulting in high levels of food in the surface layers. The observed change in vertical distribution patterns of sprat larvae might have influenced the generally higher, but more variable, recruitment in Baltic sprat in the last decade.

Transport of sprat larvae to their juvenile spawning grounds was investigated by detailed drift-model simulations for the years 1979–2002 (Hinrichsen *et al.*, 2005). Different modelling approaches, with and without diurnal vertical migration, were utilized. Data on spawning location and timing of spawning were used as input to a particle-tracking model. The most important potential nursery grounds for sprat were identified along the southeastern Baltic coast. Interannual variations were caused mainly by variable wind conditions over the Baltic Sea. The horizontal distribution of simulated larval or 0-group sprat is mostly consistent with the observed distribution of 0-group sprat obtained from hydroacoustic field surveys (Figure 7.4; Hinrichsen *et al.*, 2005).

8 Bay of Biscay anchovy

Pierre Petitgas, Andrés Uriarte, Enrique Nogueira, Jacques Massé, and Unaï Cotano

Life-history traits

Anchovy (*Engraulis encrasicolus*) is a short-lived species that demonstrates fast growth and early and high fecundity. It also suffers high natural mortality. The lifespan is 3 years, with a few percent living to a maximum of 5 years (ICES, 2007b). The annual natural mortality rate (M; ages 1–3) is variable and in the range of 0.7–2.0 year^{-1} (Uriarte *et al.*, 1996); ICES uses the value 1.2 year^{-1} (ICES, 2007b). The annual fishing mortality rate (F) estimated by ICES ranges from 0.5 to 1.6 year^{-1} (ICES, 2006b).

Spawning and growth

The fish are mature and reproductively active in their first spring at age 1 (Motos, 1996). The peak spawning season is in spring (May–June; Motos *et al.*, 1996). The onset of spawning is concurrent with the sharp seasonal increase in surface temperature. The duration of the spawning season is variable and depends on feeding (ultimately zooplankton production). In the last 20 years, major recurrent spawning grounds were identified by acoustic and egg surveys. These were coastal associated with the river plumes of the Adour and Gironde, as well as offshore near the shelf edge (south of 45°N at 2°W; Figure 8.1). Larger fish were distributed more offshore at greater depths (Motos *et al.*, 1996; Petitgas *et al.*, 2003).

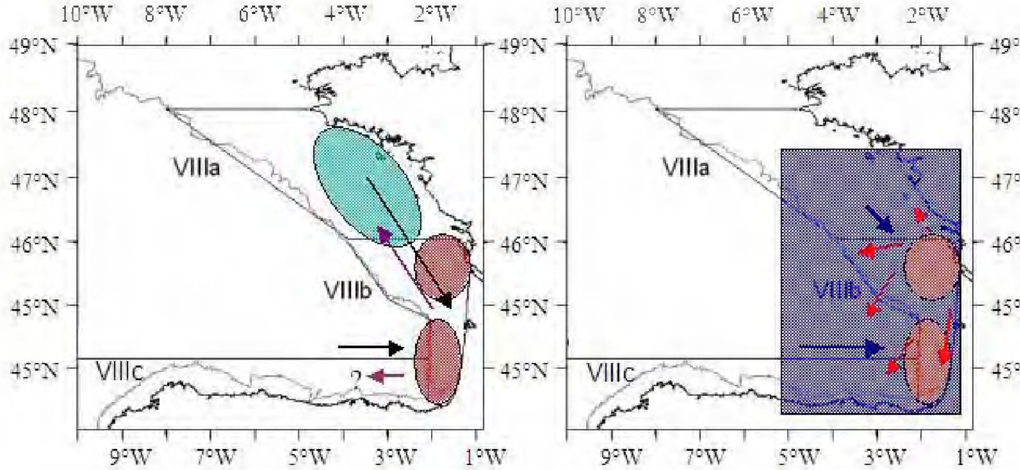

Figure 8.1. Schematic drawing of the life-cycle organization of the current anchovy population in ICES Divisions VIIIa and b. Left: spring spawning grounds (red) and autumn feeding grounds (green), summer migration (purple arrows), and early winter migration (black arrows); wintering grounds are presumed to be located close to the spring spawning grounds. Right: spring spawning grounds (red) and area containing autumn juvenile habitats (blue), summer larval drift (red arrows), and early winter juvenile arrival to the coast (blue arrows); winter juvenile habitats are coastal.

Anchovy is an indeterminate multiple-batch spawner. The average time between batches is 4–5 days, and the average number of batches in the season is roughly 20 female^{-1}, resulting in approximately 110 000–350 000 eggs spawned per female during the season (Motos, 1996). Eggs hatch within 2–5 days, and larvae metamorphose into young juveniles between 25 and 60 days post-hatch (Cermeño *et al.*, 2008). At 19.5 °C, first-feeding larvae are ca. 5 mm in length, and metamorphosis occurs between 3.5 and 4.0 cm (Garcia and Palomera, 1996; La Mesa *et al.*, 2009). Larval survival is in the order of 10^{-5} (Allain *et al.*, 2007). Daily egg mortality is in the range 0.11–0.30 d^{-1} and depends on temperature (Somarakis *et al.*, 2004). Juvenile mortality is a decreasing function of age (Lo *et al.*, 1995) and ranges from 6 to 2 $year^{-1}$ (Lehuta *et al.*, 2006). Juvenile growth is rapid, concurrent with high summer and autumn surface temperature. Most of the anchovy growth takes place during the juvenile stage before the first winter. There is high interindividual variability in growth trajectories. Average length-at-age in the spring acoustic surveys for the period 1987–2006 was 12.7 cm (age 1), 16.9 cm (age 2), and 18.2 cm (age 3; unpublished data reported annually to ICES), compatible with the data reported by Cendrero *et al.* (1981) and Uriarte *et al.* (1996).

Schooling behaviour was observed during the spring acoustic surveys (Massé, 1996). During the daytime, anchovies form small schools aligned 10–25 m above the bottom, which are often vertically separated from other species and, in particular, horse-mackerel (*Trachurus trachurus*). Occasionally, large fish only (>16 cm) form small, dense schools at the surface above the thermocline (0–20 m). At night, anchovies are found dispersed in the surface above the thermocline (0–20 m). Co-occurring species during spawning include sprat (*Sprattus sprattus*), sardine (*Sardina pilchardus*), mackerel (*Scomber scombrus*), and horse mackerel (Massé *et al.*, 1996).

Feeding

The feeding season can be defined as the time when the fish store reserves after spawning and before winter. The fat content increases in summer and autumn (July–October), diminishes in winter (November–March), and is stable throughout the spawning season (Dubreuil and Petitgas, 2009). In the last 20 years, the feeding grounds have been located in the northern part of the French shelf of Biscay (bottom depth <120 m) north of 46°N. Prey species are principally copepods and also other zooplankton organisms (Plounevez and Champalbert, 1999). Adult anchovies are filter- or snapping-feeders, depending on the size of prey. Co-occurring species during feeding include sardine, sprat, horse mackerel, and mackerel.

Anchovy continue to feed during the spawning season (Plounevez and Champalbert, 1999). Spawning duration depends on energy intake during spawning as well as reserves stored since the last feeding season. Hunter and Leong (1981) estimated that the energy dedicated to spawning is two-thirds dependent on storage.

Larval drift and nursery areas

Larvae are found in the upper surface layers (0–30 m). From the major spawning grounds located on the French shelf, larval drift is oriented mostly to the southwest (Figure 8.1). At the time of the larval period in spring and summer, the flowfield has this general orientation pattern (Allain *et al.*, 2003; M. Huret, pers. comm.). Biophysical larval-drift model results demonstrate that dispersal is large, but with three major patterns; some trajectories stay very coastal; most drift offshore outside the shelf; and others stay on-shelf off the Gironde estuary (45.5°N). This is consistent with observations of larval distributions (Cotano *et al.*, 2008; Irigoien *et al.*, 2008).

After the larval drifts, the early juveniles are mainly contained south of 46°00N and east of 5°W, offshore in the ocean, on shelf, and also close to the coast (July–September; Figure 8.1; Uriarte *et al.*, 2001a; Irigoien *et al.*, 2008). Juveniles, found independently of adults (juveniles not yet recruited to the population) in the offshore and onshelf areas, form aggregations at the surface (0–20 m) by day and night (no vertical migration; Petitgas *et al.*, 2004). The aggregations are easily disaggregated, depending on meteorological conditions. Co-occurring species of juvenile anchovies includes juveniles of horse mackerel, sardine, and mackerel.

From their offshore habitats, late juveniles recruit to coastal areas along the Spanish and French coasts in the area south of 47°N and east of 5°W (November–December; Figure 8.1). In coastal waters, juveniles are assumed to interact with the adults and recruit to the stock. Recruited juveniles form adult-like schools that are near bottom during the day and disperse at the surface at night (Petitgas *et al.*, 2004).

Migration

The spawning grounds are located in the southeast corner of Biscay, and the feeding grounds are in the northern French shelf (Figure 8.1). The feeding migration occurs after spawning, mainly in July. After the end of the feeding season, the fish are assumed to migrate back south (December) and winter close to the spawning grounds. The migration is known from the seasonal movement of the French pairtrawlers (Uriarte *et al.*, 1996) and is assumed to follow a north–south gradient in food and temperature. Food south of 46°N would become physiologically limiting at the high summer temperature (Struski *et al.*, 2009).

Juveniles that were advected as larvae offshore are presumed to head back to coastal waters traversing the shelf (Figure 8.1). Survey data reveal a gradient in size from offshore to inshore, the largest (oldest) juveniles being inshore and also northwards (Irigoien *et al.*, 2008; Petitgas *et al.*, 2004). Factors determining this migration are unknown.

Long-term trends

The Spanish fishery developed in the 1950s and declined from the early 1970s until the mid-1980s, when a French fishery developed (Figure 8.2; Villamor *et al.*, 2007). This evolution coincided with a major change in the distribution of the fishery. The decline in the 1970s was associated with a progressive reduction in the distribution area of the spring fishery from west to east along the Spanish coast, and with a progressive disappearance of the autumn fishery (Figure 8.3; Junquera, 1984). The French fishery developed predominantly in summer and autumn on the current northern feeding grounds, which were previously only lightly exploited. Recently, the stock collapsed in 2005, and the fishery remained closed until 2010.

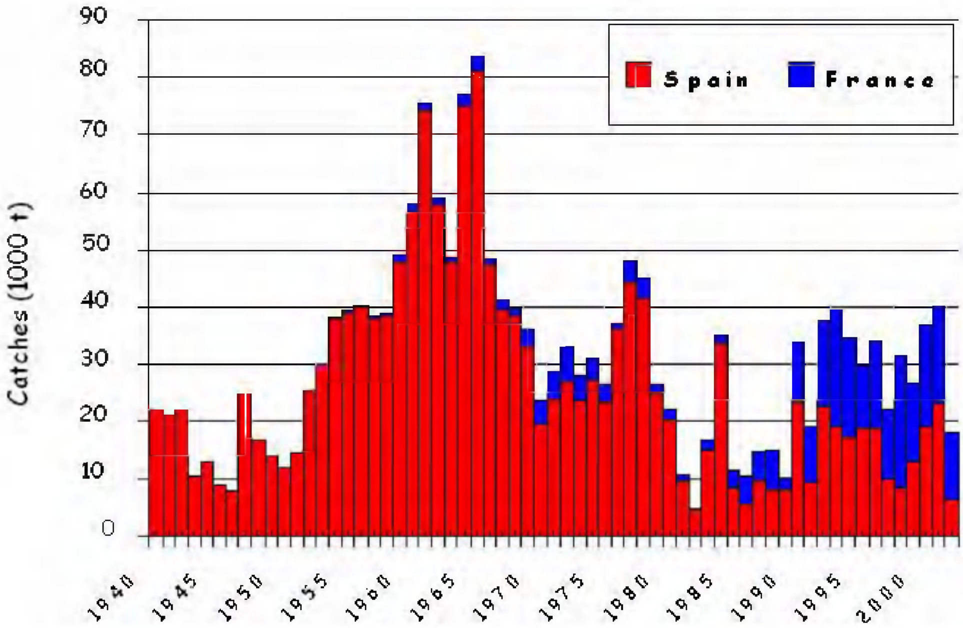

Figure 8.2. Long-term evolution of anchovy landings in Biscay (ICES Divisions VIIIc, b, and a).

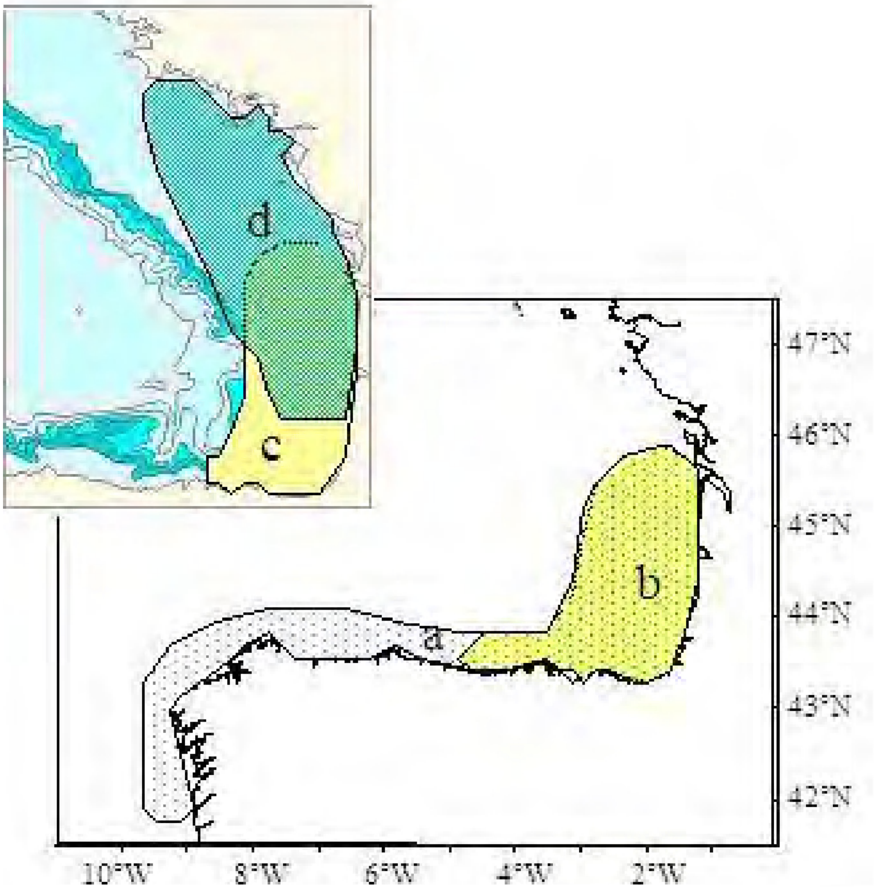

Figure 8.3. Long-term spatial and seasonal evolution of the anchovy fishery in Biscay: (a) spring fishery for 1900–1960 (mostly Spanish); (b) spring fishery for 1966–1975 (mostly Spanish); (c) spring fishery since the mid-1980s (mostly Spanish); (d) summer-autumn fishery since the mid-1980s (mostly French).

Current characteristics

The life-cycle configuration described above (Figure 8.1) has been consistent for the past 20 years since the reduction in the population along the Spanish coast: (i) spring-spawning grounds associated with the plumes of the rivers Gironde and Adour and along the French shelf break south of 46°N; and (ii) summer/autumn feeding areas on the French shelf and coastal areas from 46 to 47°N. The fate of the larvae arriving on the Spanish coast is unclear because these habitats, once productive in the 1960s and 1970s, now barely contribute to the stock. The area off the Gironde estuary in spring is an essential habitat in terms of contributing to population growth (Vaz and Petitgas, 2002) and has been suggested as an area to be protected (Villamor *et al.*, 2007). The stock has experienced repeated low recruitments since the 2002 year class, and the fishery closed in July 2005. Although the spatial extension is reduced, no new habitat loss has been described.

Potential environmental influences

In the Bay of Biscay, anticyclonic and cyclonic wind regimes alternate, activating a diversity of mesoscale oceanographic features that are potentially important for the growth and survival of the different life stages of the anchovy (Figures 8.4 and 8.5). Recruitment was positively correlated with spring (March–June) coastal upwelling along the French and Spanish coasts in the southeast corner of Biscay (46°N 4°W) under northeasterly wind conditions during spring and summer (Borja *et al.*, 1998). Such conditions would be under the control of the atmospheric East Atlantic (EA) pattern (Borja *et al.*, 2008). Recruitment variability was also negatively correlated with summer (July–August) water-column stratification breakdowns under west–southwest summer storms (Allain *et al.*, 2001). Since summer 2003, these correlations have failed to be predictive. Predation larval mortality was also listed as a potential influence (Irigoien *et al.*, 2007). Other factors acting at life-cycle stages other than larvae are also potentially important, such as winter mortality of juveniles (Dubreuil and Petitgas, 2009) and spawning strategy. The aggregation pattern of spawning adults has been identified as a significative recruitment correlate (ICES, 2007b).

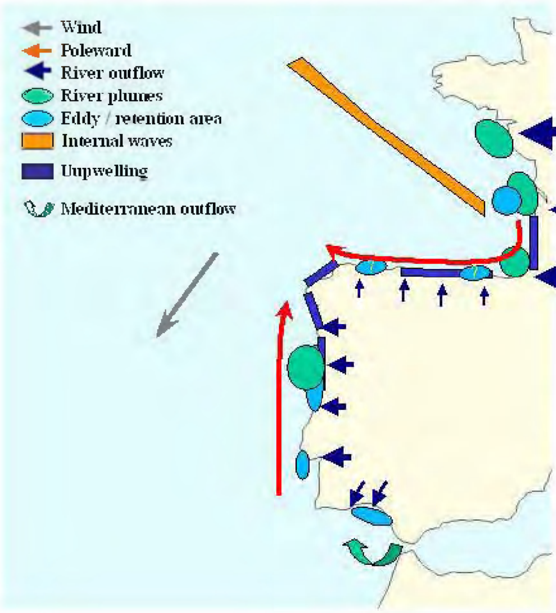

Figure 8.4. Physical processes in an anticyclonic situation (north–northeast winds). Many local upwelling events are activated along the coasts. River plumes are spread across the shelves. The poleward current is stopped. Circulation on the north coast of Spain is reversed to the west. Meeting of the two currents around Galicia generates a flow going outside the shelf.

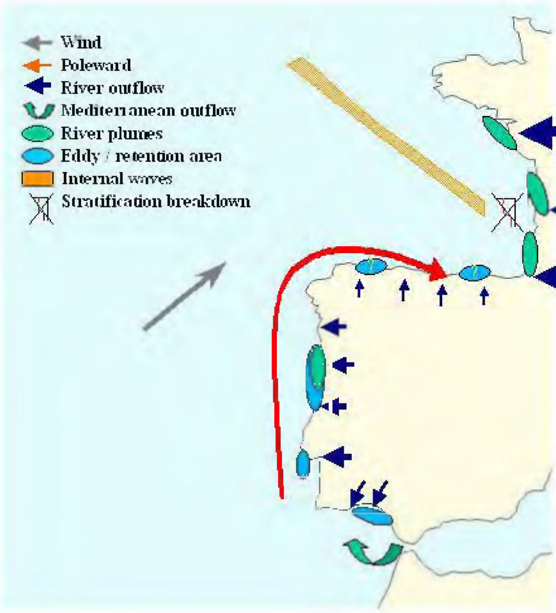

Figure 8.5. Physical processes around Iberia and in Biscay in a cyclonic situation (southwest winds). The poleward current is enhanced and interacts with river plumes in Portugal to generate retention areas. River plumes in France are concentrated along the coast, and a northward coastal flow is enhanced. Thermal stratification is broken down on the French shelf.

9 Atlanto-Iberian and Biscay sardine

Miguel Bernal, Yorgos Stratoudakis, Alexandra Silva, and Jacques Massé

Life-history traits

The lifespan of the Atlanto-Ilberian and Biscay sardine (*Sardina pilchardus*) is commonly $<$ 9 years, with a maximum of 14 years. Age-at-maturity is 1–2 years, and length-at-maturity is 14 cm. The sardine is an indeterminate multiple-batch spawner (batch fecundity 300–400 eggs g^{-1}), and metamorphosis occurs at 4–5 cm (Furnestin, 1943; Andreu and Plaza, 1962; Pérez *et al*. 1992a, 1992b; Zwolinski *et al*., 2001; Silva *et al*., 2006, 2008; Ré and Meneses, 2008).

Spawning

Time. Some mature sardines and eggs can be found year round, but the main spawning period is between October and June (peak December–March), with a latitudinal gradient in the duration and peak of the season (longer duration and earlier peak in the south; Coombs *et al*., 2006; Stratoudakis *et al*., 2007). Younger fish have a shorter spawning season (Silva *et al*., 2006).

Habitat. Spawning occurs along the shelf (with no clearly defined spawning grounds), although areas of permanent upwelling and offshore transport (e.g. the northwest Iberian corner) are generally avoided (Stratoudakis *et al*., 2003; Bernal *et al*., 2007; Planque *et al*., 2007; Zwolinski *et al*., 2010).

Schooling behaviour. Spawning takes place close to the bottom around dusk, with the probable formation of ephemeral spawning aggregations at greater depths, composed mainly of males and hydrated, running, or recently spent females (Zwolinski *et al*., 2006, 2007; Ganias *et al*., 2008).

Co-occurring species. The spawning season partially overlaps with that of mackerel (*Scomber scombrus*), chub mackerel (*Scomber colias*), and horse mackerel (*Trachurus trachurus*) off Iberia and with mackerel, horse mackerel, and anchovy (*Engraulis encrasicolus*) in Biscay (ICES, 2008a).

Growth (adult)

Time. Growth is strongly seasonal, taking place mostly outside the spawning period. Growth in length is greater in late spring and summer. Body condition and fat content of sardines peak in early autumn (when spawning resumes), and the lowest values are observed in late winter/early spring with the cessation of spawning (Bandarra *et al*., 1997; Silva *et al*., 2008). Growth in length is limited to the first 4 years of life (90% of L_∞ is achieved at age 4), whereas growth in weight continues throughout life. Growth declines from north to south resulting in clinal variation in maximum length and length-at-age (Andreu and Plaza, 1962; Silva *et al*., 2008). There is some variability in juvenile/adult growth patterns at a smaller geographical scale (Silva *et al*., 2008).

Habitat. Adults are mainly distributed over the inner and mid-shelf, with occasional excursions to the outer shelf (Zwolinski *et al*., 2010). In the Bay of Biscay, small sardines (1–2 years old) are mainly distributed in the southern area and coastal northern area, whereas large adult sardines occur mainly in the northern area along the coast and/or along the shelf break. Sardine presence is generally more likely in cooler, less saline, and more productive waters, although no significant relationship between relative sardine abundance and environmental variables has been detected so far (ICES, 2009d; Zwolinski *et al*., 2010).

Schooling behaviour. There is a clear diurnal schooling cycle, with characteristic dense schools during daylight, indiscriminately at the surface or close to the bottom, and scattered at the surface during night (Zwolinski *et al*., 2006, 2007).

Co-occurring species. Atlanto-Iberian and Bay of Biscay sardine co-occur with mackerel, occasionally sprat (*Sprattus sprattus*), horse mackerel, anchovy, bogue (*Boops boop;* all in the northern area), and with chub mackerel in the southern area (ICES, 2009d).

Nursery areas

Strong year classes are usually detected in autumn acoustic surveys in southern and western Iberia (age 0), and in spring surveys (age 1) in the southern Bay of Biscay (ICES, 2009d).

Recruits are detected in the inner shelf of western Portugal (off the Ria of Aveiro and Lisbon), in the Gulf of Cadiz (mainly off the Guadalquivir estuary), in the southern part of the Bay of Biscay, and in coastal southern Brittany (Carrera and Porteiro, 2003; ICES, 2009d; Silva *et al*., 2009). Recruitment areas coincide with areas of significant river discharge: the Loire in Brittany; the Gironde and the Adour in southern Biscay; the Minho, Douro, Mondego, and Vouga in northern Portugal; the Tagus in Lisbon; and the Guadalquivir in the Gulf of Cadiz.

Off western Portugal, sardine nursery areas may coincide with those of horse mackerel. In the Gulf of Cádiz and southern Bay of Biscay, general nursery areas for sardine coincide with those for anchovy, although some micro-scale habitat partitioning has been observed. In the coastal centre of the Bay of Biscay, they are closely mixed with small anchovy and sprat between the Loire and Gironde river plumes (ICES, 2009d).

Feeding

Time. Sardine feed throughout the year.

Predation mode. Sardines are both filter and particulate feeders, depending on prey size (Garrido *et al*., 2007). Laboratory experiments have demonstrated that particulate/filter feeding is associated with distinct behaviours (looser school organization, faster swimming, more frequent change in direction, and more energy expenditure during the former; Garrido *et al*., 2007).

Prey species. Phytoplankton and microzooplankton dominate as prey items, in terms of numbers and volume, respectively, and there are indications that the size range of prey is inversely related to sardine size (finer gillrakers in larger/older fish; Bode *et al*., 2003; Garrido *et al*., 2008). Laboratory experiments, as well as *ad hoc* field observations during daily egg production method (DEPM), or acoustic surveys, have demonstrated that fish eggs are highly appreciated as food by sardine (including cannibalistic behaviour).

Predator species. As a forage fish, sardines at different life stages are prey for many predator species, such as demersal (Preciado *et al*., 2008) and medium to large pelagic fish, marine mammals, and seabirds (Silva, 1999; M. Santos *et al*., 2004, 2007; Meynier *et al*., 2008).

Migrations

Seasonal movements are often reported by fishers, but this empirical knowledge has never been sufficiently compiled/verified to provide a description at a regional scale. Tagging experiments have provided little evidence on sardine migration patterns because of low recovery rates. The comparison between length and age structure in different areas across the Iberian–Biscay region from commercial and survey data since the 1980s provides some indirect evidence of movements around Cap Finistere in Galicia (ICES, 2006b; Silva *et al.*, 2009; see Figure 9.1 for a schematic representation). There is also some evidence from fishery and survey data of a cyclical appearance of adults to and from southern Brittany, the Cornish coast, and the English Channel. Possible movements between southern Biscay and the Cantabrian Sea are also to be considered. However, the scale of these movements and the potential fluxes of fish across the northern and southern limits of the area of sardine distribution remain unknown (also through the Strait of Gibraltar towards the Mediterranean Sea and from the Gulf of Cadiz to northwest Africa). However, recent genetic studies have provided evidence of significant isolation between particular sardine groups. Large levels of migration between Atlantic and Mediterranean sardines are unlikely across the Strait of Gibraltar (González and Zardoya, 2007). On the Atlantic side, a "Gibraltar" and a "Biscay" group are likely separated (Atarhouch *et al.*, 2006), which also agrees with asynchrony in the recruitment levels in these two groups.

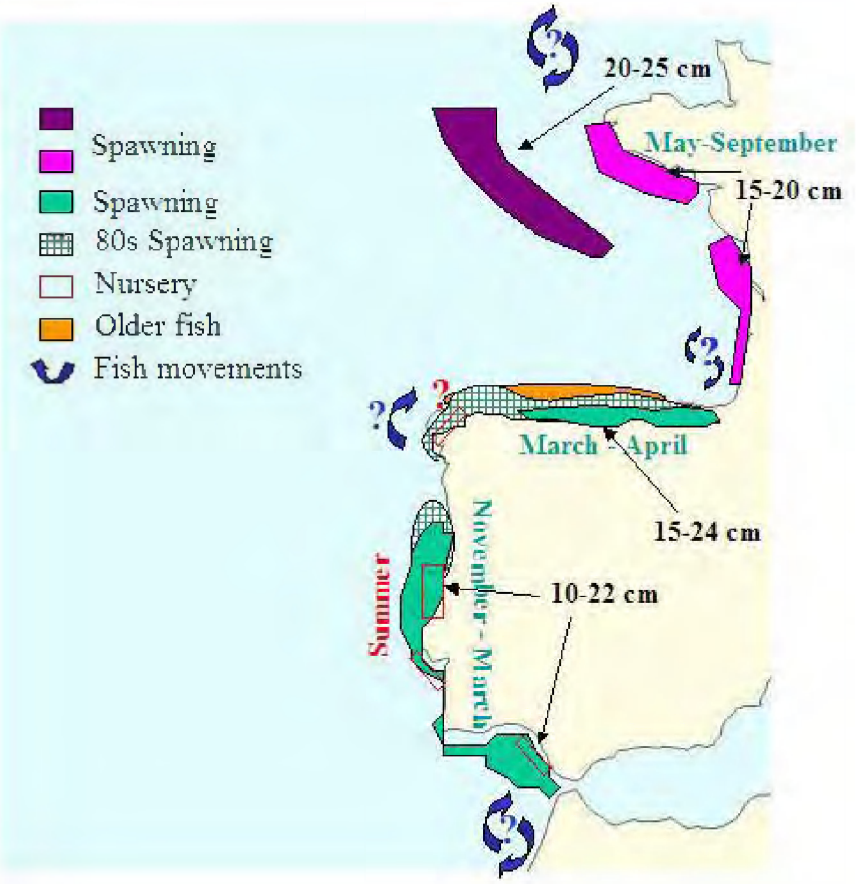

Figure 9.1. Schematic life cycle of sardine around Iberia and in Biscay.

Migration of juvenile sardine is generally considered to be minor because of significant differences in otolith microchemistry elements among recruitment sites in the study region (indicating low or no mixing between recruitment areas; Castro, 2007).

Long-term trends

Sardine was intensively exploited off Iberia throughout the 20th century, with catches fluctuating between 100 000–250 000 t. A smaller fishery (3000–66 000 t) has exploited sardine in the Bay of Biscay (ICES, 2009d). An analytical assessment (performed for the period 1978–present) indicates that the Iberian stock oscillates between high and low cycles of spawning-stock biomass (SSB; range 280 000–730 000 t) in response to pulses in recruitment every 3–7 years (ICES, 2009d). Both the total biomass and the fluctuations are on a scale smaller than those of other sardine populations throughout the world, which are usually associated with strong upwelling or other salient oceanographic features. Stronger and geographically more widespread recruitments were observed in the 1980s than in the subsequent two decades. The spawning area contracted during the 1990s, mainly as a result of a reduction in spawning activity off northern Portugal, Galicia, and northern Spain (Cantabrian coast; Bernal *et al.*, 2007), although it seems to have partially recovered in recent years.

Present characteristics

Off Iberia, the stock has recovered after an historically low SSB in 2000, resulting mainly from strong recruitments in 2000 and 2004 off northern Portugal; these year classes gradually expanded their distribution to the north (Cantabrian Sea) in the following years. The spawning area has recently expanded again in northern Portugal and western Galicia. Recent recruitments (after 2004) are considered low except in the Bay of Biscay, where both 2007 and 2008 appeared to be good year classes (ICES, 2009d).

Potential environmental influences

Sardine dynamics seem to be affected by poleward current intensity, wind strength (Borges *et al.*, 2003) and direction, upwelling (A. Santos *et al.*, 2004), river outflow, Mediterranean water outflow, and mesoscale circulation features created from the interaction of the above (especially mixed-layer depth; Oliveira and Stratoudakis, 2008; Figures 9.2 and 9.3). However, attempts to correlate sardine biomass and recruitment fluctuation with global environmental indices have, so far, provided little information on mechanistic hypotheses (Guisande *et al.*, 2004) and have proven insufficiently robust for the purpose of stock assessment and management advice. Indirect influence through environmentally driven changes in the species composition and size distribution of the trophic web is also considered to be a determinant of the distribution and relative abundance of sardine vs. other concurrent species. Sardine and anchovy have demonstrated both alternation and co-occurrence in the Bay of Biscay spring-survey data.

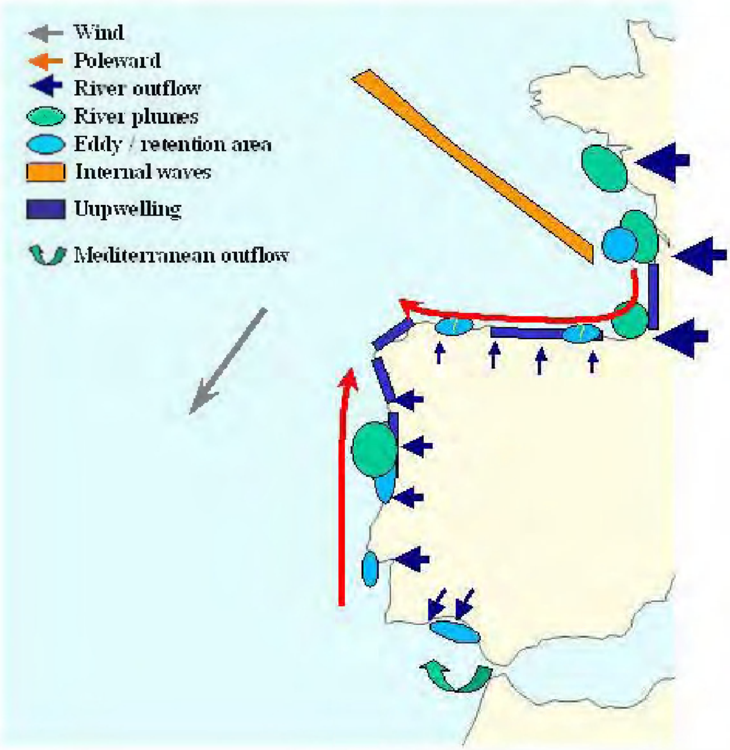

Figure 9.2. Physical processes in an anticyclonic situation (north–northeast winds). Many local upwelling events are activated along the coasts. River plumes are spread across the shelves. The poleward current is stopped. Circulation on the north coast of Spain is reversed to the west. Meeting of the two currents around Galicia generates a flow going outside the shelf.

Figure 9.3. Physical processes around Iberia and in Biscay in a cyclonic situation (southwest winds). The Poleward Current is enhanced and interacts with river plumes in Portugal to generate retention areas. River plumes in France are concentrated along the coast and a northward coastal flow is enhanced. Thermal stratification is broken down on the French shelf.

10 Northeast Atlantic mackerel

David Reid and Douglas Beare

Life-history traits

The lifespan of Northeast Atlantic mackerel (*Scomber scombrus*) is 15+ years. Sexual maturity is reached at 3 years. This species is a determinate multiple-batch spawner (Steven, 1949; Lockwood, 1988).

Spawning

Time. Spawning occurs in January–May in the southern area and in March–July in the western area (Lockwood *et al.*, 1981; Bez and Rivoirard, 2000, 2001; Beare and Reid, 2002). Spawning is closely associated with the shelf edge from 37 to 60°N. The longitudinal extent is greatest between 46 and 55°N and can extend 3–4°W of the 200 m contour, most commonly at peak spawning in April/May (Figures 10.1 and 10.2). The potential spawning area is believed to be largely identical with the area occupied (Walsh *et al.*, 1996; Dransfeld *et al.*, 2005; Ibaibarriaga *et al.*, 2007).

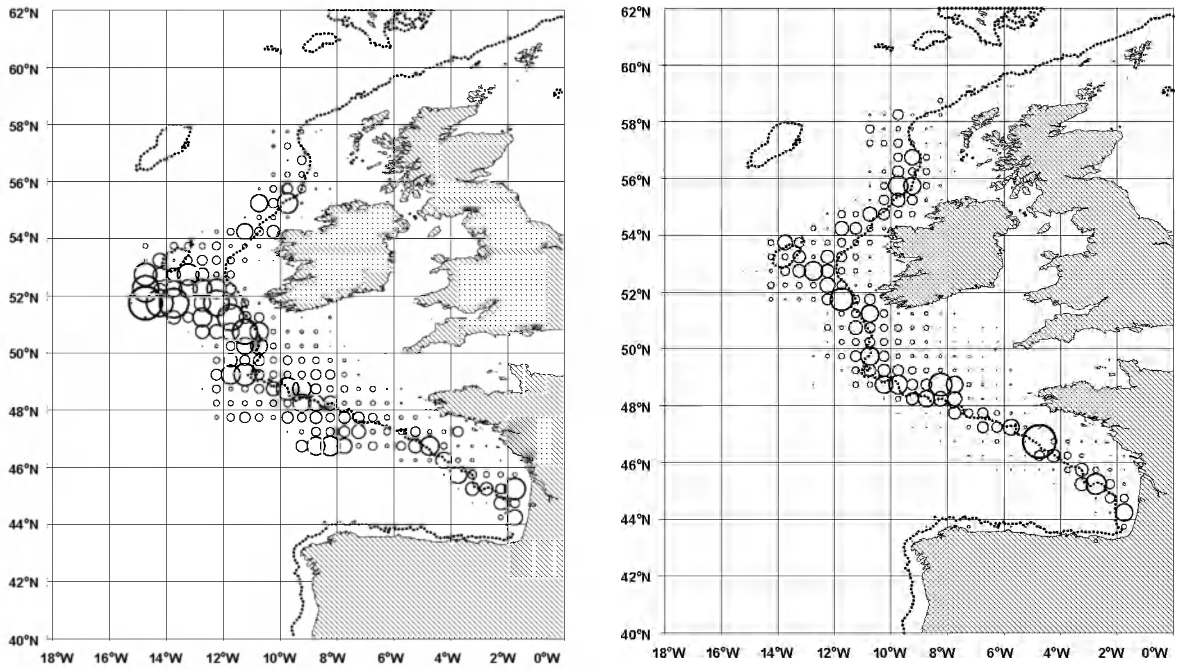

Figure 10.1. Distribution of spawning for the full survey season: (left) in 1995 and (right) in 1998. In 1995, spawning was distributed along the shelf break from 44 to 58°N, but was much more concentrated along the shelf break than in the previous year, although there was an extension again at Porcupine Bank. In 1998, spawning was distributed along the shelf break from 44 to 60°N–farther north than, in 1995. The westward extensions in Biscay and Porcupine were similar to those in 1995.

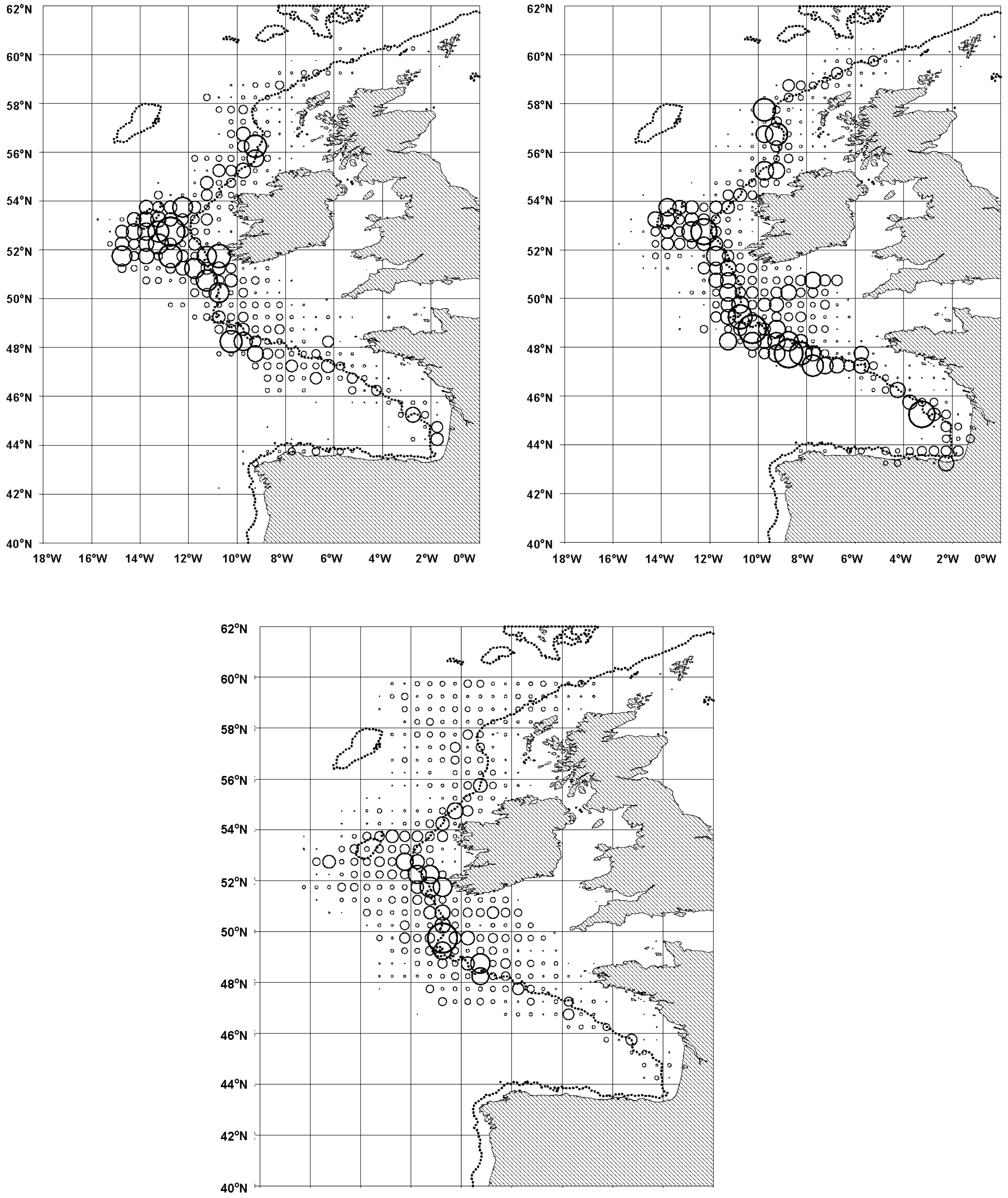

Figure 10.2. Distribution of spawning for the full survey season: (top left) in 2001; (top right) in 2004, and (bottom) in 2007. Spawning was distributed along the shelf break from 44 to 60°N–as in 2001. In 2004, spawning was mainly concentrated at the shelf break, although the usual westward extension at Porcupine can be seen. In 2004, there was no extension of spawning into the shallower waters of the Celtic Sea. The year 2007 was notable for a much wider general distribution of spawning away from that area, although the main spawning activity was again along the shelf break. This is particularly apparent in the Rockall Trough between 56 and 60°N, and also in the Celtic Sea area.

Schooling behaviour. The NEA mackerel form large, deep schools prior to spawning but are mainly dispersed or in high, small schools during the spawning season. They remain in small, high schools until aggregating in the overwintering area in the northern North Sea (in October), when they start to form very large schools in 225 m depth at the western edge of the Norwegian Deeps (Bakken and Westgaard, 1986; D. G. Reid *et al.*, 2001; Godø *et al.*, 2004; Slotte *et al.*, 2005).

Co-occurring species. During spawning, the NEA mackerel co-occur with horse mackerel (*Trachurus trachurus*, which spawns one month later) and blue whiting (*Micromesistius poutassou*, generally found over water deeper than 200 m), and possibly with sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Iberian area and Biscay, and with herring (*Clupea harengus*) in areas north of 54°N (Ibaibarriaga *et al.*, 2007).

Growth (adult)

Time. In summer/autumn, mackerel migrate to the Norwegian Sea and possibly the northern North Sea, around early July. Feeding is believed to be continuous until the overwintering aggregation in October (Steven, 1952; Lockwood, 1988; Langøy *et al.*, 2006; Martins, 2007; Villamor *et al.*, 2004a, 2004b).

Habitat. The mackerel occupy deep-water areas of the Norwegian and North seas (approximately 60–65°N 4°E–2°W), probably strongly associated with *Calanus* (Bullen, 1912; Darbyson *et al.*, 2003; Kaartvedt, 2000; Langøy *et al.*, 2006).

Co-occurring species. Autumn-spawning herring, blue whiting, and horse mackerel.

Nursery areas

The timing is not fully known, but the juvenile NEA mackerel probably arrive in the nursery areas in August/September. They remain there for their first two winters until age 2 (Figure 10.3) before recruiting to the adult stock at age 2–3, around spawning time.

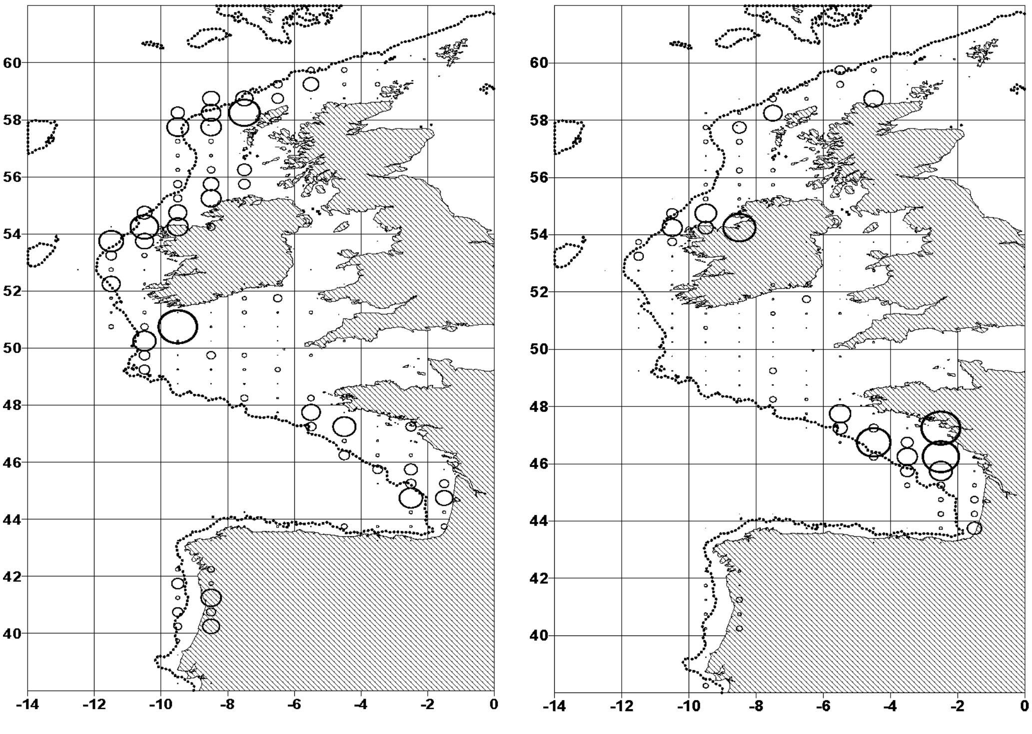

Figure 10.3. Distribution of mean catch rates of mackerel in bottom-trawl surveys carried out in the fourth quarter (1985–2006): (left) age 0 and (right) age 1. Circles are scaled to the maximum, showing the key nursery areas off Portugal, in Biscay, the southwest and northwest of Ireland, and off the Hebrides.

The nursery areas are generally demersal in shelf areas adjacent to coastlines. From south to north, juvenile fish aggregate in the following areas (Uriarte *et al.*, 2001b): (i) Spanish/Portuguese border; (ii) Bay of Biscay (between 45 and 48°N); (iii) Celtic Sea/Cornwall, mostly second-winter fish; (iv) west of Ireland (historical, but still some second-winter fish); (v) northwest Ireland; (vi) west of the Hebrides (historical); and (vii) northern edge of North Sea (recent and intermittent, mostly first-winter fish).

Nursery areas are mostly away from adult feeding areas. The status of the Cantabrian Sea as a nursery is unknown. Some juveniles are definitely found there, but juvenile distributions are inferred from bottom-trawl surveys. The bottom-trawl survey gear used in the Cantabrian Sea is selective against pelagics; therefore, the data are unreliable. The bottom-trawl survey data suggest that good recruitment may occur (e.g. 2002) when high densities of age-1 mackerel are found northwest of Ireland. High numbers of age 0 in October–December (numbers caught per hour in the western International Bottom Trawl Survey) tend to lead to large numbers of age-1 mackerel in the following year (Figure 10.4).

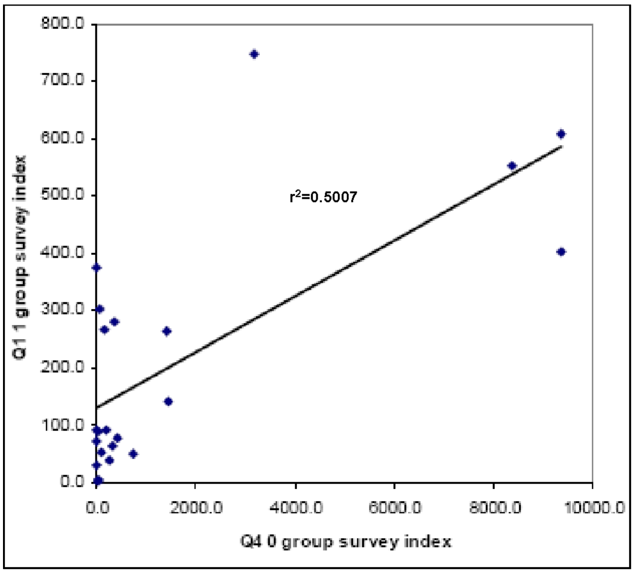

Figure 10.4. International recruit survey database (1985–2006): relationship between age 0 and age 1 the following year. (Taken from ICES, 2007b).

Co-occurring species in nursery areas include herring, possibly horse mackerel, and many demersal species.

Feeding

Predation mode. The mackerel is a filter or particulate feeder, probably mainly particulate (Bullen, 1912; Hamre, 1980; Lockwood, 1988).

Prey species. Predominantly *Calanus*, but also other crustaceans, fish larvae, and small adult fish are consumed (Steven, 1949; Kaartvedt, 2000; Olaso *et al.*, 2005; Prokopchuk and Sentyabov, 2006).

Migration

Adult mackerel overwinter in the North Sea (Viking Bank area) during October–February, after which they migrate to the spawning area. It is assumed that they turn north at the start of spawning and spawn and migrate (June–July) until spent. Following spawning, they move to the Norwegian Sea (approximately 60–65°N 4°E–2°W) during July and August. The migratory route of adult mackerel from the Cantabrian Sea in the south to the

Norwegian Sea in the north is illustrated in Figure 10.5. Papers that make reference to adult migration include Steven, 1948; Rankine and Walsh, 1982; Walsh and Martin, 1986; Iversen and Skagen, 1989; Holst and Iversen, 1992; Walsh *et al.*, 1995; D. G. Reid *et al.*, 1997, 2001, 2003, 2006; Belikov *et al.*, 1998; Nøttestad *et al.*, 1999; Uriarte and Lucio, 2001; Uriarte *et al.*, 2001b; Tenningen *et al.*, 2003; and Punzon and Villamor, 2009.

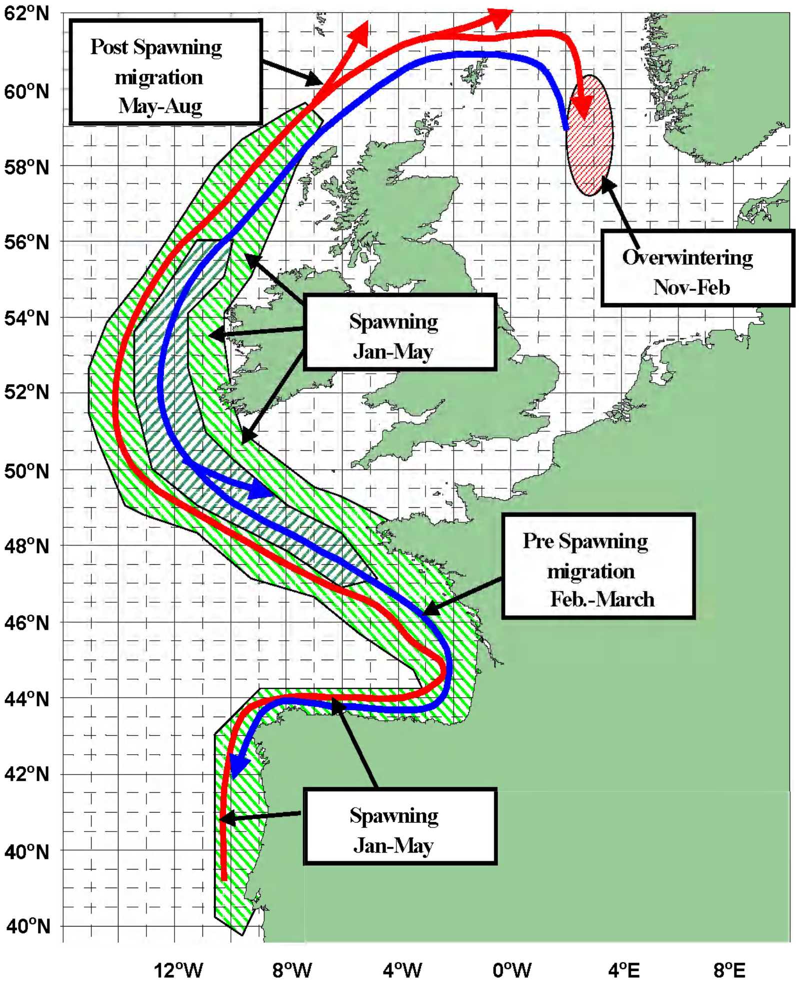

Figure 10.5. Migrations of adults of Northeast Atlantic mackerel.

After the end of larval drift, juvenile mackerel are believed to migrate actively to the nursery areas (see above; Figure 10.6). Individual-based model studies demonstrate that passive transport is insufficient to bring larvae to the known nursery grounds (Bartsch and Coombs, 2004; Bartsch *et al.*, 2004; Bartsch, 2005). Tagging data suggest that juveniles generally remain in the same area until they recruit to the adult stock (Uriarte *et al.*, 2001b). However, there is some evidence of movement of second-winter fish from the northern North Sea to the west of Scotland, and from the northwest to the west or southwest of Ireland, and into the Celtic Sea and the Cornwall area.

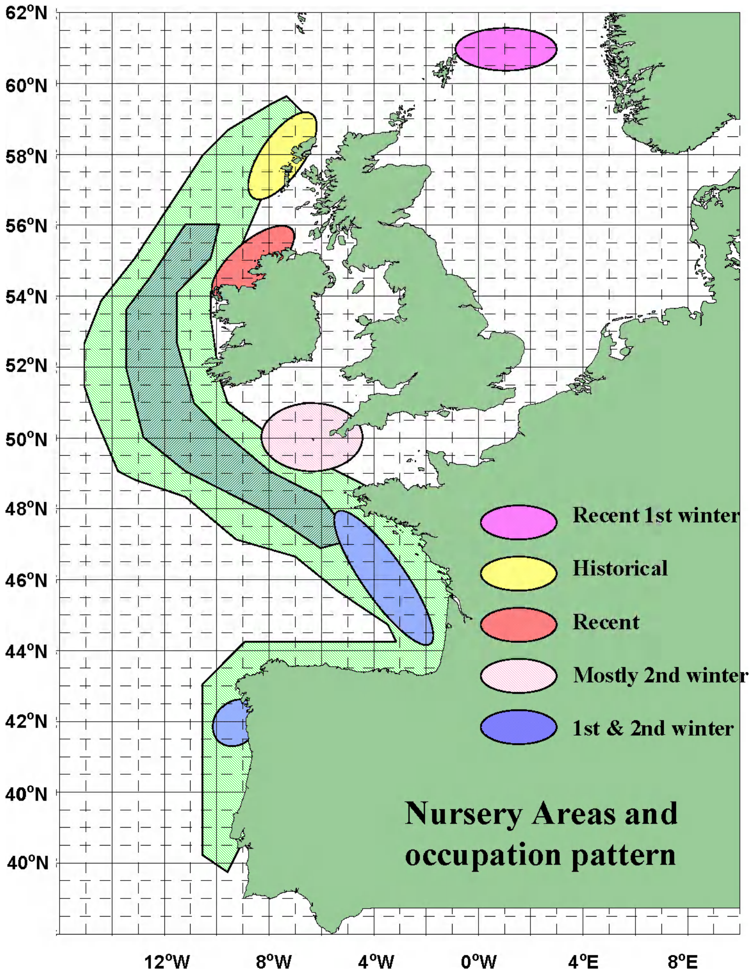

Figure 10.6. Migrations of juveniles of Northeast Atlantic mackerel.

Long-term trends

The main fishery for Northeast Atlantic mackerel and investigations of the stock have taken place mainly after the mid-1940s, although there are reports as far back as the late 19th century (Allen, 1897). This stock was only identified and exploited in the mid-1970s (Hamre, 1980; Lockwood *et al.*, 1981; Lockwood, 1988). At that time, the timing and location of spawning and post-spawning migrations were very similar to those at present (Rankine and Walsh, 1982). However, overwintering occurred west of Ireland, and fish left the North Sea in September. This departure time gradually shifted later to the current pattern from 1975 to 1990 (Walsh and Martin, 1986), and has been relatively stable since (D. G. Reid *et al.*, 2003, 2006). There is some evidence of changes in recruit distribution. In the 1980s, key areas were west of Ireland and west of the Hebrides. Both of these areas are currently not heavily occupied, with northwest Ireland and the northern North Sea becoming more important. Survey cpue data suggest that three main peaks of abundance have occurred in the northern North Sea: (i) late 1930s; (ii) late 1950s; and (iii) late 1990s (Figure 10.7). Also, the Scottish mackerel fishery changed from being a summer fishery in the 1960s to a winter fishery in the 1980s, 1990s, and 2000s (Figure 10.8).

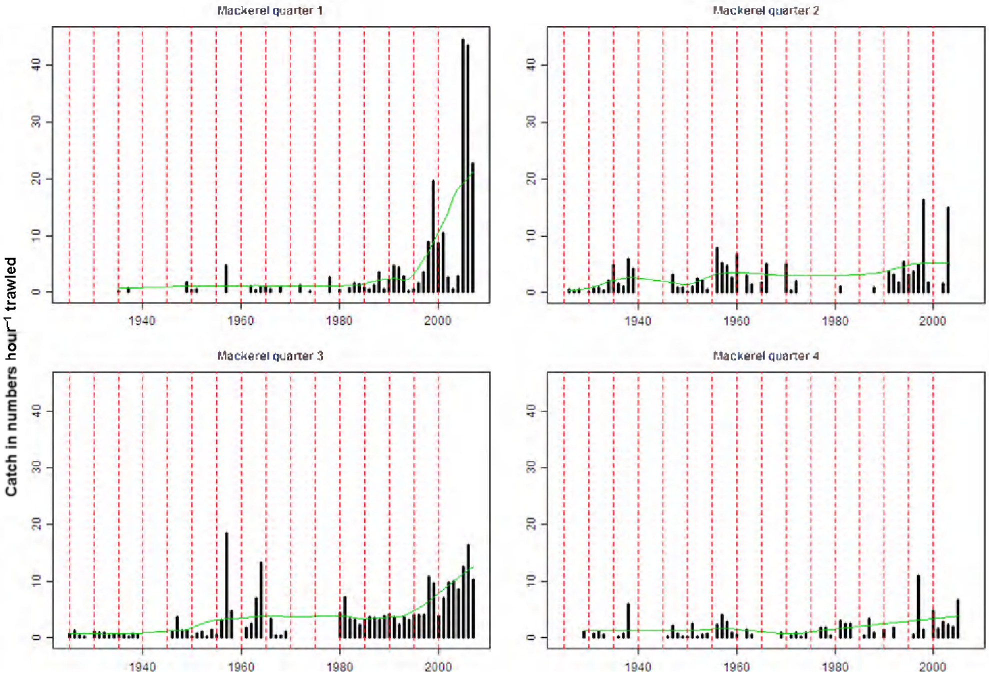

Figure 10.7. Catches of mackerel (numbers hour^{-1} trawled) in Fisheries Research Services (FRS) trawl survey database for 1925–2007 by quarter in ICES Division IVa (northern North Sea).

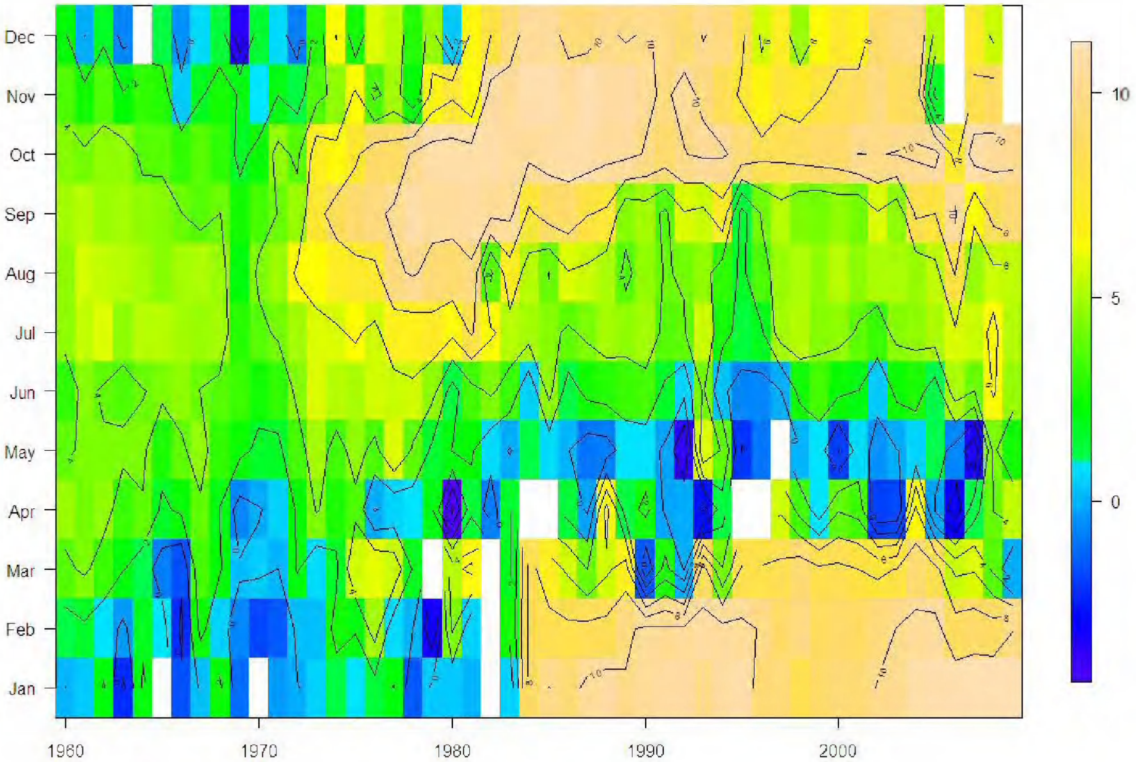

Figure 10.8. Seasonal changes in mackerel landings (log *t*) by the Scottish fleet by year (*x*-axis) and month (*y*-axis) between 1960 and 2008. The data comprise a monthly time-series, with total landings colour coded proportional to their size for each month and year combination. The objective is to illustrate how the fishery for mackerel changed from summer-dominated (early 1960s), to autumn-dominated (late 1970s, early 1980s), and to winter-dominated (mid-1980s to present).

Present characteristics

The Northeast Atlantic mackerel stock is currently (ICES, 2009e) estimated to be approximately 2.6 million t, which is about the highest in the assessment time-series (since 1980). The B_{pa} is 2.3 million t. It is currently assessed as being fished at an F of approximately 0.24; F_{pa} is 0.23. There has generally been good, stable recruitment, with rare (ca. once every 15 years) low years. The most recent poor year class was in 2000, but recruitment in 2002 was estimated as the highest in the time-series. Spawning is very widespread in both time and space (Gibraltar to Cape Wrath; January to July). There have been recent dramatic (1980–1990) changes in prespawning migration (track and time); a reversion to the earlier pattern would have significant management implications.

The Northeast Atlantic mackerel stock is considered to include a subcomponent that spawns in the North Sea (Iversen *et al.*, 1989; Gastauer *et al.*, 2009). Although this component may be genetically distinct (Nesbø *et al.*, 2000), it is managed as part of the Northeast Atlantic stock (ICES, 2009e).

Potential environmental influences

The life-cycle pattern is potentially related to a variety of physical features along the shelf break from Portugal to Shetland as well as on the shelf (Figure 10.9). Accordingly, many local factors may affect parts of the life cycle (Murray *et al.*, 1983), and at the stock level, these factors are integrated. Among the many features, there is considerable evidence that migration and distribution are modulated by temperature (Allen, 1909; Lumby, 1923; Eltink and Gerritsen, 1982). Adult fish seem to avoid water cooler than 8.5°C, and the prespawning migration seems to start when water reaches this temperature in the overwintering areas (Walsh and Martin, 1986; Walsh *et al.*, 1995; D. G. Reid *et al.*, 1997, 2001). Timing and area choice for the feeding migration and areas would suggest strong links to *Calanus* (Bullen, 1912; Kaartvedt, 2000; Darbyson *et al.*, 2003; Langøy *et al.*, 2006; Marquis *et al.*, 2006; Prokopchuk and Sentyabov, 2006). There is no real evidence from individual-based model studies for transport modulation of recruitment (Bartsch and Coombs, 2004; Bartsch *et al.*, 2004; Bartsch, 2005; Mohn *et al.*, 2007). Approximately 50% of the variability in the historical recruitment series may be explained by an index of wind-induced turbulence (Borja *et al.*, 2002).

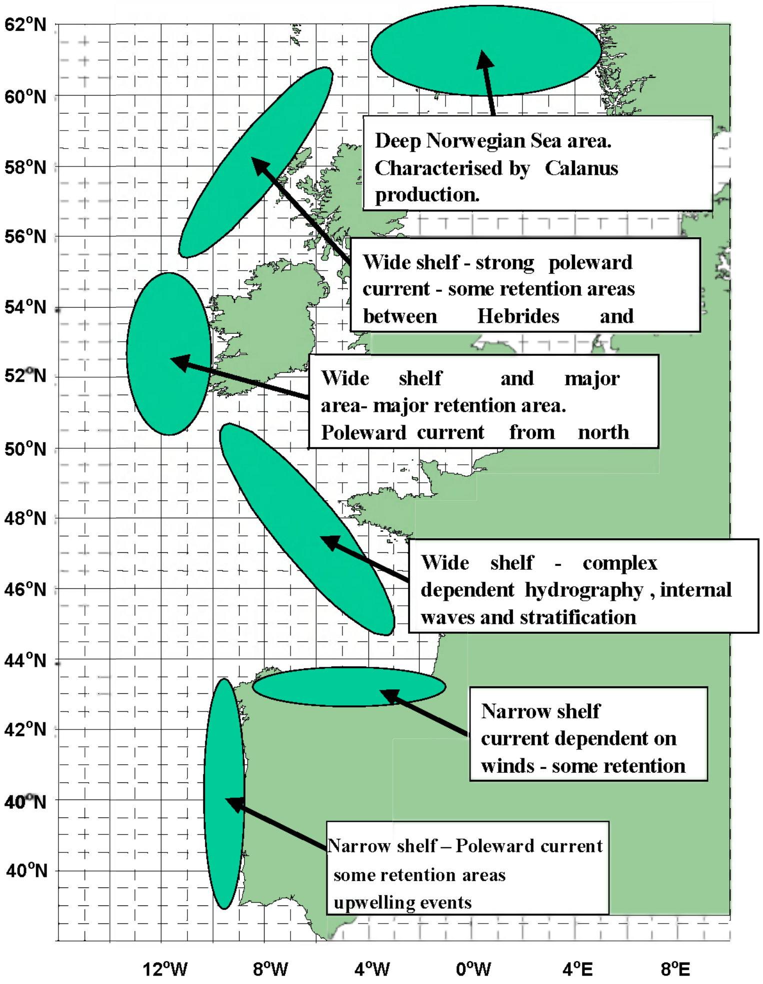

Figure 10.9. Schematics of areas occupied by Northeast Atlantic mackerel, and the potential physical processes with the potential to affect them.

Data types and sources

It is clearly essential that pan-European databases be assembled to allow the migration patterns, age structures, and long-term changes for Northeast Atlantic mackerel to be ascertained. European commercial and scientific databases were compiled at Marine Scotland to provide any information on mackerel. The databases found so far are:

- Fisheries Research Services (FRS) trawl survey: Scottish sea areas, 1925–present, patchy seasonally;
- International Bottom Trawl Survey (IBTS): North Sea, 1965–2009, patchy seasonally;
- Data Tracing Systems (DATRAS) trawl survey: North Sea and western waters, 2001–present, patchy seasonally;
- FRS market sampling: Scottish sea areas, 1960–present, good coverage seasonally;
- Scottish (and other international) commercial landings: Scottish sea areas, 1960–present, good coverage seasonally;
- International recruit trawl sampling: western continental shelf, 1980–2003, patchy seasonally;
- International egg survey: triennial, 1977–2004, good coverage seasonally; and
- Assessment working group inputs: aggregated numbers-at-age matrices.

11 Northeast Atlantic blue whiting

Mikko Heino

Life-history traits

Northeast Atlantic blue whiting (*Micromesistius poutassou*) individuals 10 years old or older are currently rare, although ages in excess of 20 years have been reported. Most blue whiting are believed to mature at 2–4 years of age, although the maturity ogive used by the Working Group on Widely Distributed Stocks (WGWIDE and, until 2007, its predecessor the Working Group on Northern Pelagic and Blue Whiting Fisheries, WGNPBW) assumes that maturation of a cohort is not complete before the age of 7 years (ICES, 2009e). The blue whiting is a batch spawner. Growth is very fast during the first year (up to 18–20 cm), but decelerates rapidly thereafter (more so in males than in females). Most fish are less than 32 cm in length, with the reported maximum length of ca. 50 cm.

Wintering

Overwintering juveniles can probably be found throughout the species' range. Adults migrate towards the spawning grounds during winter.

Spawning

Time. Spawning occurs mainly during February–April, with a seasonal northward progression.

Habitat. Blue whiting spawn in open water over great depths (>1000 m) or close to and on the shelf edge (Figure 11.1). Hátún *et al*. (2009a) demonstrated that the North Atlantic Subpolar Gyre influences spawning distribution, with a strong gyre (associated with cooler and fresher conditions west of the British Isles) resulting in a more southerly and easterly distribution than with a weak gyre.

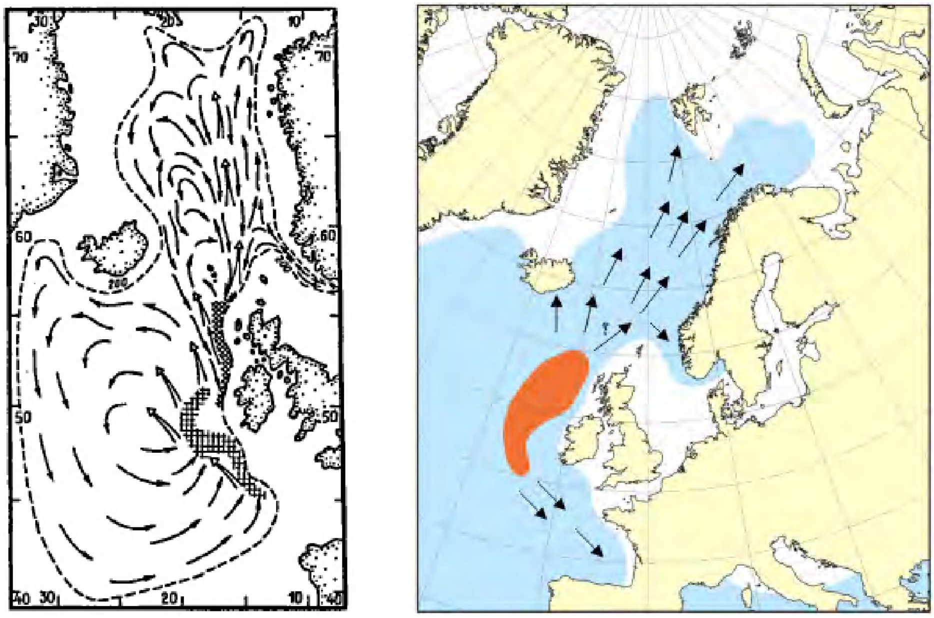

Figure 11.1. Migration of blue whiting. Left: the migration pattern of adult blue whiting, as suggested by Isaev *et al*. (1992). The hatched area shows the main spawning grounds. The current understanding does not fully support the pattern suggested for the component spawning around Porcupine Bank by not accounting for the Bay of Biscay component. The migrations in the west are also virtually unknown. Right: the current understanding of drift patterns of blue whiting larvae.

Schooling behaviour. Dense spawning aggregations are formed during the spawning season, typically at 300–600 m depth. Diurnal movements are small. Sexual dimorphism in the pelvic fin (Andersen and Jákupsstova, 1978) suggests that mating pairs are formed during spawning.

Co-occurring species. During spawning include mesopelagic fish such as hatchetfish (*Sternoptyx* spp.), lanternfish (Myctophidae), and, in recent years, dealfish (*Trachipterus arcticus*).

Feeding

Time. Late spring and summer is the main feeding period for blue whiting, but some feeding may occur throughout the year. Very little feeding occurs during the February–April spawning season.

Habitat. Traditionally, the Norwegian Sea has been considered to be the main feeding area; other areas include south of Iceland and along the continental shelf edge from the Bay of Biscay to the Barents Sea.

Predation mode. Blue whiting is a snapping feeder.

Prey species. Crustaceans (large copepods, amphipods, krill), small cephalopods, small fish, and fish larvae (Bailey, 1982; Monstad, 2004; Prokopchuk and Sentyabov, 2006; Dolgov *et al*., 2010).

Schooling behaviour. Blue whiting form loose layers or schools that demonstrate diurnal migrations. Juveniles can be found in surface waters at night.

Co-occurring species. Saithe (*Pollachius virens*), redfish (*Sebastes* spp.), and various mesopelagic fish below 200 m; herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) above 200 m; and demersal fish on the shelf areas.

Migrations

Mature blue whiting migrate to the spawning grounds west of the British Isles during winter (Figure 11.1). In spring to early summer, the post-spawning migration brings the adults back to the feedings areas. However, Hátún *et al*. (2009b) have demonstrated that during the post-spawning migration, more blue whiting migrate west of the Faroe Islands when the Subpolar Gyre is weak. Exact migration patterns, along with stock structure, are not well known.

Larval drift and nursery areas

Hatched larvae drift northward towards the Norwegian Sea and Iceland, or southward towards the Bay of Biscay (Figure 11.1; Bailey, 1982). The direction of drift depends on the spawning area. Hydrographic modelling suggests that the line separating northern and southern drift varies from year to year, but is usually at the northern part of Porcupine Bank (Skogen *et al*., 1999). Larval otolith-growth histories also support the hypothesis that larvae originating in a specific spawning area tend to drift together to the same nursery area (Brophy and King, 2007). By February in the year after spawning, blue whiting probably originating in the main spawning area are found in surveys in the Barents Sea (Figure 11.2; Heino *et al*., 2008). A proportion of the northward-drifting larvae enter the North Sea, and 0-group blue whiting are caught there by the third quarter of the spawning year (Figures 11.3 and 11.4). The main nursery areas are in the Norwegian Sea, south of Iceland, southwest Barents Sea, and the Bay of Biscay. The deeper parts of shelf areas around the Faroe Islands, the British Isles, and the North Sea also function as nursery areas.

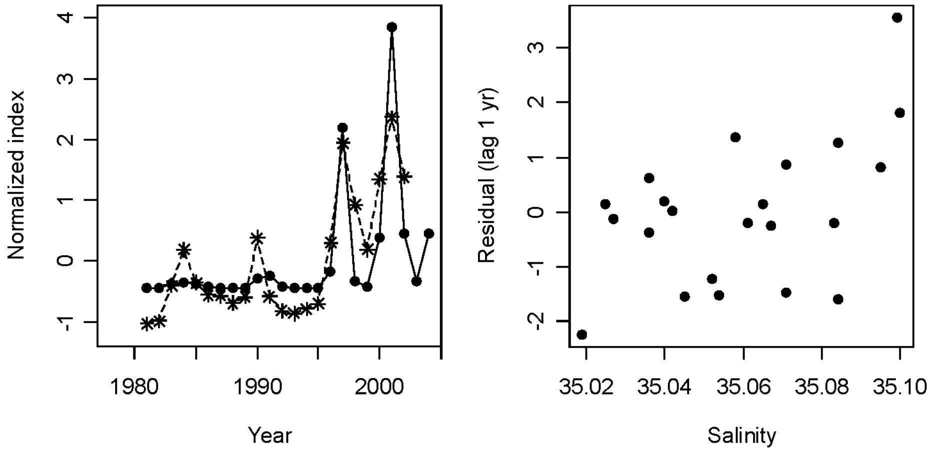

Figure 11.2. Left: abundance index of 1-group blue whiting, based on the Barents Sea winter survey conducted by IMR (Norway; unbroken line), and recruitment in the main Atlantic blue whiting stock (dashed line; ICES, 2004b). Right: Residuals from the log (abundance index)~log (recruitment) regression are positively correlated with salinity in the Fugloya–Bear Island section ($r = 0.49$). High salinity on this section is presumed to indicate a large inflow of Atlantic water into the Barents Sea, which should facilitate the entry of young blue whiting into the survey area. See also Heino *et al.* (2008).

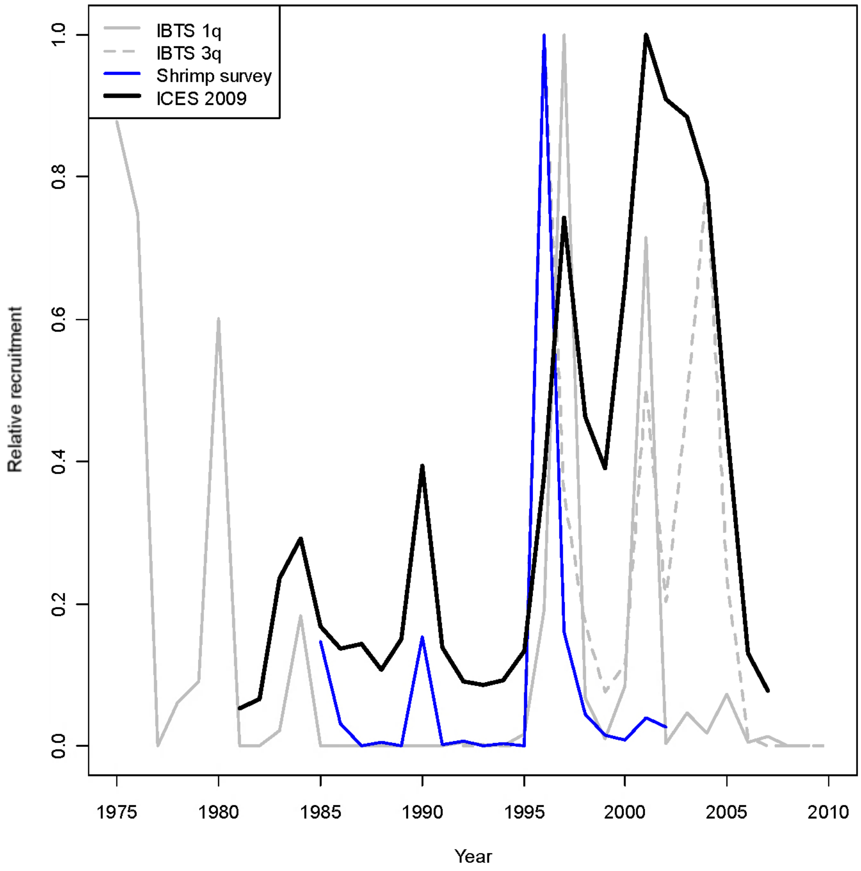

Figure 11.3. Relative recruitment indices of blue whiting in North Sea surveys compared with recruitment in the latest stock assessment (ICES, 2009e). The International Bottom Trawl Survey (IBTS) during the third quarter (1991–2009) and Norwegian shrimp survey in the fourth quarter (1984–2002) caught 0-group blue whiting; these time-series have been shifted forward by 1 year to match recruitment (age 1) in the assessment (1981–2007) and the first quarter IBTS (1975–2009). All time-series have been scaled to a maximum of 1. Strong recruitment events have been captured by at least one of the surveys, but there are large differences in how single surveys have captured recruitment signals in the main Atlantic stock. This suggests that environmental conditions are important for determining numbers of recruits entering the North Sea and how they are subsequently distributed.

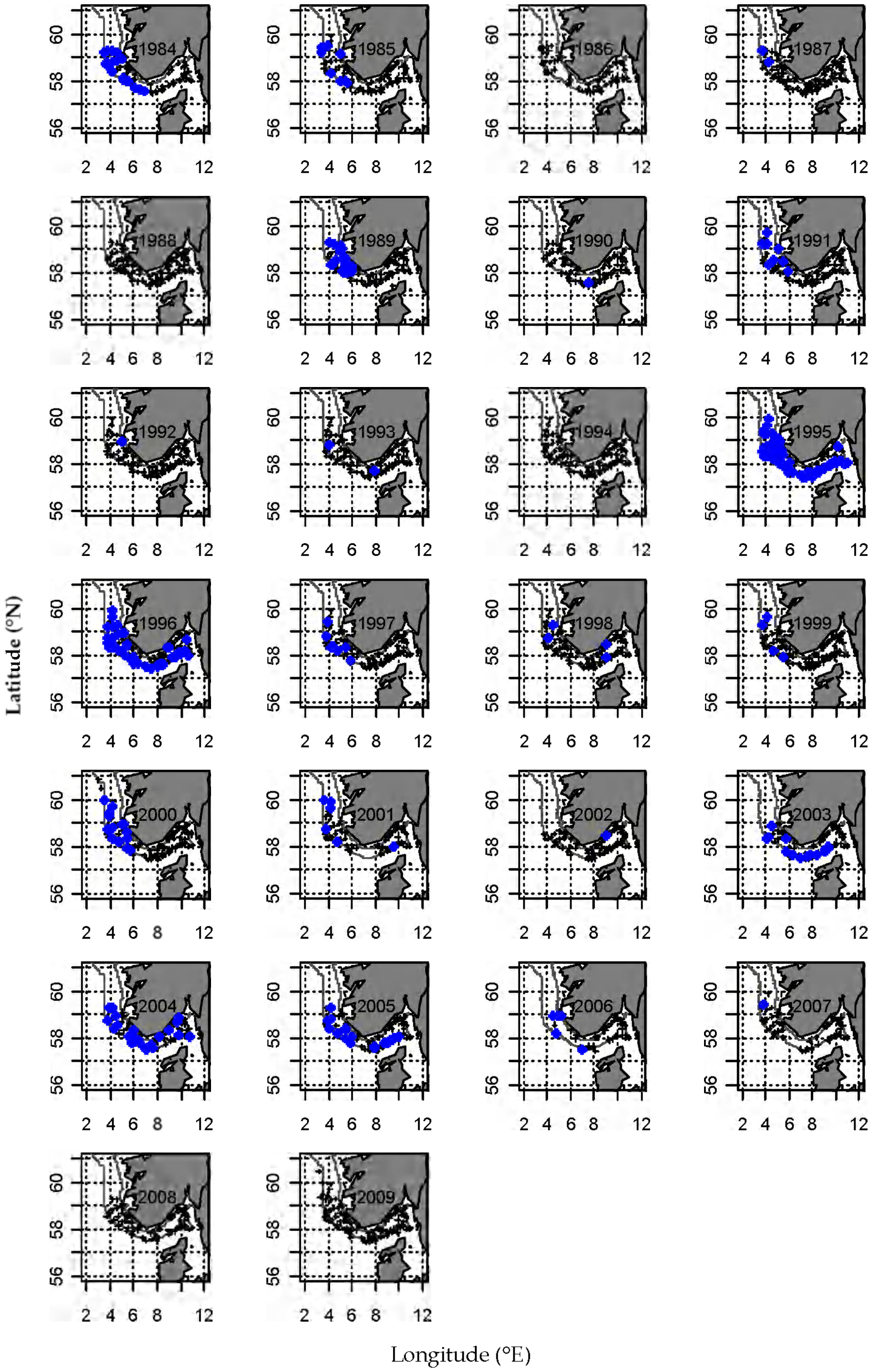

Figure 11.4. Distribution of trawl stations (crosses) and stations with likely 0-group blue whiting (blue dots) in the North Sea shrimp survey conducted by IMR (Norway). The 0-group blue whiting tend to occur in the western parts of the survey area and also, in some years, in the southern slopes of deep waters in the Skagerrak. Since 2002, the survey gear and timing of the survey have undergone changes.

Long-term trends

Stock size. Little is known about stock size prior to 1981, the first year in the current ICES assessment time-series. The stock was relatively stable until the late 1990s, after which it increased owing to a period of strong recruitment. Figures for the latest years in the assessment are uncertain, but suggest that the stock is in decline from the historical high reached around 2003.

Recruitment. During the period 1996–2005, recruitment (age 1, corresponding to the 1995–2004 year classes) was considerably higher than previously observed. What were "weak" year classes during this period would have been considered "strong" before 1995. In 2007–2009, recruitment appeared weak by any standard. No stock-wide recruitment estimates exist prior to 1981, but data from the International Bottom Trawl Survey (first quarter) in the North Sea indicate that there was a period of strong recruitment in the 1970s (Figure 11.3). Drivers of changes in recruitment are poorly known (an ICES Workshop on Blue Whiting Recruitment held 10–12 November 2009 focussed on this topic; see ICES, 2009f).

Body size and growth. At the level of the whole stock, there are indications of declining weights-at-age (ICES, 2008b). Interpretation of this trend is complicated by the aggregated nature of the data and potential biases in age readings.

Present characteristics

The stock is still relatively large because of the period of strong recruitment that ended just a few years ago. With declining recruitment, the numbers of young blue whiting are declining, and the average age of blue whiting is increasing.

Potential environmental influences

Hydrographic conditions during the spawning season affect the relative amounts of eggs and larvae drifting to northern and southern nursery areas. A particular spawning area may seed northern areas in one year and southern areas in another (Skogen *et al.*, 1999).

The large inflow of warm Atlantic water into the Barents Sea (as indicated by a positive salinity anomaly on the Fugløya–Bear Island section) has a positive effect on the abundance of blue whiting in the Barents Sea one year later (Heino *et al.*, 2008; Figure 11.2).

The strength of year classes, as 0- or 1-group, in the North Sea is linked only to the strength of year classes in the main Atlantic stock. High abundance in the North Sea tends to coincide with strong year classes in the main stock. However, some strong year classes do not show up strongly in the North Sea. The success of surveys in different parts of the North Sea and at different times of the year in catching recruits is highly variable (Figures 11.3 and 11.4). This suggests environmentally driven variation in the transport of larvae into the North Sea as well as their subsequent distribution.

The North Atlantic Subpolar Gyre influences spawning distribution (Hátún *et al.*, 2009a), and its strength is correlated with landings (Hátún *et al.*, 2009b).

The North Atlantic Subpolar Gyre is probably also influencing recruitment. The strength of the gyre started to decline (the gyre index started to increase) at the same time as recruitment increased (Hátún *et al.*, 2009a, 2009b). As this change is associated with an increased inflow of Atlantic water into the Norwegian Sea through the Faroe–Shetland Channel, a main dispersal route of eggs and larvae to the Norwegian Sea, it is likely that these changes are causally linked. However, the mechanism is not trivial, because earlier periods of high gyre index did not witness greatly enhanced recruitment, nor is the recent decline in recruitment explained by this link.

There is evidence to suggest density-dependent juvenile growth in the Norwegian Sea, indicating that growth of young blue whiting can be food-limited (Figure 11.5).

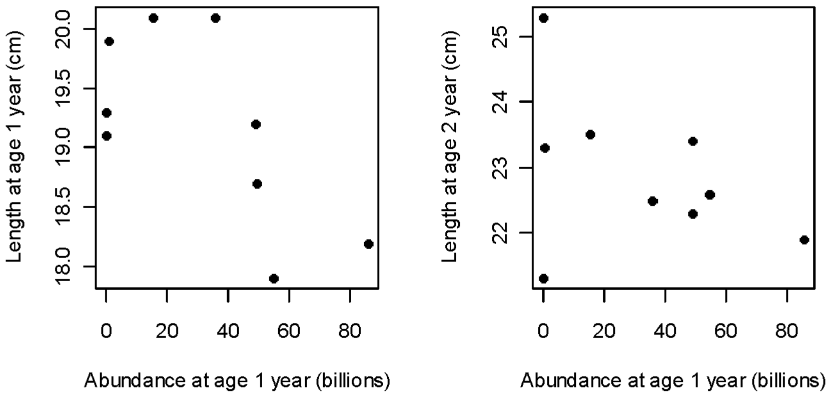

Figure 11.5. Relationship between abundance (2000–2008) and length-at-age in the International Pelagic Ecosystem Survey in the Norwegian Sea, May 2000–2009. Left: For age 1, the relationship is for the observations in the same year. Right: for age 2 years, length-at-age is plotted against a cohort's abundance in the previous year. There is a negative relationship that is approaching statistical significance (*p* = 0.057) at age 1 year; there is no clear relationship at age 2 years (*p* = 0.29).

12 Conceptual schemes of life-cycle spatial structures

Pierre Petitgas, Miguel Bernal, and Yorgos Stratoudakis

The life cycles of the different species populations examined have different spatial scales and structures. Harden Jones (1968) conceptualized the great variety in life-cycle patterns in a migration triangle, in which larval passive drifts were balanced by adult active migrations (contranatant vs. denatant migrations). Here, we specify the structural differences between life-cycle patterns because of their potential consequences on population dynamics, linkage with environmental features, and spatial management strategies. Differences between life-cycle patterns are summarized below using schematic diagrams.

Differences in life-cycle patterns

In the case studies examined, differences in the life-cycle patterns could result from the following characteristics:

- spatial scale of population extension (fish length and lifespan);
- discreteness/continuity of habitats for different life-cycle stages (geographical setting);
- mixing/separation of population contingents at different stages/times of the life cycle (contingent structure).

Anchovy (*Engraulis encrasicolus*) and sprat (*Sprattus sprattus*) formed discrete populations, with a limited spatial extension (Table 12.1; Figure 12.1). In contrast, the populations of mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*) have a more diffuse spatial extent on the scale of ICES waters, with adults making large-scale annual migrations (Figure 12.2). Mackerel have several discrete nursery grounds and large continuous spawning grounds where population components are mixed (Table 12.1). Herring (*Clupea harengus*) have several discrete spawning grounds, where population components are separated, and large continuous nursery and feeding grounds, where population components are mixed (Table 12.1). The life cycle of sardine (*Sardina pilchardus*) has some characteristics in common with anchovy and sprat and some with mackerel (Table 12.1; Figure 12.2). Sardines started to reproduce at a small size, and small sardines (<18 cm) demonstrate discrete local populations. At a later age, large sardines recruit to a mixed population component and undergo larger-scale migrations covering the extent of the various local populations (Table 12.1; Figure 12.2). The change in behaviour between small and large sardines may be related to a change in diet and swimming capacity as the fish grow larger.

Table 12.1. Structural differences between pelagic species life cycles in ICES waters, as characterized by differences in the spatial extent of populations, the life phases where population components are mixed or isolated, and the habitats where population components are isolated. Sardines demonstrate a mixture of spatial extents as the fish move to a different population contingent as they grow.

SPECIES	SPATIAL SCALE	MIXED COMPONENTS	DISCRETE HABITATS
Anchovy and Sprat	Small	Juvenile, feeding	Spawning
Herring	Large	Juvenile, feeding	Spawning
Mackerel	Large	Spawning, feeding	Juvenile
Sardine	Older fish: large Young fish: small	Spawning, feeding –	– Spawning, juvenile

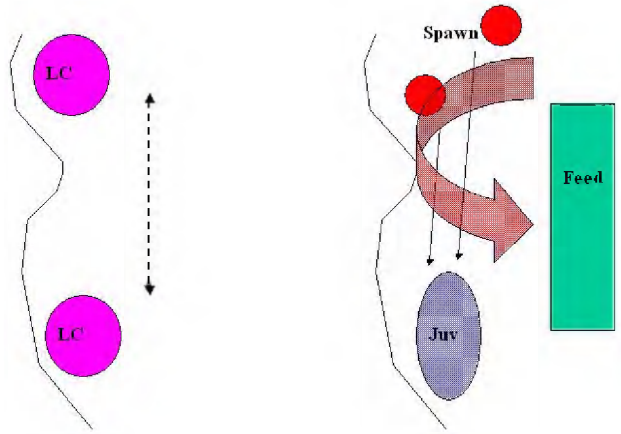

Figure 12.1. Life-cycle schematic diagrams for: (left) anchovy and sprat, and (right) herring. LC = life cycle, Juv = juvenile. Dashed line (left) represents vagrancy at larval and adult stages. Red arrow (right) corresponds to the adult feeding migration, which overlaps with juveniles habitats. Black arrows correspond to larval drift. The scales along abscissa and ordinate are similar in both figures.

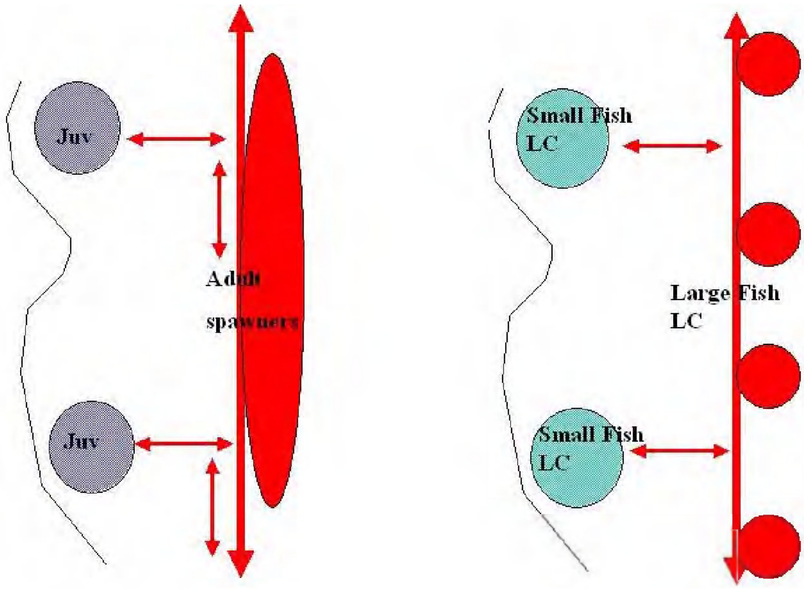

Figure 12.2. Life-cycle schematic diagrams for: (left) mackerel and (right) sardine. LC = life cycle, Juv = juvenile. Juveniles of mackerel are located on discrete habitats. Spawners undergo migrations (the bigger the fish, the larger the migration) over a large continuous area and form one large reproductive component. Small sardines form discrete local populations; larger sardines form a large-scale continuous population with continuous spawning grounds. The scales along abscissa and ordinate are similar in both figures.

Mechanisms supporting life-cycle patterns

The life cycles of the different species include similar basic processes: larval drift, feeding, juvenile and adult growth and survival, adult migration, spawning, and overwintering. Differences between life-cycle spatial patterns relate to the spatial scale and connectivity between the different habitats involved in these basic processes. The persistence of such connectivity can be sustained by environmental drivers and fish behaviour, including imprinting and social learning (Wynne-Edwards, 1962; Harden Jones, 1968; McCleave *et al.*, 1984; McQuinn, 1997; Corten, 2002; Petitgas *et al.*, 2006). The encounter between juveniles and adults is critical for life-cycle closure if it is sustained by learned behaviours. Anchovy juveniles have been observed to change their schooling behaviour when mixed with adults (Figure 12.3; Petitgas, 2007). In Norwegian spring-spawning herring, young mature fish from the marine component have been reported to school and mix with older fish from the coastal component and to adopt the local traditional spawning habitats (Johannessen *et al.*, 2009). Adequate behaviour (feeding, predator avoidance) and the exchange of information between fish in order to acquire these behavioural characteristics, would ultimately be selected for, because they result in spatial memory across generations at the population level, which would increase individual fitness (Giske *et al.*, 1998). In that context, different factors explaining differences in life-cycle patterns are as follows.

- Geographical and environmental settings, which determine the discreteness and number of suitable feeding, spawning, and nursery habitats (e.g. herring around Ireland demonstrate discrete populations, whereas herring in the North Sea are components within one population).
- Lifespan and asymptotic length, which affect the spatial scale at which the population can develop in space and colonize a variety of habitats (e.g. small fish such as anchovy and sprat, do not form large-scale continuous populations, as do mackerel and blue whiting).
- Life-history traits (short-lived vs. long-lived) and reproduction strategy (semelparous vs. iteroparous), which affect the repetition of migration routes during an individual fish's lifespan and, therefore, the selective importance of imprinting or social learning.
- Phenotypic plasticity in growth and maturation, which determines diversity in growth trajectories between individuals, potentially leading to varied migratory behaviours and habitat-use patterns.
- Aggregation and schooling behaviour, overlap of length classes across ages, and overlap in feeding habitats of adults and juveniles, which determine conditions for information-sharing across generations and, therefore, learning.

These characteristics may contribute to the persistence of distinct contingents within a single population (e.g. Secor, 1999), where individuals from different contingents mix and separate in space and time (e.g. spring/autumn spawners, repeat homing to spawning grounds, migratory vs. resident forms). Based on similar processes, populations can be connected within a metapopulation (e.g. McQuinn, 1997; Smedbol and Wroblewski, 2002).

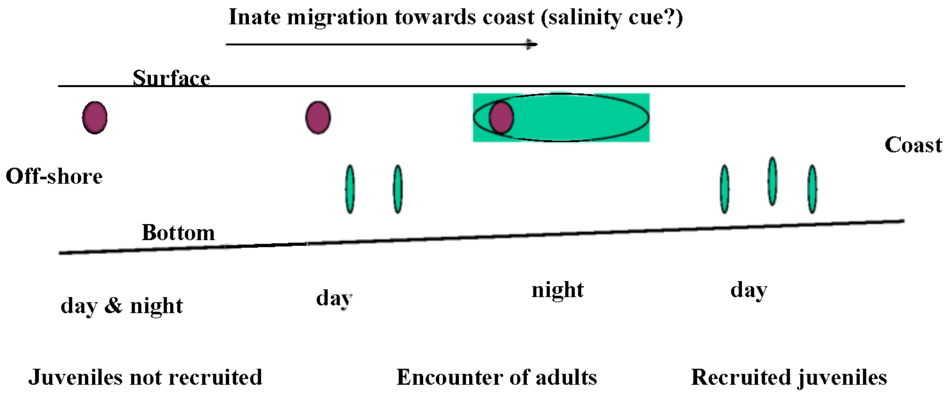

Figure 12.3. Schematic diagram showing how juveniles of anchovy in the Bay of Biscay may encounter adults in the coastal areas by spatial overlap and switch from juvenile-like schooling behaviour to adult-like schooling behaviour. At night at the surface, juveniles and adults are mixed. At dawn, when schools are formed, juveniles aggregate with adults and are entrained in adult-like schools. Purple: juvenile schools by day and night; green near bottom: adult-like schools during day; green at surface: adult-like disaggregated schools at night. (ICES, 2007c).

Consequences for understanding population response to climate change

As life-cycle patterns differ in their spatial organization, they can be expected to demonstrate specific variability with hydro-climate (Table 12.2). For instance, environmental drivers that determine recruitment variability may not be the same for all species, depending on the space–time spawning windows, meaning that adult spawning behaviour is also a control for recruitment variation. Further, habitat and length overlaps between young and old fish are critical for maintaining the young in the tradition of the existing life-cycle pattern. Environmental impacts may disrupt overlaps across generations and jeopardize life-cycle closure or favour the colonization of new habitats. Therefore, social behaviour may modulate the connectivity between habitats. To predict the responses of populations to environmental changes, it is clearly necessary to integrate over the entire life cycle, and to consider changes in habitats and connectivity for all life stages (Table 12.2).

Table 12.2. Impact of environmental changes on habitat-use patterns for pelagic species within ICES waters.

SPECIES	VARIATION IN YEAR-CLASS STRENGTH	VARIATION IN LARGE ADULT MIGRATION	VARIATION IN SPAWNING COMPONENT
Anchovy	Burst/loss of local population	–	–
Sprat	Burst/loss of local population	–	Loss of winter spawners
Herring	Loss of spawning grounds	Failure of encounter between young/old fish	Loss of winter spawners
Mackerel	Burst/loss of nursery grounds	Variation in spawning sites Failure of encounter between young/old fish	–
Sardine	Burst/loss of local population (small fish)	Variation in spawning sites Failure of encounter between young/old fish	–

13 Perspectives

Use of operational oceanographic products in modelling habitat and recruitment

The different life-cycle patterns examined demonstrate a consistent match between seasonal oceanographic features and the habitats used by different life stages of the fish. From the knowledge documented here, it would be possible to construct a sequence of quantitative habitat models for the successive life stages, which could be useful from a climate-change perspective. When searching for relationships between patterns in the physical environment and fish distributions, the questions of scale and behaviour are central (ICES, 2008c). Realistic simulations of past and present situations derived from coupled physical–biogeochemical models are now available to allow the availability of suitable habitats to be mapped (ICES, 2009g; Struski *et al.*, 2009). The strength of these models is that the simulated environment resolves a range of spatio-temporal scales in the oceanographic features. These patterns can also be useful as correlates of recruitment.

Full life-cycle modelling

The fish populations examined here have complex life cycles comprising different life stages that exploit a variety of habitats. Larval dispersal and fish movements close the life cycles by spatially connecting habitats occupied by different life stages. Each life stage has particular habitat requirements, and the availability of these requirements in space and time may change depending on hydro-climatic changes. In order to predict the responses of populations to environmental changes, it is clearly necessary to integrate many processes over the entire life cycle. Mechanisms and controls of changes in spatial distributions and migration patterns have been reviewed by ICES (2008c). A sequence of habitat models and connectivity pathways can be integrated into matrix-like population models (Heath *et al.*, 2008; Christensen *et al.*, 2009). However, approaches involving complex individual-based models (IBMs) are also of interest. Dynamic full life-cycle IBMs are being developed, coupled with lower trophic ecosystem models, that integrate habitat availability, bioenergetic requirements, larval drift, fish movements, growth, and survival (Werner *et al.* 2001; Megrey *et al.*, 2007). An important aspect yet to be completely resolved is the modelling of fish movement and related behaviour.

The importance of behaviour

In Section 12, it was emphasized how learned behaviours contribute to the determination of persistent life-cycle patterns. Fish can learn and memorize efficient behaviours from their more experienced congeners (Dodson, 1988; Brown and Laland, 2003), which results in a group-level memory or tradition (McQuinn, 1997; Corten, 2001a, 2001b). Based on historical patterns, Petitgas *et al.* (2006) suggests mapping indices of population memory as well as those of habitat suitability to update spatial distributions of populations when environmental conditions change. In effect, suitable habitats may remain unoccupied when knowledge of migration routes is lost, for example, after a stock collapse (e.g. Corten, 2001a, 2001b). Giske *et al.* (1998) elaborated a modelling framework where fish movement and habitat-selection behaviours are guided by proximate environmental cues and are also ultimately selected for depending on their resulting fitness. G. Huse and Ellingsen (2008) modelled the Barents Sea capelin (*Mallotus villosus*) population response to a climate-change scenario based on this approach.

Future research directions

Future directions for the further development of predictive tools include:

- monitoring habitat suitability using operational oceanographic products;

- predicting successful spawning windows in space and time under different climate scenarios using biophysical larvae IBMs;
- predicting fish growth and reproductive potential under different climate scenarios using bioenergetic models forced by three-dimensional ecosystem model outputs;
- integrating behavioural processes into models of fish spatial distributions in order to predict the effective occupation of potentially suitable habitats.

Therefore, it is expected that operational oceanographic products and bioenergetic budgets will be used in habitat modelling, that the importance of behaviour in shaping life-cycle patterns will be recognized, and that full life-cycle population models will be developed in order to predict population responses to climate change. As fish populations are depleted, their internal structure and individual-level phenotypic diversity become important drivers of their future evolution. Therefore, complex process models cannot be avoided, requiring the acquisition of new data on movements, vital rates, and bioenergetics across a range of ecosystems. In addition, it is also essential that regional and pan-European research, survey, and commercial databases be assembled so that migration patterns, age structures, and long-term changes can be ascertained.

14 References

Alheit, J., and Hagen, E. 1996. The Bohuslän herring periods: are they controlled by climate variations or local phenomena? ICES Document CM 1996/O:6.

Alheit, J., and Hagen, E. 1997. Long-term climate forcing of European herring and sardine populations. Fisheries Oceanography, 6: 130–139.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous regime shifts in the Central Baltic and the North Sea in 1987–88. ICES Journal of Marine Science, 67: 1205–1215.

Allain, G., Petitgas, P., and Lazure, P. 2001. The influence of mesoscale ocean processes on anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay estimated with a three-dimensional hydrodynamic model. Fisheries Oceanography, 10: 151–163.

Allain, G., Petitgas, P., Grellier, P., and Lazure, P. 2003. The selection process from larval to juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. Fisheries Oceanography, 12: 407–418.

Allain, G., Petitgas, P., Lazure, P., and Grellier, P. 2007. Biophysical modelling of larval drift, growth and survival for the prediction of anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay (NE Atlantic). Fisheries Oceanography, 16: 489–505.

Allen, E. J. 1897. Report on the present state of knowledge with regard to the habits and migrations of the mackerel *Scomber scombrus*. Journal of the Marine Biological Association of the UK, 5: 1–29.

Allen, E. J. 1909. Mackerel and sunshine. Journal of the Marine Biological Association of the UK, 8: 394–406.

Andersen, K. P., and Jákupsstova, S. H. 1978. Sexual dimorphism and morphological differences in blue whiting (*Micromesistius poutassou*). ICES Document CM 1978/H:46.

Andreu, B., and Plaza, M. 1962. Estudio de la edad y crecimiento de la sardina (*Sardina pilchardus* Walb.) del NW de España. Investigaciónes Pesqueras, 21: 49–95.

Aneer, G. 1985. Some speculations about the Baltic Herring (*Clupea harengus membras*) in connection with the eutrophication of the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 42(Suppl. 1): 83–90.

Aneer, G. 1987. High natural mortality of Baltic herring (*Clupea harengus*) eggs caused by algal exudates. Marine Biology, 94: 163–169.

Aneer, G., and Nellbring, S. 1982. A SCUBA-diving investigation of Baltic herring (*Clupea harengus membras*) spawning grounds in the Askö–Landsort area, Northern Baltic proper. Journal of Fish Biology, 21: 433–442.

Anthony, V. C., and Fogarty, M. J. 1985. Environmental effects on recruitment, growth and vulnerability of Atlantic herring (*Clupea harengus harengus*) in the Gulf of Maine Region. Canadian Journal of Fisheries and Aquatic Sciences, 42: 158–173.

Aro, E. 1989. A review of fish migration patterns in the Baltic. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 190: 72–96.

Arrhenius, F., and Hansson, S. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series, 96: 125–137.

Atarhouch, T., Rüber, L., Gonzalez, E., Albert, E., Rami, M., Dakkak, A., and Zardoya, R. 2006. Signature of an early genetic bottleneck in a population of Moroccan sardines (*Sardina pilchardus*). Molecular Phylogenetics and Evolution, 39: 373–383.

Axenrot, T., and Hansson, S. 2003. Predicting herring recruitment from young-of-the-year densities, spawning-stock biomass, and climate. Limnology and Oceanography, 48: 1716–1720.

Bailey, R. S. 1982. The population biology of blue whiting in the North Atlantic. Advances in Marine Biology, 19: 257–355.

Bainbridge, V., and Forsyth, D. C. T. 1972. An ecological survey of a Scottish herring fishery. Part V: The plankton of the northwestern North Sea in relation to the physical environment and the distribution of the herring. Bulletins of Marine Ecology, 8: 21–52.

Bakken, E., and Westgaard, T. 1986. Intermixture of the North Sea and western mackerel. ICES Document CM 1986/H:65.

Bakun, A., and Weeks, S. J. 2006. Adverse feedback sequences in exploited marine ecosystems: are deliberate interruptive actions warranted? Fish and Fisheries, 7: 316–333.

Bandarra, N., Batista, I., Nunes, M., Empis, J., and Christie, W. 1997. Seasonal changes in lipid composition of sardine (*Sardina pilchardus*). Journal of Food Science, 62: 40–42.

Bartsch, J. 2005. The influence of spatio-temporal egg production variability on the modelled survival of the early life history stages of mackerel (*Scomber scombrus*) in the eastern North Atlantic. ICES Journal of Marine Science, 62: 1049–1060.

Bartsch, J., and Coombs, S. H. 2004. An individual-based model of the early life history of mackerel (*Scomber scombrus*) in the eastern North Atlantic, simulating transport, growth and mortality. Fisheries Oceanography, 13: 365–379.

Bartsch, J., Reid, D. G., and Coombs, S. H. 2004. Simulation of mackerel (*Scomber scombrus*) recruitment with an individual-based model and comparison with field data. Fisheries Oceanography, 13: 380–391.

Batty, R. S., Blaxter, J. H. S., and Libby, D. A. 1986. Herring (*Clupea harengus*) filter-feeding in the dark. Marine Biology, 91: 371–375.

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.

Baumann, H., Hinrichsen, H-H., Möllmann, C., Köster, F. W., Malzahn, A. M., and Temming, A. 2006a. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Canadian Journal of Fisheries and Aquatic Sciences, 63: 2191–2201.

Baumann, H., Hinrichsen, H-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L. W., and Temming, A. 2006b. Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. Fisheries Oceanography, 15: 465–476.

Baumann, H., Peck, M. A., Götze, H. E., and Temming, A. 2007. Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. Journal of Fish Biology, 70: 853–866.

Baumann, H., Peck, M. A., and Herrmann, J. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, *Sprattus sprattus*. Marine and Freshwater Research, 56: 539–547.

Baumann, H., Voss, R., Hinrichsen, H-H., Mohrholz, V., Schmidt, J. O., and Temming, A. 2008. Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fishery Research, 91: 1–14.

Baxter, I. G., and Hall, W. B. 1960. The fecundity of the Manx herring and a comparison of the fecundities of autumn spawning groups. ICES Document CM 1960/H:55. 8 pp.

Beare, D. J., and Reid, D. G. 2002. Investigating spatio-temporal change in spawning activity by Atlantic mackerel between 1977 and 1998 using generalized additive models. ICES Journal of Marine Science, 59: 711–724.

Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fisheries Oceanography, 12: 270–283.

Beggs, S., Allen, M., and Schön, P. J. 2009a. Stock identification of 0-group herring in the Irish Sea (VIIaN) using otolith microstructure and shape analysis, Working Document 8. *In* Report of the Herring Assessment Working Group for the Area South of 62°N. ICES Document CM 2009/ACOM:03. 648 pp.

Beggs, S., Schön, P. J., McCurdy, W., Peel, J., McCorriston, P., and McCausland, I. 2009b. Seasonal origin of 1-ring+ herring in the Irish Sea (VIIaN) management area during the annual acoustic survey. AFBI, Belfast, N. Ireland, UK, Working Document 1. *In* Report of the Herring Assessment Working Group for the Area South of 62°N. ICES Document CM 2009/ACOM:03. 648 pp.

Belikov, S. V., Jakupsstovu, S. H., Shamrai, E., and Thomsen, B. 1998. Migration of mackerel during summer in the Norwegian Sea. ICES Document CM 1998/AA:8.

Bernal, M., Stratoudakis, Y., Coombs, S., Angélico, M., Lago de Lanzós, A., Porteiro, C., Sagarminaga, Y., *et al.* 2007. Sardine spawning off the European Atlantic coast: characterization of and spatio-temporal variability in spawning habitat. Progress in Oceanography, 74: 210–227.

Bez, N., and Rivoirard, J. 2000. On the role of sea surface temperature on the spatial distribution of early stages of mackerel using inertiograms. ICES Journal of Marine Science, 57: 383–392.

Bez, N., and Rivoirard, J. 2001. Transitive geostatistics to characterise spatial aggregations with diffuse limits: an application on mackerel ichtyoplankton. Fisheries Research, 50: 41–58.

Bierman, S. M., Dickey-Collas, M., van Damme, C. J. C., van Overzee, H. J., Pennock-Vos, M. G., Tribuhl, S. V., and Clausen, L. A. W. 2010. Between-year variability in the mixing of North Sea herring spawning components leads to pronounced variation in the composition of the catch. ICES Journal of Marine Science, 67: 885–896.

Bjerkan, P. 1917. Age, maturity and quality of North Sea herrings during the years 1910–13. Report on Norwegian Fishery and Marine Investigations, III(1). 119 pp.

Blaxter, J. H. S., and Hunter, J. R. 1982. The biology of clupeoid fishes. Advances in Marine Biology, 20: 1–223.

Bode, A., Carrera, P., and Lens, S. 2003. The pelagic foodweb in the upwelling ecosystem of Galicia (NW Spain) during spring: natural abundance of stable carbon and nitrogen isotopes. ICES Journal of Marine Science, 60: 11–22.

Boeke, J. 1906. Eier und Jugendformen von Fischen der südlichen Nordsee. Verhandelingen u.h. Rijksinstituut v.h. Onderzoek der Zee, 1(4): 3–35.

Borges, M., Santos, A., Crato, N., Mendes, H., and Mota, B. 2003. Sardine regime shifts off Portugal: a time series analysis of catches and wind conditions. Scientia Marina, 67: 235–244.

Borja, A., Fontan, A., Saenz, J., and Valencia, V. 2008. Climate, oceanography, and recruitment: the case of Bay of Biscay anchovy (*Engraulis encrasicolus*). Fisheries Oceanography, 17: 477–493.

Borja, A., Uriarte, A., and Egaña, J. 2002. Environmental factors and recruitment of mackerel, *Scomber Scombrus* L. 1758, along the Northeast Atlantic coasts of Europe. Fisheries Oceanography, 11: 116–127.

Borja, A., Uriarte, A., Egaña, J., Motos, L., and Valencia, V. 1998. Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay. Fisheries Oceanography, 7: 375–380.

Bowers, A. B., and Holliday, F. G. T. 1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). Marine Research (Scotland), 5: 1–15.

Bowers, A. B., and Williamson, D. I. 1951. Food of larval and early post larval stages of autumn-spawned herring in Manx waters. Annual Report of the Port Erin Marine Biology Station, 63: 17–26.

Bracken, J. 1963. Herring investigations in Donegal Bay (1962 and 1963). ICES Document CM 1963/Herring Committee No. 111. 4 pp.

Bracken, J. 1964. Report on Donegal herring investigations 1963/1964. ICES Document CM 1964/Herring Committee No. 88. 5 pp.

Bracken, J., and Phillips, D. 1968. Donegal Bay herring investigations 1967/68. University College Dublin. 4 pp.

Brander, K. 1998. Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. Oceanologica Acta, 23: 485–496.

Breslin, J. J. 1998. The location and extent of the main herring (*Clupea harengus*) spawning grounds around the Irish coast. Master's Thesis. University College Dublin, Ireland.

Breslin, J. J. 1999. Celtic Sea Acoustic Survey Report July 1999. Marine Institute, Dublin, Unpublished Report. 16 pp.

Bridger, J. P. 1961. On the fecundity and larval abundance of Downs herring. Fishery Investigations (MAFF, London), Series II, 23: 1–30.

Brophy, D., and Danilowicz, B. S. 2002. Tracing populations of Atlantic herring (*Clupea harengus* L.) in the Irish and Celtic seas using otolith microstructure. ICES Journal of Marine Science, 59: 1305–1313.

Brophy, D., and Danilowicz, B. S. 2003. The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (*Clupea harengus* L.). ICES Journal of Marine Science, 60: 1103–1113.

Brophy, D., Danilowicz, B. S., and King, P. A. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 63: 607–616.

Brophy, D., and King, P. A. 2007. Larval otolith growth histories show evidence of stock structure in Northeast Atlantic blue whiting (*Micromesistius poutassou*). ICES Journal of Marine Science, 64: 1136–1144.

Brown, C., and Laland, K. 2003. Social learning in fishes: a review. Fish and Fisheries, 4: 280–288.

Brunel, T., and Dickey-Collas, M. 2010. Effects of temperature and density dependence on Atlantic herring growth: a macro-ecological analysis. Marine Ecology Progress Series, 405: 15–28.

Bullen, G. E. 1912. Some notes upon the feeding habits of mackerel and certain clupeoids in the English Channel. Journal of the Marine Biological Association of the UK, 9: 394–403.

Burd, A. C. 1978. Long term changes in North Sea herring stocks. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 137–153.

Burd, A. C. 1984. Density dependent growth in North Sea herring. ICES Document CM 1984/H:4.

Burd, A. C. 1985. Recent changes in the central and southern North Sea herring stocks. Canadian Journal of Fisheries and Aquatic Sciences, 42(Suppl 1): 192–206.

Burd, A. C., and Bracken, J. 1965. Studies on the Dunmore East Herring Stock 1. A population assessment. Journal du Conseil International pour l'Exploration de la Mer, 29: 277–301.

Burd, A. C., and Howlett, G. J. 1974. Fecundity studies on North Sea herring. Journal du Conseil International pour l'Exploration de la Mer, 35: 107–120.

Burke, N. 2008. Atlantic herring (*Clupea harengus*) around the Irish coastline; tracing populations of the past and present. PhD thesis. Galway Mayo Institute of Technology, Galway, Ireland.

Burke, N., Brophy, D., and King, P. 2008. Shape analysis of otolith annuli in Atlantic herring (*Clupea harengus*); a new method for tracking fish populations. Fisheries Research, 91: 133–143.

Burke, N., Brophy, D., Schön, P. J., and King, P. A. 2009. Temporal trends in the stock composition and abundance of juvenile Atlantic herring (*Clupea harengus*) in the Irish Sea. ICES Journal of Marine Science, 66: 1749–1753.

Cardinale, M., and Arrhenius, F. 2000. Decreasing weight-at-age of Atlantic herring (*Clupea harengus*) from the Baltic Sea between 1986 and 1996: a statistical analysis. ICES Journal of Marine Science, 57: 882–893.

Cardinale, M., Casini, M., and Arrhenius, F. 2002. The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources, 15: 273–281.

Cardinale, M., Casini, M., Arrhenius, F., and Håkansson, N. 2003. Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources, 16: 283–292.

Cardinale, M., Möllmann, C., Bartolino, V., Casini, M., Kornilovs, G., Raid, T., Margonski, P., *et al.* 2009. Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. Marine Ecology Progress Series, 388: 221–234.

Carrera, P., and Porteiro, C. 2003. Stock dynamic of the Iberian sardine (*Sardina pilchardus*, W.) and its implication on the fishery off Galicia (NW Spain). Scientia Marina, 67: 245–258.

Casini, M., Bartolino, V., Molinero, J. C., and Kornilovs, G. 2010. Linking fisheries, trophic interactions and climate: threshold dynamics drive herring (*Clupea harengus*) growth in the central Baltic Sea. Marine Ecology Progress Series, 413: 185–187.

Casini, M., Cardinale, M., and Arrhenius, F. 2004. Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. ICES Journal of Marine Science, 61: 1267–1277.

Casini, M., Cardinale, M., and Hjelm, J. 2006. Inter-annual variation in herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) condition in the central Baltic Sea: what gives the tune? Oikos, 112: 638–650.

Castro, B. 2007. Element composition of sardine (*Sardina pilchardus*) otoliths along the Atlantic coast of the Iberian Peninsula. ICES Journal of Marine Science, 64: 512–518.

Cendrero, O., Cort, J., and Cardenas, E. 1981. Revisión de algunos datos sobre la biología de la anchoa, *Engraulis encrasicolus* (L.) del Mar Cantábrico. Boletin del Instituto Espanol de Oceanografia, 311: 118–123.

Cermeño, P., Uriarte, A., Morales Nin, B., Cotano, U., and Alvarez, P. 2008. Setting up interpretation criteria for ageing juvenile European anchovy otoliths. Scientia Marina, 72: 733–742.

Checkley, D. M. 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Marine Ecology Progress Series, 9: 245–253.

Christensen, A., Mosegaard, H., and Jensen, H. 2009. Spatially resolved fish population analysis for designing MPAs: influence on inside and neighbouring habitats. ICES Journal of Marine Science, 66: 56–63.

Clarke, M. W., and Egan, A. 2008. Pair trawl survey for young herring. Irish Fisheries Investigations.

Coombs, S., Smyth, T., Conway, D., Halliday, N., Bernal, M., Stratoudakis, Y., and Alvarez, P. 2006. Spawning season and temperature relationships for sardine (*Sardina pilchardus*) in the eastern North Atlantic. Journal of the Marine Biological Association of the UK, 86: 1245–1252.

Corten, A. 1999a. A proposed mechanism for the Bohuslän herring periods. ICES Journal of Marine Science, 56: 207–220.

Corten, A. 1999b. The reappearance of spawning herring on Aberdeen Bank in 1983 and its relationship to environmental conditions. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2051–2061.

Corten, A. 2000. A possible adaptation of herring feeding migrations to a change in timing of the *Calanus finmarchicus* season in the eastern North Sea. ICES Journal of Marine Science, 57: 1261–1270.

Corten, A. 2001a. Herring and Climate. PhD thesis, Rijksuniversiteit Groningen, the Netherlands. 228 pp.

Corten, A. 2001b. Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. Fisheries Research, 50: 189–204.

Corten, A. 2002. The role of conservatism in herring migrations. Reviews in Fish Biology and Fisheries, 11: 339–361.

Cotano, U., Irigoien, X., Etxebeste, E., Alvarez, P., Zarauz, L., Mader, J., and Ferrer, L., 2008. Distribution, growth and survival of anchovy larvae (*Engraulis encrasicolus* L.) in relation to hydrodynamic and trophic environment in the Bay of Biscay. Journal of Plankton Research, 30: 67–481.

Cushing, D. H. 1955. On the autumn-spawned herring races in the North Sea. Journal du Conseil Permanent International pour l'Exploration de la Mer, 21: 44–59.

Cushing, D. H. 1967. The grouping of herring populations. Journal of the Marine Biological Association of the UK, 47: 193–208.

Cushing, D. H. 1992. A short history of the Downs stock of herring. ICES Journal of Marine Science, 49: 437–443.

Cushing, D. H. 1996. Towards a Science of Recruitment in Fish Populations. Excellence in Ecology No. 7. Ecology Institute, Oldendorf/Luhe, Germany. 175 pp.

Cushing, D. H., and Bridger, J. P. 1966. The stock of herring in the North Sea, and changes due to fishing. Fishery Investigations (MAFF, London) Series II, 25(1): 1–123.

Cushing, D. H., and Burd, A. C. 1957. On the herring of the southern North Sea. Fishery Investigations (MAFF, London) Series II, 20(11): 1–31.

Daan, N., Rijnsdorp, A. D., and van Overbeeke, G. R. 1985. Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. Transactions of the American Fisheries Society, 114: 499–506.

van Damme, C. J. G., Dickey-Collas, M., Rijnsdorp, A. D., and Kjesbu, O. S. 2009. Fecundity, atresia and spawning strategies of Atlantic herring. Canadian Journal of Fisheries and Aquatic Sciences, 66: 2130–2141.

Darbyson, E., Swain, D. P., Chabot, D., and Castonguay, M. 2003. Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. Journal of Fish Biology, 63: 1235–1257.

de Groot, S. J. 1980. The consequences of marine gravel extraction on the spawning of herring, *Clupea harengus* Linné. Journal of Fish Biology, 16: 605–611.

Dickey-Collas, M., Bolle, L. J., van Beek, J. K. L., and Erftemeijer, P. L. A. 2009b. Variability in transport of fish eggs and larvae. II. The effects of hydrodynamics on the transport of Downs herring larvae. Marine Ecology Progress Series, 390: 183–194.

Dickey-Collas, M., Clarke, M., and Slotte, A. 2009a. Linking herring: do we really understand plasticity? ICES Journal of Marine Science, 66: 1649–1651.

Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., Corten, A., *et al.* 2010. Lessons learned from stock collapse and recovery of North Sea herring: a review. ICES Journal of Marine Science. 67: 000–000. doi: 10.1093/icesjms/fsq033.

Dickmann, M., Möllmann, C., and Voss, R. 2007. Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – implications for survival. Marine Ecology Progress Series, 342: 277–289.

Dodson, J. 1988. The nature and role of learning in the orientation and migratory behaviour of fishes. Environmental Biology of Fishes, 23: 161–182.

Dolgov, A., Johannessen, E., Heino, M., and Olsen, E. 2010. Trophic ecology of blue whiting in the Barents Sea. ICES Journal of Marine Science, 67: 483–493.

Dragesund, O., Johannessen, A., and Ulltang, Ø. 1997. Variation in migration and abundance of Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia, 82: 97–105.

Dransfeld, L., Dwane, O., Molloy, J., Gallagher, S., and Reid, D. G. 2005. Estimation of mackerel (*Scomber scombrus* L., 1758) and horse mackerel (*Trachurus trachurus* L., 1758) daily egg production outside the standard ICES survey area. ICES Journal of Marine Science, 62: 1705–1710.

Dubreuil, J., and Petitgas, P. 2009. Energy density of anchovy *Engraulis encrasicolus* in the Bay of Biscay. Journal of Fish Biology, 74: 521–534.

Ellis, T., and Nash, R. D. M. 1997. Predation by sprat and herring on pelagic fish eggs in a plaice spawning area in the Irish Sea. Journal of Fish Biology, 50: 1195–1202.

Eltink, A., and Gerritsen, J. 1982. Growth, spawning and migration of western mackerel. ICES Document CM 1982/H:31.

Engelhard, G. H., and Heino, M. 2004. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. Fisheries Research, 66: 299–310.

Farran, G. P. 1927. The reproduction of *Calanus finmarchicus* off the south coast of Ireland. Journal du Conseil Permanent International pour l'Exploration de la Mer, 2: 132–143.

Farran, G. P. 1930. Fluctuations in the stock of herrings on the north coast of Donegal. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 65: 124–128.

Farran, G. P. 1937. The herring fisheries off the north coast of Donegal. Journal of the Department of Agriculture for Ireland, 34: 262–270.

Farran, G. P. 1938. On the size and numbers of the ova of Irish herrings. Journal du Conseil Permanent International pour l'Exploration de la Mer, 13: 91–100.

Farran, G. P. 1944. The herring fishery in Eire 1921–1941. Journal of the Department of Agriculture for Ireland, 41: 3–36.

Fiksen, Ø., and Folkvord, A. 1999. Modelling growth and ingestion processes in herring *Clupea harengus* larvae. Marine Ecology Progress Series, 184: 273–289.

Fiksen, Ø., and Slotte, A. 2002. Stock-environment recruitment models for Norwegian spring spawning herring. Canadian Journal of Fisheries and Aquatic Sciences, 59: 211–217.

Flinkman, J. 1999. Interactions between plankton and planktivores of the northern Baltic Sea: selective predation and predation avoidance. Doctoral thesis, University of Helsinki, Finland.

Fonselius, S., and Valderrama, J. 2003. One hundred years of hydrographic measurements in the Baltic Sea. Journal of Sea Research, 49: 229–241.

Fox, C. J. 2001. Recent trends in stock–recruitment of Blackwater herring (*Clupea harengus* L.) in relation to larval production. ICES Journal of Marine Science, 58: 750–762.

Furnestin, J. 1943. Contribution à l' etude biologique de la sardine Atlantique (*Sardina pilchardus*, Walbaum). Revue des Travaux de l'Office Scientifique et Techniques des Pêches Maritimes, 13: 211–340.

Ganias, K., Nunes, C., and Stratoudakis, Y. 2008. Using late ovarian atresia to describe the spawning history of sardine, *Sardina pilchardus*. Journal of Sea Research, 60: 244–249.

García, A., and Palomera, I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Scientia Marina, 60: 155–166.

Garrido, S., Ben-Hamadou, R., Oliveira, P., Cunha, M., Chícharo, M., and van der Lingen, C. 2008. Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. Marine Ecology Progress Series, 354: 245–256.

Garrido, S., Marcalo, A., Zwolinski, J., and van der Lingen, C. 2007. Laboratory investigations on the effect of prey size and concentration on the feeding behaviour of *Sardina pilchardus*. Marine Ecology Progress Series, 330: 189–199.

Gastauer, S., Ybema, S., Couperus, B., and van Damme, C. J. D. 2009. Use of historical acoustic survey data to estimate the stock abundance of mackerel in the North Sea. ICES Document CM 2009/I:09.

Geffen, A. J. 2009. Advances in herring biology: from simple to complex, coping with plasticity and adaptability. ICES Journal of Marine Science, 66: 1688–1695.

Giske, J., Huse, G., and Fiksen, Ø. 1998. Modelling spatial dynamics of fish. Reviews in Fish Biology and Fisheries, 8: 57–91.

Godø, O. R., Hjellvik, V., Iversen, S. A., Slotte, A., Tenningen, E., and Torkelsen, T. 2004. Behaviour of mackerel schools during summer feeding migration in the Norwegian Sea, as observed from fishing vessel sonars. ICES Journal of Marine Science, 61: 1093–1099.

Gonzalez, E., and Zardoya, R. 2007. Relative role of life-history traits and historical factors in shaping genetic population structure of sardines (*Sardina pilchardus*). BMC Evolutionary Biology, 7: 197.

Grainger, R. 1976. The inter-relationship of populations of autumn spawning herring off the west coast of Ireland. Resource Record Paper, Irish Sea Fisheries Board, Dublin, Fisheries Development Division. 21 pp.

Grainger, R. J. 1980a. The distribution and abundance of early herring (*Clupea harengus* L.) larvae in Galway Bay in relation to oceanographic conditions. Proceedings of the Royal Irish Academy, Section B, 80: 1–60.

Grainger, R. J. 1980b. Irish west coast herring fluctuations and their relation to oceanographic conditions (abstract only). Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 444.

Grainger, R., and McArdle, E. 1985. Surveys for herring larvae off the northwest and west coasts of Ireland in 1982 and 1983. Ireland Department of Agriculture and Fisheries, Fishery Leaflet, 124. 11 pp.

Guiblin, P., Rivoirard, J., and Simmonds, E. J. 1996. Spatial distribution of length and age for Orkney-Shetland herring. ICES Document CM 1996/D:14. 20 pp.

Guisande, C., Vergara, A., Riveiro, I., and Cabanas, J. 2004. Climate change and abundance of the Atlantic-Iberian sardine (*Sardina pilchardus*). Fisheries Oceanography, 13: 91–101.

Hamre, J. 1980. Biology, exploitation, and management of the Northeast Atlantic mackerel. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 212–242.

Hansson, S., Larsson, U., and Johansson, S. 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. Journal of Plankton Research, 12: 1099–1116.

Harden Jones, F. R. 1968. Fish Migration. Edward Arnold Ltd, London. 325 pp.

Hardy, A. C. 1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. Fishery Investigations, (MAFF, London), Series II, 7(3): 1–39.

Harma, C., Brophy, D., and Clarke, M. 2009. Temporal trends in stock composition of Celtic Sea herring. ICES Document CM 2009/H:08.

Haslob, H., Clemmesen, C., Schaber, M., Hinrichsen, H-H., Schmidt, J. O., Voss, R., Kraus, G., *et al.* 2007. Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series, 349: 303–306.

Hatfield, E. M. C., Zuur, A. F., Boyd, J., Campbell, N., Chubb, J., Collins, C. M., Coughlan, J., *et al.* 2007. The scientific implications of the EU Project WESTHER (Q5RS–2002–01056) to the assessment and management of the herring stocks to the west of the British Isles. ICES Document CM 2007/L:11.

Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., Sandø, A. B., Drange, H., Hansen, B., Jacobsen, J. A., and Bloch, D., *et al.* 2009b. Large bio-geographical shifts in the north-eastern Atlantic Ocean:

From the Subpolar Gyre, via plankton, to blue whiting and pilot whales. Progress in Oceanography, 80: 149–162.

Hátún, H., Payne, M. R., and Jacobsen, J. A. 2009a. The North Atlantic Subpolar Gyre regulates the spawning distribution of blue whiting (*Micromesistius poutassou*). Canadian Journal of Fisheries and Aquatic Sciences, 66: 759–770.

Heath, M. 1989. Transport of larval herring (*Clupea harengus* L.) by the Scottish Coastal Current. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 85–91.

Heath, M., Kunzlik, P., Gallego, A., Holmes, S., and Wright, P. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod – the dynamic consequences of natal fidelity. Fisheries Research, 93: 92–116.

Heath, M., and 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., and Richardson, K. 1989. Comparative study of early life survival variability of herring, *Clupea harengus*, in the North-Eastern Atlantic. Journal of Fish Biology, 35(Suppl. A): 49–57.

Heath, M., Scott, B., and Bryant, A. D. 1997. Modelling the growth of herring from four different stocks in the North Sea. Journal of Sea Research, 38: 413–436.

Heincke, F. 1898. Naturgeschichte des Herings. Abhandlung des Deutschen Seefisch, Ver. II.

Heino, M., Engelhard, G. H., and Godø, O. R. 2008. Migrations and hydrography determine the abundance fluctuations of blue whiting (*Micromesistius poutassou*) in the Barents Sea. Fisheries Oceanography, 17: 153–163.

Hempel, G., and Schubert, K. 1969. Sterblichkeitsbestimmungen an einem Eiklumpen des Nordsee-Herings (*Clupea harengus* L.). Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung, 20: 79–83.

Hinrichsen, H-H., Kraus, G., Voss, R., Stepputtis, D., and Baumann, H. 2005. The general distribution pattern and mixing probability of Baltic sprat juvenile populations. Journal of Marine Systems, 58: 52–66.

Hinrichsen, H-H., Lehmann, A., Petereit, C., and Schmidt, J. O. 2007. Correlation analyses of Baltic Sea winter water mass formation and its impact on secondary and tertiary production. Oceanology, 49: 381–395.

Hjøllo, S. S., Skogen, M. D., and Svendsen, E. 2009. Exploring currents and heat within the North Sea using a numerical model. Journal of Marine Systems, 78: 180–192.

Hodgson, W. C. 1936. The recent state of knowledge concerning the origin and distribution of herring populations in western European waters. The Southern Bight. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 100: 19.

Hodgson, W. C. 1951. Fisheries of the North-east Atlantic: Herring Atlas. ICES: Copenhagen. 14 pp.

Holst, J. C. 1996. Long term trends in the growth and recruitment pattern of the Norwegian spring-spawning herring (*Clupea harengus* Linnaeus 1758). PhD thesis, University of Bergen, Norway. ISBN 82–77444–032–4.

Holst, J. C., and Iversen, S. A. 1992. Distribution of Norwegian spring-spawning herring and mackerel in the Norwegian Sea in late summer, 1991. ICES Document CM 1992/H:13.

Holst, J. C., and Slotte, A. 1998. Effects of juvenile nursery on geographic spawning distribution in Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 55: 987–996.

Hubold, G. 1978. Variations in growth rate and maturity of herring in the Northern North Sea in the years 1955–1973. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 154–163.

Hulme, T. J. 1995. The use of vertebral counts to discriminate between North Sea herring stocks. ICES Journal of Marine Science, 52: 775–779.

Hunter, J. R., and Leong, R. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fishery Bulletin US, 79: 215–230.

Huse, G., and Ellingsen, I. 2008. Capelin migrations and climate change – a modelling analysis. Climate Change, 87: 177–197.

Huse, G., Fernö, A., and Holst, J. C. 2010. Establishment of new wintering areas in herring co-occurs with peaks in the "first time/repeat spawner" ratio. Marine Ecology Progress Series, 409: 189–198.

Huse, G., Railsback, S., and Fernö, A. 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. Journal of Fish Biology, 60: 571–582.

Huse, I., and Korneliussen, R. 2000. Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). ICES Journal of Marine Science, 57: 903–910.

Husebø, Å., Slotte, A., and Stenevik, E. K. 2007. Growth of juvenile Norwegian spring spawning herring related to temperature and acoustic abundance in their coastal and fjord nursery areas. ICES Journal of Marine Science, 64: 1161–1172.

Husebø, Å., Stenevik, E. K., Slotte, A., Fossum, P., Salthaug, A., Vikebø, F., Aanes, S., *et al*. 2009. Effects of hatching time on year-class strength in Norwegian spring-spawning herring (*Clupea harengus*). ICES Journal of Marine Science, 66: 1710–1717.

Ibaibarriaga, L., Irigoien, X., Santos, M., Motos, L., Fives, J. M., Franco, C., Lago De Lanzo S. A., *et al*. 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. Fisheries Oceanography, 16: 284–293.

ICES. 1965. The North Sea Herring. ICES Cooperative Research Report No. 4. 57 pp.

ICES. 1994. Report of the Study Group on Herring Assessment and Biology in the Irish Sea and Adjacent Waters, 21–25 February 1994, Belfast, Northern Ireland. ICES Document CM 1994/H:5. 69 pp.

ICES. 2004a. Report of the Study Group on Regional Scale Ecology of Small Pelagics, 23–26 February 2004, Nantes, France. ICES Document CM 2004/G:06. 52 pp.

ICES. 2004b. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group, 27 April–4 May 2004 ICES, Copenhagen. ICES Document CM 2004/ACFM:24. 294 pp.

ICES. 2005. Report of the Study Group on Regional Scale Ecology of Small Pelagics, 28 February–2 March 2005, Plymouth, UK. ICES Document CM 2005/G:06. 106 pp.

ICES. 2006a. Report of the Study Group on Regional Scale Ecology of Small Pelagics, 27 February–2 March 2006, Galway, Ireland. ICES Document CM 2006/LRC:05. 49 pp.

ICES. 2006b. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine, and Anchovy (WGHMSA), 5–14 September 2006, Galway, Ireland. ICES Document CM 2006/ACFM:36. 601 pp.

ICES. 2006c. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy, 6–15 September 2005, Vigo, Spain. ICES Document CM 2006/ACFM:08. 615 pp.

ICES. 2007a. Report of the Herring Assessment Working Group South of 62°N (HAWG), 13–22 March 2007, ICES Headquarters. ICES Document CM 2007/ACFM:11. 538 pp.

ICES. 2007b. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (WGMHSA), 4–13 September 2007, ICES Headquarters. ICES Document CM 2007/ACFM:31. 712 pp.

ICES. 2007c. Report of the Workshop on Testing the Entrainment Hypothesis (WKTEST), 4–7 June 2007, Nantes, France. ICES Document CM 2007/LRC:10. 111 pp.

ICES. 2008a. Report of the Working Group on Acoustic and Egg Survey for Sardine and Anchovy in ICES Areas VIII and IX (WGACEGG), 24–28 November 2008, Nantes, France. ICES Document CM 2008/LRC:17. 181 pp.

ICES. 2008b. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 2–11 September 2008, ICES Headquarters Copenhagen. ICES Document CM 2008/ACOM:13. 691 pp.

ICES. 2008c. Report of the ICES/GLOBEC Working Group on Life Cycle and Ecology of Small Pelagic Fish (WGLESP). By correspondence. ICES Document CM 2008/LRC:13. 22 pp.

ICES. 2009a. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG), 17–25 March 2009, ICES Headquarters, Copenhagen. ICES Document CM 2009/ACOM:03. 638 pp.

ICES. 2009b. Report on the Working Group on Multispecies Assessment Methods (WGSAM), 5–9 October 2009, ICES Headquarters, Copenhagen. ICES Document CM 2009/RMC:10. 111 pp.

ICES. 2009c. Report of the Baltic Fisheries Assessment Working Group, 22–28 April 2009, ICES Headquarters, Copenhagen. ICES Document CM 2009/ACOM:07. 626 pp.

ICES. 2009d. Report of the Working Group on Anchovy and Sardine, 15–20 June 2009, ICES Headquarters, Copenhagen. ICES Document CM 2009/ACOM:13. 354 pp.

ICES. 2009e. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 2–8 September 2009, Copenhagen, Denmark. ICES Document CM 2009/ACOM:12. 563 pp.

ICES. 2009f. Report of the Workshop on Blue Whiting Recruitment (WKBLUR), 10–12 November 2009, ICES Headquarters, Copenhagen. ICES Document CM 2009/RMC:09. 66 pp.

ICES. 2009g. Report of the Working Group on Operational Oceanographic Products for Fisheries and Environment (WGOOFE), 15–17 June 2009, Aberdeen, United Kingdom; 16–18 November 2009, IJmuiden, The Netherlands. ICES Document CM 2009/OCC:03. 18 pp.

Iles, T. D. 1984. Allocation of resources to gonad and soma in Atlantic herring *Clupea harengus* L. *In* Fish Reproduction: Strategies and Tactics, pp. 331–348. Ed. by G. W. Potts and R. J. Wootton. Academic Press, London. 410 pp.

Irigoien, X., Cotano, U., Boyra, G., Santos, M., Alvarez, P., Uriarte, A., Ferrer, L., *et al.* 2008. From egg to juvenile in the Bay of Biscay: spatial patterns of anchovy (*Engraulis encrasicolus*) recruitment in a non-upwelling region. Fisheries Oceanography, 17: 446–462.

Irigoien, X., Fiksen, Ø., Cutano, U., Uriarte, A., Alvarez, P., Arrizabalaga, H., Boyra, G., *et al.* 2007. Could Biscay Bay anchovy recruit through a spatial loophole? Progress in Oceanography, 74: 132–148.

Isaev, N. A., Seliverstov, A. S., Tretyak, V. L., and Korzhev, V. A. 1992. Population dynamics of the Hebrides and Porcupine populations of blue whiting, *Micromesistius poutassou*, and their rational exploitation. Journal of Ichthyology, 32: 32–42.

Iversen, S. A., Eltink, A., Kirkegaard, E., and Skagen, D. W. 1989. The egg production and spawning stock size of the North Sea mackerel and horse mackerel stocks in 1988. ICES Document CM 1989/H:16.

Iversen, S. A., and Skagen, D. W. 1989. Migration of western mackerel to the North Sea 1973–1988. ICES Document CM 1989/H:20.

Jennings, S., and Beverton, R. J. H. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.). ICES Journal of Marine Science, 48: 117–125.

Johannessen, A., Blom, G., and Folkvord, A. 2000. Differences in growth between spring and autumn spawned herring (*Clupea harengus* L.) larvae. Sarsia, 85: 461–466.

Johannessen, A., Nøttestad, L., Fernö, A., Langård, L., and Skaret, G. 2009. Two components of Northeast Atlantic herring within the same school during spawning: support for the existence of a metapopulation? ICES Journal of Marine Science, 66: 1740–1748.

Jørgensen, H. B. H., Hansen, M. M., and Loeschcke, V. 2005. Spring-spawning herring (*Clupea harengus* L.) in the southwestern Baltic Sea: do they form genetically distinct spawning waves? ICES Journal of Marine Science, 62: 1065–1075.

Junquera, S. 1984. Pêche de l'anchois (*Engraulis encrasicolus*) dans le Golfe de Gascogne et sur le littoral atlantique de Galice depuis 1920. Revue des Travaux de l'Institut des Pêches Maritimes, 48: 133–142.

Kääriä, J., Rajasilta, M., Kurkilahti, M., and Soikkeli, M. 1997. Spawning bed selection by the Baltic herring (*Clupea harengus membras*) in the Archipelago of SW Finland. ICES Journal of Marine Science, 54: 917–923.

Kaartvedt, S. 2000. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. ICES Journal of Marine Science, 57: 1819–1824.

Karasiova, E., and Voss, R. 2004. Long-term variability of cod and sprat eggs abundance in ichthyoplankton of the Baltic Sea. ICES Document CM 2004/L:07. 30 pp.

Kenny, A. J., Skjoldal H. R., Engelhard, G. H, Kershaw, P. I., and Reid, J. B. 2009. An integrated approach for assessing the relative significance of human pressures and environmental forcing on the status of large marine ecosystems. Progress in Oceanography, 81: 132–148.

Köster, F. W., Hinrichsen, H-H., Schnack, D., St John, M. A., MacKenzie, B. R., Tomkiewicz, J., Möllmann, C., *et al.* 2003a. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock–recruitment relationships. Scientia Marina, 67(Suppl. 1): 129–154.

Köster, F. W., Möllmann, C., Neuenfeldt, S., Vinther, M., St John, M. A., Tomkiewicz, J., Voss, R., *et al.* 2003b. Fish stock development in the Central Baltic Sea (1976–2000) in relation to variability in the physical environment. ICES Marine Science Symposia, 219: 294–306.

La Mesa, M., Donato, F., Giannetti, G., and Arneri, E. 2009. Growth and mortality rates of European anchovy (*Engraulis encrasicolus*) in the Adriatic sea during the transition from larval to juvenile stages. Fisheries Research, 96: 275–280.

Laine, P., and Rajasilta, M. 1998. Changes in the reproductive properties of Baltic herring females during the spawning season. Fisheries Research, 36: 67–73.

Laine, P., and Rajasilta, M. 1999. The hatching success of Baltic herring eggs and its relation to female condition. Journal of Experimental Marine Biology and Ecology, 273: 61–73.

Langøy, H., Nøttestad, L., Skaret, G., Broms, C. T. A., and Fernö, A. 2006. Feeding ecology of Atlantic mackerel (*Scomber scombrus*) in the Norwegian Sea. ICES Document CM 2006/F:12.

Last, J. M. 1989. The food of herring *Clupea harengus*, in the North Sea, 1983–1986. Journal of Fish Biology, 34: 489–501.

Lehuta, S., Petitgas, P., and Mahévas, S. 2006. Assessing the potential effect of management scenarios for anchovy fishery of the Bay of Biscay using ISIS-Fish simulation tool. ICES Document CM 2006/R:10.

Lo, N., Smith, P., and Butler, J. 1995. Population growth of northern anchovy and pacific sardine using stage-specific matrix models. Marine Ecology Progress Series, 127: 15–26.

Lockwood, S. J. 1988. The mackerel – its biology, assessment and the management of a fishery. Fishing News Books Ltd, Farnham, UK. 181 pp.

Lockwood, S. J., Nichols, J. H., and Dawson, W. A. 1981. The mackerel (*Scomber scombrus*) spawning in the Bay of Biscay, Celtic Sea and west of Ireland. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 178: 171–173.

Lumby, J. R. 1923. The relation between catches of mackerel and the surface temperature *in situ*. Journal of the Marine Biological Association of the UK, 13: 236–242.

Lynch, D. 2009. Long-term changes in biological parameters of herring in the Celtic Sea and southwest of Ireland. MSc Thesis. Trinity College, Dublin, Ireland.

MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate: sprat in the Baltic Sea. Ecology, 85: 784–794.

Mackinson, S., and Daskalov, G. 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. Cefas, Lowestoft, Science Series, Technical Report No. 142. 195 pp.

Maravelias, C. D. 2001. Habitat associations of Atlantic herring in the Shetland area: influence of spatial scales and geographic segmentation. Fisheries Oceanography, 10: 259–267.

Maravelias, C. D., and Reid, D. G. 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Marine Ecology Progress Series, 147: 1–9.

Maravelias, C. D., Reid, D. G., Simmonds, E. J., and Haralabous, J. 1996. Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring. Canadian Journal of Fisheries and Aquatic Sciences, 53: 1497–1505.

Marquis, E., Petitgas, P., Niquil, N., and Dupuy, C. 2006. Influence of the small pelagic fish on the structure and functioning of the planktonic foodweb on the continental shelf of the Bay of Biscay. ICES Document CM 2006/F:09.

Martins, M. M. 2007. Growth variability in Atlantic mackerel (*Scomber scombrus*) and Spanish mackerel (*Scomber japonicus*) off Portugal. ICES Journal of Marine Science, 64: 1785–1790.

Massé, J. 1996. Acoustic observations in the Bay of Biscay: schooling, vertical distribution, species assemblages and behaviour. Scientia Marina, 60(Suppl. 2): 227–234.

Massé, J., Koutsikopoulos, C., and Patty, W. 1996. The structure and spatial distribution of pelagic fish schools in multispecies clusters: an acoustic study. ICES Journal of Marine Science, 53: 155–160.

McCleave, J., Arnold, G., Dodson, J., and Neill, W. (Eds). 1984. Mechanisms of Migration in Fishes. Plenum Press, New York. 574 pp.

McKenzie, K. 1985. The use of parasites as biological tags in population studies of herring (*Clupea harengus* L.) in the North Sea and to the north and west of Scotland. Journal du Conseil International pour l'Exploration de la Mer, 42: 33–64.

McPherson, A. A., Stephenson, R. L., and Taggart, C. T. 2003. Genetically different Atlantic herring *Clupea harengus* spawning waves. Marine Ecology Progress Series, 247: 303–309.

McQuinn, I. 1997. Metapopulations and the Atlantic herring. Reviews in Fish Biology and Fisheries, 7: 297–329.

Megrey, B., Rose, K., Klumb, R., Hay, D., Werner, F., Eslinger, D., and Smith, S. 2007. A bioenergetics-based population dynamics model of Pacific herring (*Clupea harengus pallasi*) coupled to a lower trophic level nutrient-phytoplankton-zooplankton model: description, calibration and sensitivity analysis. Ecological Modelling, 202: 144–164.

Melvin, G. D., and Stephenson, R. L. 2007. The dynamics of a recovering fish stock: Georges Bank herring. ICES Journal of Marine Science, 64: 69–82.

Meynier, L., Pusineri, C., Spitz, J., Santos, M. B., Pierce, G. J., and Ridoux, V. 2008. Diet and feeding ecology of the common dolphin, *Delphinus delphis*, in the Bay of Biscay: importance of fat fish. Marine Ecology Progress Series, 354: 267–276.

Misund, O. A., Vilhjalmsson, H., Jakupsstovu, S. H. I., Røttingen, I., Belikov, S., Asthorsson, O., Blindheim, J., *et al.* 1998. Distribution, migration and abundance of Norwegian spring-spawning herring in relation to the temperature and zooplankton biomass in the Norwegian Sea as recorded by coordinated surveys in spring and summer 1996. Sarsia, 83: 117–127.

Mohn, C., Dransfeld, L., and White, M. 2007. Hindcasting planktonic egg drift patterns of Atlantic mackerel in Irish shelf and oceanic waters. ICES Document CM 2007/G:29.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2004a. Herring and sprat growth changes in the Central Baltic Sea. ICES Document CM 2004/L:27.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2004b. Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology, 65: 1563–1581.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F. W., and Hinrichsen, H-H. 2003b. The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fisheries Oceanography, 12: 360–368.

Möllmann, C., Köster, F. W., Kornilovs, G., and Sidrevics, L. 2003a. Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea. ICES Marine Science Symposia, 219: 220–230.

Molloy, J. 1979. Fecundities of Celtic Sea autumn and winter spawning herring. ICES Document CM 1979/H:47. 5 pp.

Molloy, J. 1980. The assessment and management of the Celtic Sea herring stock. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 159–165.

Molloy, J. 1983. The occurrence of winter and spring spawning herring off the northwest coast of Ireland. ICES Document CM 1983/H:60.

Molloy, J. 1984. Density dependent growth in Celtic Sea herring. ICES Document CM 1984/H:30. 13 pp.

Molloy, J. 1989. The closure of herring spawning grounds in the Celtic Sea and Div. VIIj. Ireland Department of Agriculture and Fisheries, Fishery Leaflet 145. 7 pp.

Molloy, J. 2006. The herring fisheries of Ireland 1900–2005. Marine Institute, Galway.

Molloy, J., and Barnwall, E. 1988. Herring larval surveys off the west and northwest coasts 1984–1986. Ireland Department of Agriculture and Fisheries, Fishery Leaflet 142. 8 pp.

Molloy, J., Barnwall, E., and Morrison, J. 1993. Herring tagging experiments around Ireland, 1991. Marine Institute, Ireland, Fishery Leaflet 154. 7 pp.

Molloy, J., and Corten, A. 1975. Young herring surveys in Irish seas. ICES Document CM 1975/H:11. 20 pp.

Molloy, J., and Cullen, A. 1981. The fat content of Irish herring. Ireland Department of Agriculture and Fisheries, Fishery Leaflet 107. 7 pp.

Molloy, J., and Kelly, C. 2000. Herring in VIaS and VIIbc, a review of fisheries and biological information. Report of the workshop between Scientists and Fishermen, Killybegs Fishermen's Organisation, Bruach Na Mara, July 2000.

Monstad, T. 2004. Blue whiting. *In* The Norwegian Sea Ecosystem, pp. 263–288. Ed. by H. R. Skjoldal. Tapir Academic Press, Trondheim.

Motos, L. 1996. Reproductive biology and fecundity of the Bay of Biscay anchovy population (*Engraulis encrasicolus* L.). Scientia Marina, 60(Suppl. 2): 195–207.

Motos, L., Uriarte, A., and Valencia, V. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus,* L.). Scientia Marina, 60(Suppl. 2): 117–140.

Murray, T., LeDuc, S., and Ingham, M. 1983. Impact of climatic factors on early life stages of Atlantic mackerel, *Scomber scombrus*, L.: an application of meteorological data to a fishery problem. Journal of Climate and Applied Meteorology, 22: 57–68.

Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence and variability using meta-analytic approaches. ICES Journal of Marine Science, 58: 937–951.

Nash, R. D. M., and 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, 14: 279–291.

Nash, R. D. M., Dickey-Collas, M., and Kell, L. T. 2009. Stock and recruitment in North Sea herring (*Clupea harengus*): compensation and depensation in the population dynamics. Fisheries Research, 95: 88–97.

Nesbø, C. L., Rueness, E. K., Iversen, S. A., Skagen, D. W., and Jakobsen, K. S. 2000. Phylogeography and population history of Atlantic mackerel (*Scomber scombrus* L.): a genealogical approach reveals genetic structuring among the eastern Atlantic stocks. Proceedings of the Royal Society of London, Series B, Biological Sciences, 267: 281–292.

Nichols, J. H. 2001. Management of North Sea herring and prospects for the new millennium. *In* Herring: Expectations for a New Millennium. pp. 645–665. Ed. by F. Funk, J. Blackburn, D. Day, A. J. Paul, R. Stephenson, R. Toresen, and D. Witherell. University of Alaska Sea Grant, AK-SG-01-04, Fairbanks. 800 pp.

Nilsson, L. A. F., Thygesen, U. H., Lundgren, B., Nielsen, B. F., Nielsen, J. R., and Beyer, J. E. 2003. Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. Aquatic Living Resources, 16: 317–324.

Nissling, A. 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. Hydrobiologia, 514: 115–123.

Nøttestad, L., Aksland, M., Beltestad, A., Fernö, A., Johannessen, A., and Misund, O. A. 1996. Schooling dynamics of Norwegian spring-spawning herring (*Clupea harengus*) in a coastal spawning area. Sarsia, 80: 277–284.

Nøttestad, L., Giske, J., Holst, J. C., and Huse, G. 1999. A length-based hypothesis for feeding migrations in pelagic fish. Canadian Journal of Fisheries and Aquatic Sciences, 56: 26–34.

Oeberst, R., Klenz, B., Gröhsler, T., Dickey-Collas, M., Nash, R. D. M., and Zimmermann, C. 2009. When is year-class strength determined in western Baltic herring? ICES Journal of Marine Science, 66: 1667–1672.

Ojaveer, E., and Lehtonen, H. 2001. Fish stocks in the Baltic Sea: finite or infinite resource? Ambio, 30: 217–221.

Olaso, I., Gutierrez, J. L., Villamor, B., Carrera, P., Valdes, L., and Abaunza, P. 2005. Seasonal changes in the north-eastern Atlantic mackerel diet (*Scomber scombrus*) in the north of Spain (ICES Division VIIIc). Journal of the Marine Biological Association of the UK, 85: 415–418.

Oliveira, P., and Stratoudakis, Y. 2008. Mesoscale advection off the Iberian and the northern African Atlantic coasts: potential implications for sardine recruitment and population structure. Remote Sensing of Environment, 112: 3376–3387.

Orlowski, A. 2000. Diel dynamics of acoustic measurements of Baltic fish. ICES Journal of Marine Science, 57: 1196–1203.

Oskarsson, G. J., Kjesbu, O. S., and Slotte, A. 2002. Predictions of realised fecundity and spawning time in Norwegian spring spawning herring (*Clupea harengus* L.). Journal of Sea Research, 48: 59–79.

Otterlind, G. 1976. Fish stocks and fish migration in the Baltic Sea environment. Ambio Special Report, 4: 89–101.

Parmanne, R., Popov, A., and Raid, T. 1997. Fishery and biology of herring (*Clupea harengus* L.) in the Gulf of Finland: a review. Boreal Environment Research, 2: 217–227.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana, 10: 29–59.

Parrish, B. B., Saville, A., Craig, R. E., Baxter, I. G., and Priestley, R. 1959. Observations on herring spawning and larval distribution in the Firth of Clyde in 1958. Journal of the Marine Biological Association of the UK, 38: 445–453.

Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaug, T., Gallego, A., Gröger, J., Licandro, P., *et al.* 2009. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. ICES Journal of Marine Science, 66: 272–277.

Peltonen, H., Vinni, M., Lappalainen, A., and Pönni, J. 2004. Spatial feeding patterns of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.), and the three-spined stickleback (*Gasterosteus aculeatus* L.) in the Gulf of Finland, Baltic Sea. ICES Journal of Marine Science, 61: 966–971.

Pérez, N., Figueiredo, I., and Lo, N. 1992a. Batch fecundity of *Sardina pilchardus* (Walb.) off the Atlantic Iberian coast. Boletin del Instituto Espanol de Oceanografia, 8: 155–162.

Pérez, N., Figueiredo, I., and Macewicz, B. 1992b. The spawning frequency of sardine, *Sardina pilchardus* (Walb.) off the Atlantic Iberian coast. Boletin del Instituto Espanol de Oceanografia, 8: 175–189.

Petereit, C., Haslob, H., Kraus, G., and Clemmesen, C. 2008. The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk-sac larvae. Marine Biology, 154: 295–306.

Petitgas, P. 2007. Bay of Biscay anchovy: do adults facilitate the adoption by recruits of schooling behaviour and habitat occupation? *In* Report of the Workshop on Testing the Entrainment Hypothesis (WKTEST), 4–7 June 2007, Nantes, France, pp. 89–95. ICES Document CM 2007/LRC:10. 111 pp.

Petitgas, P., Beillois, P., Massé, J., and Grellier, P. 2004. On the importance of adults in maintaining population habitat occupation of recruits as deduced from observed schooling behaviour of age-0 anchovy in the Bay of Biscay. ICES Document CM 2004/J:13.

Petitgas, P., Huret, M., Léger, F., Peck, M. A., Dickey-Collas, M., and Rijnsdorp, A. D. 2009. Patterns and schedules in hindcasted environments and fish life cycles. ICES Document CM 2009/E:25.

Petitgas, P., Massé, J., Grellier, P., and Beillois, P. 2003. Variation in the spatial distribution of fish length: a multi-annual geostatistics approach on anchovy in Biscay 1983–2002. ICES Document CM 2003/Q:15.

Petitgas, P., Reid, D., Planque, B., Nogueira, E., O'Hea, B., and Cotano, U. 2006. The entrainment hypothesis: an explanation for the persistence and innovation in spawning migrations and life cycle spatial patterns. ICES Document CM 2006/B:07.

Planque, B., Bellier, E., and Lazure, P. 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Fisheries Oceanography, 16: 16–30.

Plounevez, S., and Champalbert, G. 1999. Feeding behaviour and trophic environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. Estuarine, Coastal and Shelf Science, 49: 177–191.

Postuma, K. H., and Zijlstra, J. J. 1974. Larval abundance in relation to stock size, spawning potential and recruitment in North Sea herring. *In* The Early Life History of Fish, pp. 113–128. Ed. by J. H. S. Blaxter. Springer-Verlag, Berlin. 765 pp.

Poulsen, B. 2008. Dutch Herring. An Environmental History c. 1600–1860. Aksant, Amsterdam. 264 pp.

Preciado, I., Velasco, F., and Olaso, I. 2008. The role of pelagic fish as forage or the demersal fish community in the southern Bay of Biscay. Journal of Marine Systems, 72: 407–417.

Prokopchuk, I., and Sentyabov, E. 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES Journal of Marine Science, 63: 117–127.

Punzon, A., and Villamor, B. 2009. Does the timing of the spawning migration change for the southern component of the Northeast Atlantic Mackerel (*Scomber scombrus*, L. 1758)? An approximation using fishery analyses. Continental Shelf Research, 29: 1195–1204.

Rajasilta, M., Eklund, J., Hänninen, J., Kurkilahti, M., Kääriä, J., Rannikko, P., and Soikkeli, M. 1993. Spawning of herring (*Clupea harengus membras* L.) in the Archipelago Sea. ICES Journal of Marine Science, 50: 233–246.

Rankine, P. A., and Walsh, M. 1982. Tracing the migrations of Minch mackerel. Scottish Fisheries Bulletin, 47: 8–13.

Ré, P., and Meneses, I. 2008. Early Stages of Marine Fishes Occurring in the Iberian Peninsula. IPIMAR/IMAR, Lisbon. 282 pp.

Redeke, H. C., and van Breemen, P. J. 1907. Die Verbreitung der planktonischen Eier und Larven einiger Nützfische in der südlichen Nordsee. Verhandelingen u.h. Rijksinstituut v.h. Onderzoek der Zee, II: 3–37.

Reid, D. G., Eltink, A., and Kelly, C. 2003. Inferences on the changes in pattern in the prespawning migration of the western mackerel (*Scomber scombrus*) from commercial vessel data. ICES Document CM 2003/Q:19.

Reid, D. G., Eltink, A., Kelly, C. J., and Clark, M. 2006. Long-term changes in the pattern of the prespawning migration of the western mackerel (*Scomber scombrus*) since 1975, using commercial vessel data. ICES Document CM 2006/B:14.

Reid, D. G., Turrell, W. R., Walsh, M., and Corten, A. 1997. Cross-shelf processes north of Scotland in relation to the southerly migration of western mackerel. ICES Journal of Marine Science, 54: 168–178.

Reid, D. G., Walsh, M., and Turrell, W. R. 2001. Hydrography and mackerel distribution on the shelf edge west of the Norwegian deeps. Fisheries Research, 50: 141–150.

Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M., and Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fisheries Oceanography, 12: 260–269.

Roel, B. A., O'Brien, C. M., and Basson, M. 2004. Management options for the Blackwater herring, a local spring-spawning stock in the Thames Estuary. ICES Journal of Marine Science, 61: 297–307.

Rönkkönen, S., Ojaveer, E., Raid, T., and Viitasalo, M. 2004. Long-term changes in Baltic herring (*Clupea harengus membras*) growth in the Gulf of Finland. Canadian Journal of Fisheries and Aquatic Sciences, 61: 219–229.

Sætre, R., Toresen, R., and Anker-Nilssen, T. 2002. Factors affecting the recruitment variability of the Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 59: 725–736.

Santos, A., Peliz, A., Dubert, J., Oliveira, P., Angelico, M., and Ré, P. 2004. Impact of a winter upwelling event on the distribution and transport of sardine eggs and larvae off western Iberia: a retention mechanism. Continental Shelf Research, 24: 149–165.

Santos, M., Fernández, R., López, A., Martínez, J., and Pierce, G. 2007. Variability in the diet of bottlenose dolphin, *Tursiops truncatus*, in Galician waters, north-western Spain, 1990–2005. Journal of the Marine Biological Association of the UK, 87: 231–241.

Santos, M., Pierce, G., López, A., Martínez, J., Fernández, M., Ieno, E., Mente, E., *et al.* 2004. Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationship with prey abundance. ICES Document CM 2004/Q:09.

Savage, R. E. 1937. The food of North Sea herring 1930–1934. Ministry of Agriculture, Fisheries and Food, Fishery Investigations, London, II, 15: 5. 60 pp.

Savage, R. E., and Wimpenny, R. S. 1936. Phytoplankton and the herring. Fishery Investigations, London, Series II, 15: 1. 88 pp.

Saville, A. 1978. The growth of herring in the northwestern North Sea. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 164–171.

Schmidt, J. O., van Damme, C. J. G., Röckmann, C., and Dickey-Collas, M. 2009. Recolonisation of spawning grounds in a recovering fish stock: recent changes in North Sea herring. Scientia Marina, 73: 153–157.

Secor, D. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fisheries Research, 43: 13–34.

Segers, F. H. I. D., Dickey-Collas, M., and Rijnsdorp, A. D. 2007. Prey selection by North Sea herring (*Clupea harengus* L.), with special regard to fish eggs. ICES Journal of Marine Science, 64: 60–68.

Silva, A., Carrera, P., Massé, J., Uriarte, A., Santos, M., Oliveira, P., Soares, E., *et al.* 2008. Geographic variability of sardine growth across the northeastern Atlantic and the Mediterranean Sea. Fisheries Research, 90: 56–69.

Silva, A., Santos, M., Caneco, B., Pestana, G., Porteiro, C., Carrera, P., and Stratoudakis, Y. 2006. Temporal and geographic variability of sardine maturity at length in the north-eastern Atlantic and the western Mediterranean. ICES Journal of Marine Science, 63: 663–676.

Silva, A., Skagen, D., Carrera, P., Massé, J., Santos, M., Uriarte, A., Marques, V., *et al.* 2009. Geographic variability in sardine (*Sardina pilchardus*, Walb.) dynamics in the Iberia-Biscay region. ICES Journal of Marine Science, 66: 495–508.

Silva, M. 1999. Diet of common dolphins, *Delphinus delphis*, off the Portuguese continental coast. Journal of the Marine Biological Association of the UK, 87: 231–241.

Simmonds, E. J. 2007. Comparison of two periods of North Sea herring stock management: success, failure, and monetary value. ICES Journal of Marine Science, 64: 686–692.

Sinclair, M. 1988. Marine Populations: an Essay on Population Regulation and Speciation. University of Washington Press, Seattle. 252 pp.

Sinclair, M. 2009. Herring and ICES: a historical sketch of a few ideas and their linkages. ICES Journal of Marine Science, 66: 1652–1661.

Skaret, G. 2007. Collective behaviour of herring during spawning. PhD thesis, Department of Biology, University of Bergen, Norway.

Skaret, G., Axelsen, B. E., Nøttetstad, L., Fernö, A., and Johannessen, A. 2002. Herring as cannibals. Journal of Fish Biology, 61: 1050–1052.

Skaret, G., Nøttestad, L., Fernö, A., Johannessen, A., and Axelsen, B. E. 2003. Spawning of herring: day or night, today or tomorrow? Aquatic Living Resources, 16: 299–306.

Skogen, M. D., Monstad, T., and Svendsen, E. 1999. A possible separation between a northern and a southern stock of the Northeast Atlantic blue whiting. Fisheries Research, 41: 119–131.

Slotte, A. 1999a. Effects of fish length and condition on spawning migration in Norwegian spring-spawning herring (*Clupea harengus* L.). Sarsia, 84: 111–127.

Slotte, A. 1999b. Differential utilisation of energy during wintering and spawning migration in Norwegian spring-spawning herring (*Clupea harengus* L.). Journal of Fish Biology, 54: 338–355.

Slotte, A. 2001. Factors influencing location and time of spawning in Norwegian spring-spawning herring: an evaluation of different hypotheses. *In*: Herring: Expectations for a New Millennium, pp. 255–278. Ed. by F. Funk, J. Blackburn, D. Hay, A. J. Paul, R. Stephenson, R. Toresen, and D. Witherell. University of Alaska Sea Grant, AK-SG-01-04, Fairbanks. 800 pp.

Slotte, A., and Fiksen, Ø. 2000. State-dependent spawning migration in Norwegian spring-spawning herring (*Clupea harengus* L.). Journal of Fish Biology, 56: 138–162.

Slotte, A., Johannessen, A., and Kjesbu, O. S. 2000. Effects of fish size on spawning time in Norwegian spring spawning herring (*Clupea harengus* L.). Journal of Fish Biology, 56: 295–310.

Slotte, A., Korneliussen, R., and Skagen, D. 2005. Three-dimensional distribution of Northeast Atlantic mackerel in the northern North Sea during autumn related to ambient temperature. ICES Document CM 2005/U:04.

Smedbol, R., and Wroblewski, J. 2002. Metapopulation theory and northern cod population structure: interdependence of subpopulations in recovery of a groundfish population. Fisheries Research, 55: 161–174.

Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., and Motos, L. 2004. Daily egg production of anchovy in European waters. ICES Journal of Marine Science, 61: 944–958.

Stepputtis, D. 2006. Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) — causes and consequences. PhD thesis. University of Kiel, Germany. 153 pp.

Steven, G. A. 1948. Contributions to the biology of the mackerel *Scomber scombrus*. I. Mackerel migrations in the English Channel and the Celtic Sea. Journal of the Marine Biological Association of the UK, 27: 517–539.

Steven, G. A. 1949. Contributions to the biology of the mackerel *Scomber scombrus*. II. A study of the fishery in the SW of England with special reference to spawning, feeding and fishermen. Journal of the Marine Biological Association of the UK, 38: 555–581.

Steven, G. A. 1952. Contributions to the biology of the mackerel *Scomber scombrus*. III. Age and growth. Journal of the Marine Biological Association of the UK, 30: 549–569.

Stratoudakis, Y., Bernal, M., Borchers, D., and Borges, F. 2003. Changes in the distribution of sardine eggs and larvae off Portugal, 1985–2000. Fisheries Oceanography, 12: 49–60.

Stratoudakis, Y., Coombs, S., Lago de Lanzós, A., Halliday, N., Costas, G., Caneco, B., Franco, C., *et al.* 2007. Sardine (*Sardina pilchardus*) spawning seasonality in European waters of the Northeast Atlantic. Marine Biology, 152: 201–212.

Struski, C., Petitgas, P., and Huret, M. 2009. Long-term hindcast and climate change forecast of habitat unsuitability using bioenergetics and physical–biogeochemical models: anchovy in the Bay of Biscay and the North Sea. ICES Document CM 2009/E:22.

Tenningen, E., Godø, O. R., Iversen, S., Slotte, A., Hjellvik, V., and Torkelsen, T. 2003. Comparison of Northeast Atlantic mackerel (*Scomber scombrus*) distribution patterns in the Norwegian Sea using lidar, sonar and trawl. ICES Document CM 2003/V:04.

Toresen, R., and Østvedt, O. J. 2000. Variation in abundance of Norwegian spring spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries, 1: 231–256.

Torstensen, E., and Gjøsæter, J. 1995. Occurrence of 0-group sprat (*Sprattus sprattus*) in the littoral zone along the Norwegian Skagerrak coast 1945–1992, compared with the occurrence of 0-group herring (*Clupea harengus*). Fisheries Research, 21: 409–421.

Uriarte, A., Alvarez, P., Iversen, S., Molloy, J., Villamor, B., Martins, M. M., and Myklevoll, S. 2001b. Spatial pattern of migration and recruitment of Northeast Atlantic mackerel. ICES Document CM 2001/O:17.

Uriarte, A., and Lucio, P. 2001. Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. Fisheries Research, 50(1–2): 129–139.

Uriarte, A., Prouzet, P., and Villamor, B. 1996. Bay of Biscay and Ibero Atlantic anchovy populations and their fisheries. Scientia Marina, 60(Suppl. 2): 237–255.

Uriarte, A., Sagarminaga, Y., Scalabrin, C., Valencia, V., Cermeño, P., de Miguel, E., Gomez Sanchez, J. A., Jimenez, M., *et al.* 2001a. Ecology of anchovy juveniles in the Bay of Biscay 4 months after peak spawning: do they form part of the plankton? ICES Document CM 2001/W:20.

van Damme, C. J. G., Dickey-Collas, M., Rijnsdorp, A. D., and Kjesbu, O. S. 2009. Fecundity, atresia and spawning strategies of Atlantic herring. Canadian Journal of Fisheries and Aquatic Sciences. 66(12): 2130–2141.

Vaz, S., and Petitgas, P. 2002. Study of the Bay of Biscay anchovy population dynamics using spatialized age-specific matrix models. ICES Document CM 2002/O:07.

Villamor, B., Abaunza, P., and Farina, A. C. 2004a. Growth variability of mackerel (*Scomber scombrus*) off north and northwest Spain and a comparative review of the growth patterns in the Northeast Atlantic. Fisheries Research, 69: 107–121.

Villamor, B., Abaunza, P., Petitgas, P., Massé, J., and Uriarte, A. 2007. Bay of Biscay anchovy: a resource in crisis. ICES Insight, 44: 9–10.

Villamor, B., Bernal, M., and Hernandez, C. 20

04b. Models describing mackerel (*Scomber scombrus*) early life growth in the North and Northwest of the Iberian Peninsula in 2000. Scientia Marina, 68: 571–583.

Voss, R. 2002. Recruitment processes in the larval phase: the influence of varying transport on cod and sprat larval survival. PhD thesis. University of Kiel, Germany. 138 pp.

Voss, R., Clemmesen, C., Baumann, H., and Hinrichsen, H-H. 2006. Baltic sprat larvae: coupling food availability, larval condition and survival. Marine Ecology Progress Series, 308: 243–254.

Voss, R., Dickmann, M., Hinrichsen, H-H., and Floeter, J. 2008. Environmental factors influencing larval sprat *Sprattus sprattus* feeding during spawning time in the Baltic Sea. Fisheries Oceanography, 17: 219–230.

Voss, R., Köster, F. W., and Dickmann, M. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research, 63: 97–111.

Voss, R., Schmidt, J. O., and Schnack, D. 2007. Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration? ICES Journal of Marine Science, 64: 956–962.

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. Fishery Investigations, London, Series II, 7: 1–73.

Walsh, M., and Martin, J. H. A. 1986. Recent changes in the distribution and migrations of the western mackerel stock in relation to hydrographic changes. ICES Document CM 1986/H:17.

Walsh, M., Reid, D. G., and Turrell, W. R. 1995. Understanding mackerel migration off Scotland: Tracking with echosounders and commercial data, and including environmental correlates and behaviour. ICES Journal of Marine Science, 52: 925–939.

Walsh, M., Skogen, M., Reid, D. G., Svendsen, E., and Mcmillan, J. A. 1996. The relationship between the location of western mackerel spawning, larval drift and recruit distributions: A modelling study. ICES Document CM 1996/S:33.

Ware, D. M., and Tanasichuck, R. W. 1989. Biological basis of maturation and wave spawning in Pacific herring (*Clupea harengus-pallasi*). Canadian Journal of Fisheries and Aquatic Sciences, 46: 1776–1784.

Werner, F., Quinlan, J., Lough, R., and Lynch, D. 2001. Spatially explicit individual based modeling of marine populations: a review of the advances in the 1990s. Sarsia, 86: 411–421.

Wheeler, J. P., and Winters, G. H. 1984. Homing of Atlantic herring (*Clupea harengus harengus*) in Newfoundland waters as indicated by tagging data. Canadian Journal of Fisheries and Aquatic Sciences, 41: 108–117.

Winters, G. H., and Wheeler, J. P. 1987. Recruitment dynamics of spring-spawning herring in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 44: 882–900.

Winters, G. H., and Wheeler, J. P. 1996. Environmental and phenotypic factors affecting the reproductive cycle of Atlantic herring. ICES Journal of Marine Science, 53: 73–88.

Wynne-Edwards, V. 1962. Animal Dispersion in Relation to Social Behaviour. Oliver and Boyd, Edinburgh. 653 pp.

Zheng, J. 1996. Herring stock–recruitment relationship and recruitment patterns in the North Atlantic and Northeast Pacific Oceans. Fisheries Research, 26: 257–277.

Zijlstra, J. J. 1958. On the herring races spawning in the southern North Sea and English Channel. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 143: 134–145.

Zijlstra, J. J. 1969. On the racial structure of North Sea autumn-spawning herring. Journal du Conseil Permanent International pour l'Exploration de la Mer, 33: 67–80.

Zwolinski, J., Mason, E., Oliveira, P., and Stratoudakis, Y. 2006. Fine-scale distribution of sardine (*Sardina pilchardus*) eggs and adults during a spawning event. Journal of Sea Research, 56: 294–304.

Zwolinski, J., Morais, A., Marques, V., Stratoudakis, Y., and Fernandes, P. 2007. Diel variation in the vertical distribution and schooling behaviour of sardine (*Sardina pilchardus*) off Portugal. ICES Journal of Marine Science, 64: 963–972.

Zwolinski, J. P., Oliveira, P. B., Quintino, V., and Stratoudakis, Y. 2010. Sardine potential habitat and environmental forcing off western Portugal. ICES Journal of Marine Science, 67: 1553–1564.

Zwolinski, J., Stratoudakis, Y., and Soares, E. 2001. Intra-annual variation in the batch fecundity of sardine off Portugal. Journal of Fish Biology, 58: 1633–1645.

15 List of acronyms and abbreviations

IBM	individual-based model
IBTS	International Bottom Trawl Survey
IMARES	Netherlands Institute of Marine Research
IMR	Norwegian Institute of Marine Research
MSVPA	multispecies virtual population analysis
NAO	North Atlantic Oscillation
NEA	Northeast Atlantic
NSS	Norwegian spring-spawning herring
SSB	spawning-stock biomass
SST	sea surface temperature

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