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Food for Thought

Recruitment depressions in North Sea herring

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Two periods of sustained low recruitment have been observed in North Sea herring in recent history; one from 1971 to 1979 and one that started in 2002 and continued up until the most recent year for which information is available (2010). This paper compares both periods of recruitment depression and considers the possible causes for each of them. The first depression (1971–1979) has been commonly ascribed to insufficient egg production by the depleted parent stock. However, recruitment to the central and northern populations was probably also affected by an environmental factor. There are indications of a reduced Atlantic inflow into the northwestern North Sea at the time of the depression. This could have affected survival of the larvae by slowing down their transport to the nursery areas in the southeastern North Sea. For the second period (2002–2010), the low recruitment has been ascribed to an increase in temperature and/or a regime shift in the ecosystem. An alternative explanation could be predation by the large stock of adult herring on its own larvae.

Keywords: Cannibalism, environment, North Sea herring, recruitment.

Introduction

In recent history, recruitment to the North Sea herring stock (*Clupea harengus* L.) has shown two periods of sustained depression. The first of these depressions occurred from 1971 to 1979 (the years refer to the year of birth of the year classes). Recruitment during this period dropped to an extremely low level (Figure 1), and this depression may therefore be called a "recruitment failure". It resulted in a collapse of the stock and a closure of all directed herring fisheries in the North Sea from 1977 to 1981/1983 (Dickey-Collas *et al.*, 2010).

The second period of low recruitment started in 2002 and it continued at least until 2010, the last year for which a recruitment estimate is available (ICES, 2012). This recruitment depression also affected the industry, be it to a lesser extent than the first one. The total allowable catch (TAC) for North Sea herring was severely reduced for some years. Landings dropped to < 50% of the long-term average, but then increased again (Figure 2).

The first recruitment depression occurred at a time when the spawning stock size of North Sea herring was at an all-time low (Figure 1). Most scientists therefore ascribed the recruitment failure to the depletion of spawning stock and refrained from looking for other causes. However, the depletion of the spawning stock probably was not the only cause of the poor recruitment. The first signs of recovery occurred in 1978 in the southernmost population; the population that was the smallest of all North Sea populations at the time of the stock collapse (Corten 1986a). Also, recruitment before 1979 was much lower for a given stock size than after that year (Figure 1). These two observations suggest that recruitment prior to 1980 was affected not only by low egg production, but also by an unknown environmental factor (Bailey, 1991).

Also for the second depression (2002–2010), there is still uncertainty about the underlying cause. A large number of potential causes has been considered by earlier authors, such as poor larval feeding, predation, and poor hatching conditions (ICES, 2006, 2007), a regime shift in plankton of the North Sea (Payne *et al.* 2009), and increased larval mortality resulting from high water temperatures (Fässler *et al.*, 2011; Hufnagl and Peck, 2011). The temperature hypothesis is considered the most plausible explanation so far, since the recruitment depression coincided with a period of elevated water temperatures in the central and northern North Sea. However, it should be noted that recent water

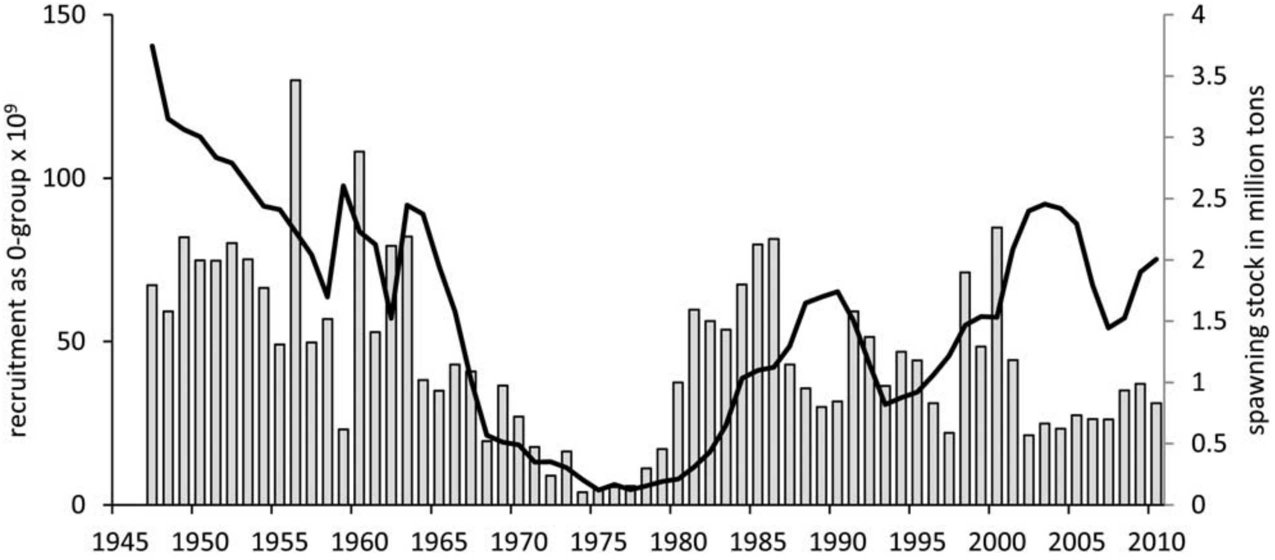

Figure 1. Spawning stock (drawn line) and recruitment produced by that stock (bars) for North Sea herring. Data from ICES (2012).

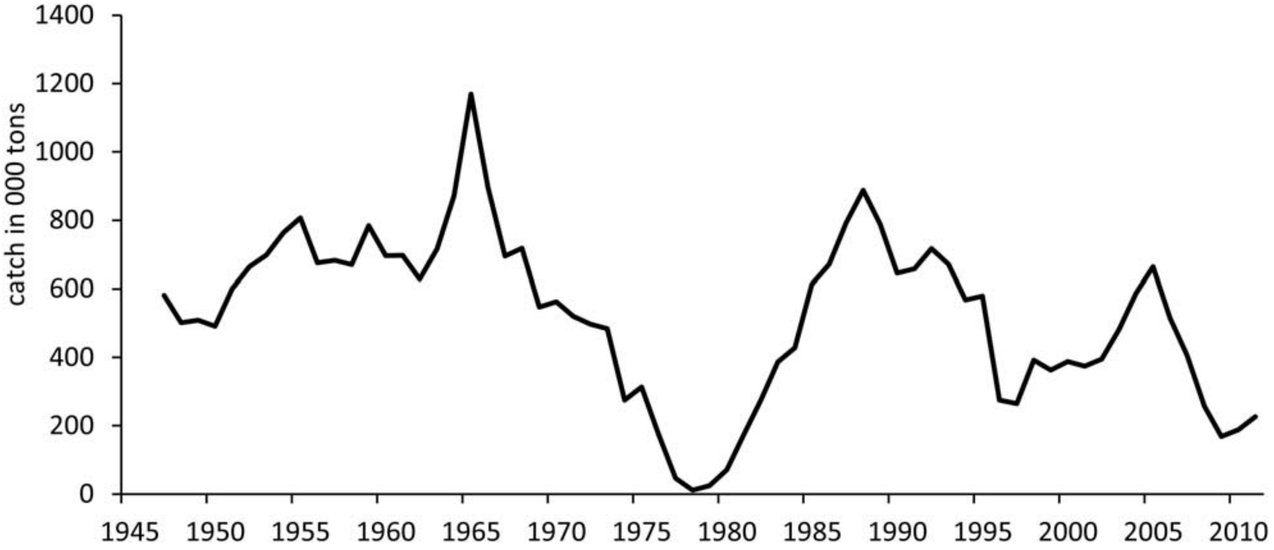

Figure 2. Total landings of North Sea herring. Note that the depression in 1996 – 1997 was not caused by low recruitment but by a tightening of management measures after a period of relaxation. Data from ICES (2012).

temperatures in the central and northern North Sea have not been much higher than those in 1981 – 1984 (Fässler *et al*., 2011), a period in which a series of strong year classes was produced (Figure 1). High temperatures, therefore, are not always detrimental to recruitment. This means that uncertainty also remains as to the cause of the latest recruitment depression.

The purpose of this paper is to review existing hypotheses for both recruitment depressions and to identify the most likely cause(s) for each of them. The basic assumption in this analysis is that the cause of a sustained recruitment depression should exhibit the same persistence over time as the recruitment depression itself. This rules out variations in environmental parameters caused by local meteorological conditions. These local conditions normally show strong interannual variations, so they are unlikely to cause sustained recruitment depressions.

In general, the factors that may depress recruitment consistently over a series of years may be grouped into three categories: (i) low egg production by the parent stock; (ii) predator populations that persist over several years; and (iii) environmental effects related to changes in the nearby ocean.

Low egg production by a depleted parent stock is a factor that will not change drastically from one year to another. This factor, therefore, is normally the first cause that is considered.

The second potential cause is predators that live for a number of years and that may remove the larvae or juveniles over a considerable part of their distribution area. Such predators are most probably plankton-eating pelagic fish with a lifespan of several years.

The third potential cause of persistent changes in recruitment is oceanic effects. Changes in the ocean are normally more persistent than changes in the peripheral seas. This is due to the large volume, heat content, and momentum of the ocean currents. An example of a long-lasting change in the North Atlantic was the "Great Salinity Anomaly" that affected most of the North Atlantic over a period of 15 years (Dickson *et al*., 1988). This salinity anomaly was just one example of long-term variability in the North Atlantic. Another example was the changes in the Atlantic water in the English Channel in the early 1930s (Russell, 1935). Long-term variations in the North Atlantic may affect fish stocks in adjacent areas that are under the influence of Atlantic waters.

In this paper, the two recruitment depressions in recent history will be considered from the above perspective. Existing hypotheses for their causes will be reviewed and compared with the criteria for potential causes described above. For the second period (2002–2010), a new hypothesis will be presented in addition to the theories already advanced so far.

The 1971–1979 recruitment failure

During the 1971–1979 recruitment failure, spawning stock biomass was at an extremely low level (Figure 1). Low egg production is therefore commonly considered as the main cause of the recruitment failure during this period. However, there was a remarkable change in the ratio between recruitment and spawning stock size by the end of this period (Bailey, 1991; Bailey and Steele, 1992; Nash *et al*., 2009). Before 1980, recruitment was much lower for a given stock size than after that year (Figure 1). Therefore, it seemed that recruitment prior to 1980 was affected not only by the low spawning stock size, but also by an environmental factor (Corten, 1984, 1986a).

In an analysis of the collapse and recovery of the individual North Sea populations, Corten (1986a) noted that the first signs of recovery occurred in the southern population, which was the smallest of all North Sea populations at the time of the stock collapse. In this population, larval production already showed a small recovery in 1980/81 (ICES, 1981; Schmidt *et al*., 2009), which led to a reopening of the fishery in the English Channel in 1981. The larger spawning populations of the central and northern North Sea did not show signs of recovery until 2 years later, and the fishery in this area remained closed until 1983. The slow recovery of recruitment in these areas, despite a relatively large spawning stock, indicated that egg production was not the only limiting factor for recruitment.

A critical factor for the survival of the larvae born in the central and northern North Sea is their transport in winter across the North Sea towards the nursery areas in the eastern North Sea (Figure 3). Although some larvae may be retained in coastal waters along the western board of the North Sea, the most important nurseries are found in the shallow and productive waters of the eastern North Sea. This is evident from the high densities of juvenile (1-ringed) herring found in this area during the International Bottom Trawl Survey (IBTS). The larvae have to arrive in the eastern North Sea in early spring to take advantage of the spring plankton bloom. If their passage across the North Sea takes too much time, they risk starvation or being eaten by predators. There is evidence that this winter transport of larvae across the North Sea was interrupted for a number of years prior to 1980. Results of a sampling programme of herring larvae with Methot Isaacs–Kidd (MIK) trawls during winter in the open North Sea, started in 1977, showed a peculiar distribution of the larvae during the first 3 years of the programme (1977–1979). In these years, most of the larvae in February were still found in the western North Sea, and very few had reached the southeastern North Sea (Corten, 1986a). The absence of larvae from this latter area was surprising, as it was known from the literature that normally the bulk of the larvae should have reached the German Bight by February (Bückmann, 1950). However, starting from 1980, larvae appeared in increasing numbers in the German Bight and Skagerrak by February. The corresponding year classes also turned out to be of increasing strength. These observations suggested that the poor recruitment in the years prior to 1980 was caused not only by insufficient egg production, but also by a reduced transport of the larvae towards their nursery areas.

Unfortunately, the sampling of herring larvae in the open North Sea was started only in 1977, whereas the recruitment failure had been in progress already since 1971. We do not know, therefore, whether the abnormal distribution of herring larvae in the open North Sea occurred already from the start of the recruitment failure. However, evidence for a disruption of larval transport in the earlier years is available from a sampling programme of late herring larvae in the inlets of the Dutch Waddenzee (Corten and Van der Kamp, 1979; Corten, 1986a). This region is part of the herring nursery area in the eastern North Sea (Figure 3), and larvae from the central North Sea spawning grounds normally arrive here in February–March. The Dutch sampling programme covered the period 1967–1984, and its results showed that virtually no larvae from the central North Sea reached the Dutch coastal waters in 1973–1980 (Figure 4). These observations therefore support the theory that larval transport in the open North Sea was disrupted prior to 1980, and that this disruption had been in progress already several years prior to the start of the MIK sampling programme.

Corten (1986a) assumed that the disrupted transport of the larvae was caused by a sustained reduction of North Sea circulation, and that this reduction would have had an oceanic origin. The residual circulation of the North Sea is the result of a number of factors such as local wind stress, oceanic inflow along it borders (Dooley, 1974, 1983), and local density gradients (Hill *et al*., 2008). Whereas local wind stress and density gradients are unlikely to produce sustained changes in North Sea circulation over a number of years, the oceanic inflow might do so (Turrell, 1992; Turrell *et al*., 1992).

Long-term changes in North Atlantic inflow would affect the herring spawning grounds in the northwestern North Sea that are situated in the path of the inflowing Atlantic water (Figure 3). It is likely that the larvae born at these sites travel on the Atlantic inflow during the first part of their journey across the North Sea. This means that their chances of reaching the nursery areas in the eastern North Sea may depend on the strength of this inflow.

Hydrographic data show that the period from 1975 to 1980 was anomalous in the North Sea, and was characterized by reduced temperatures and salinities (Turrell, 1992; Turrell *et al*., 1992, 1996). These authors propose that there was a reduction of the transport of Atlantic water into the North Sea at that time. Results from the international JONSDAP '76 survey did not show any Atlantic inflow at the time of this survey, which clearly indicated an anomalous situation (Turrell *et al*., 1992).

Indications for a persistent decrease of Atlantic inflow into the northwestern North Sea prior to 1980 are also provided by ecological data. The annual results of the Continuous Plankton Recorder Survey show a significant reduction of the transport of

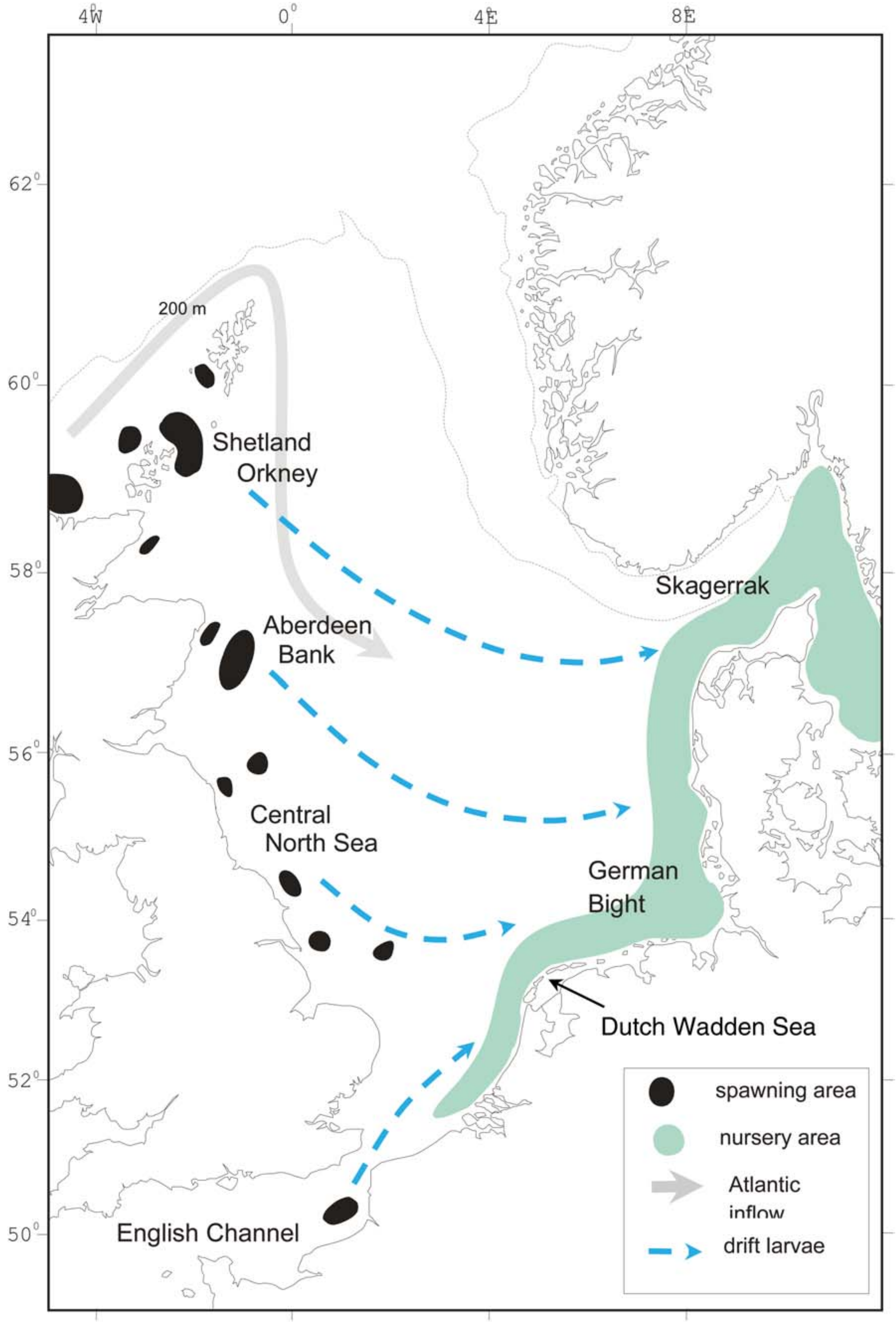

Figure 3. Drift routes of herring larvae from the hatching areas in the northwestern, western, and southern North Sea to the main nursery area in the eastern North Sea. Also indicated is the position of the Dutch sampling in the Wadden Sea.

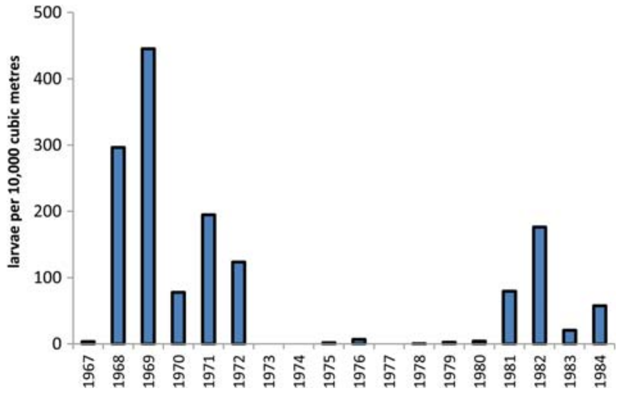

Figure 4. Abundance of herring larvae originating from central North Sea spawning grounds in the Dutch Wadden Sea in 1967–1984. Data from Corten (1986a).

oceanic warm-water plankton species from the west of Scotland into the North Sea in 1971–1978 (Robinson and co-workers 1975–1985, summarized by Corten, 1986b). After 1979–1980, there was a reversal of this long-term trend, with warm-water oceanic species penetrating into the North Sea in increasing numbers. In a further study on plankton indicator species in the northwestern North Sea, Corten (1999) looked at two characteristic plankton indicator species for Atlantic water in the North Sea, the copepods *Candacia armata* and *Metridia lucens*. It appeared that the abundance of both species in the northwestern North Sea had been abnormally low in the years 1965–1979 (Figure 5). Considering that the two species occupy different ecological niches, *C. armata* being a carnivore and *M. lucens* a herbivore, this simultaneous depression in both species was probably not related to intraspecific dynamics but to a more general hydrographic change in the area. The drop in abundance was not seen in the adjacent part of the North Atlantic, so the author interpreted the low abundance in the North Sea as an indication of a reduced Atlantic inflow into the North Sea.

Additional indications for a persistent reduction of the Atlantic inflow into the northwestern North Sea in the mid 1970s are provided by some fish stocks. Turrell (1992) mentions that the numbers of young sandeels (*Ammoditus marinus* Raitt) taken by research vessels in midwater trawls in the coastal waters of Shetland increased during the years 1974–1979, and decreased again in subsequent years. The temporary increase of sandeel recruitment gave rise to a commercial fishery for sandeels, and record numbers of seabirds in the Shetland area. Turrell (1992) suggested that the temporary increase in sandeel recruitment was caused by a reduction or cessation of the inflow of Atlantic water east of Shetland. Such a cessation of the residual current would reduce the loss of larvae out of Shetland coastal waters.

A similar explanation was given by Corten (1986a, 1990) for the temporary expansion of the sprat stock in the northwestern North Sea during the 1970s. Just like sandeel (and in contrast to herring), sprat is a coastal species that depends for its recruitment on larvae that are retained in nearby coastal waters. Larvae born in the Shetland area that are carried away by the residual currents towards the German Bight will be lost to their parent population. The unusual expansion of the sprat population in the northwestern North Sea in the 1970s must have been due to an abnormally strong recruitment (ICES, 1990). A reduced water circulation in the northwestern North Sea, that would retain more sprat larvae in the area, could be an explanation for this exceptional recruitment.

The above observations support the theory of a reduction of the Atlantic inflow into the northwestern North Sea in the 1970s. This reduction of Atlantic inflow has probably affected the survival of the herring larvae born in the western and northwestern North Sea by reducing their transport across the North Sea. An alternative possibility is that the reduced Atlantic inflow has affected feeding conditions of the larvae. Whatever the precise mechanism of the effect on larval survival may have been, it is likely that the major hydrographic and ecological change in the northwestern North Sea in the 1970s also affected herring recruitment, and that the recruitment failure, therefore, cannot be attributed solely to the low spawning stock.

The 2002–2010 recruitment depression

A review of existing hypotheses

The post-2000 recruitment depression in herring coincided with similar recruitment problems in sandeel and Norway pout. In order to investigate the cause of this phenomenon, ICES established a special working group, the "Study Group on Recruitment Variability in North Sea Planktivorous fish" (SGRECVAP). Large numbers of hypotheses were considered by this group during its first meeting in 2006, including poor larval feeding, predation on larvae, and poor hatching conditions (ICES, 2006). During its subsequent meeting (ICES, 2007), the group concluded that the poor recruitment in North Sea herring was probably related to an increase of water temperature at the spawning sites in the central and northern North Sea, which could have affected frontal development and thereby food supply for the larvae.

Payne *et al*. (2009) also considered a number of possible explanations for the poor recruitment in North Sea herring. They noted that contemporary warming of the North Sea had caused significant ecological changes, and they referred to a recently identified regime shift in the plankton of the central North Sea in around 2000 (Edwards *et al*., 2007) which showed close temporal agreement with the reduced larval survival. More recently, however, Alvarez-Fernandez *et al*. (2012) estimated the latest regime shift in the North Sea to have occurred around 1998, i.e. 3 years before the drop in herring recruitment. The herring year classes born in 1998 and 2000 were even far above average (Figure 1), so the regime shift postulated by Alvarez-Fernandez *et al*. (2012) does not coincide with the start of the herring recruitment depression.

Perhaps it was not regime shift itself but the underlying increase in water temperature that caused the recent recruitment depression in herring. Fässler *et al*. (2011) estimated daily mortality of early herring larvae by combining data from the International Herring Larval Surveys with a temperature-based growth model to estimate larval age. They found that the central and northern components of North Sea herring after 2000 shared an increasing trend in mortality that was significantly correlated with ambient water temperatures experienced by the larvae during the first 30 d after hatching. The modelled ambient temperature of the larvae showed a strong increase in 2002 (Figure 6), which corresponds more accurately with the onset of the recruitment depression.

The relationship between larval mortality and temperature was further analysed in a modelling study by Hufnagl and Peck (2011).

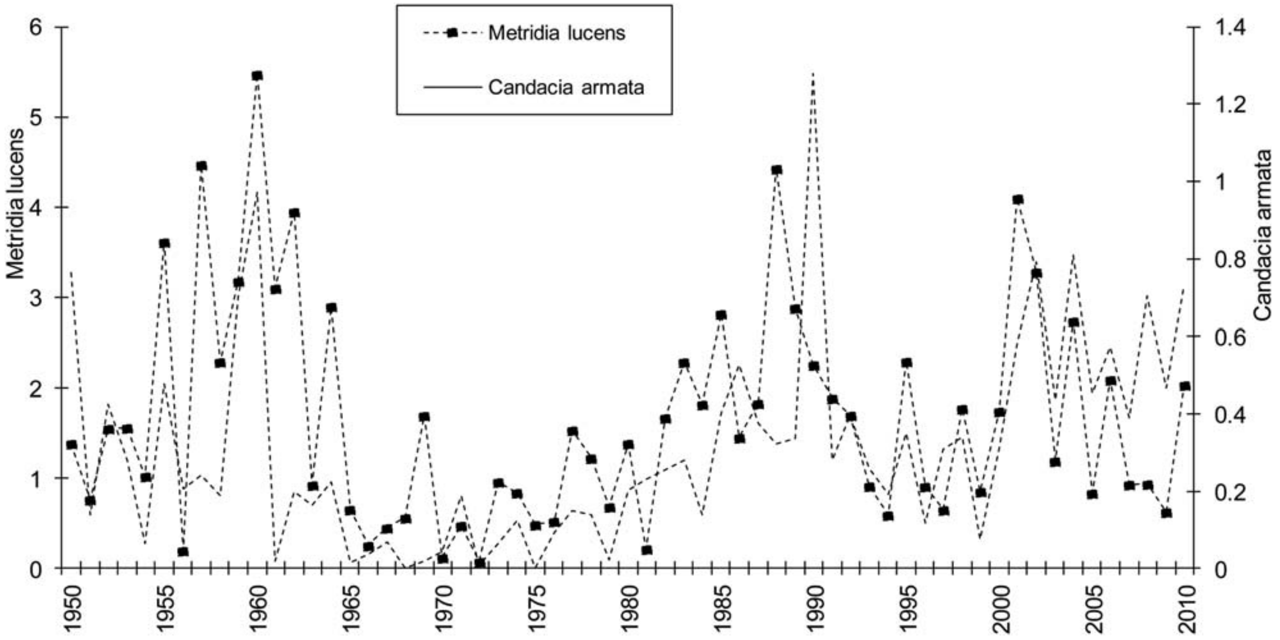

Figure 5. Abundance of two Atlantic plankton species, *Candacia armata* and *Metridia lucens*, in the northwestern North Sea as measured in the Continuous Plankton Recorder survey. Abundance is expressed in mean numbers per sample for the second half of the year. Data were kindly provided by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS).

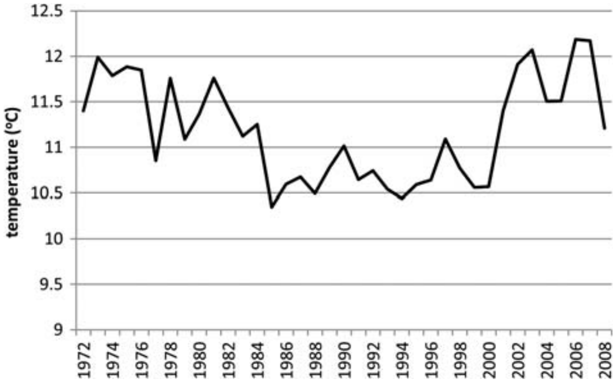

Figure 6. Mean ambient temperatures of herring larvae in the central and northern North Sea. Adapted from Fässler *et al.* (2011; original data kindly provided by S. Fässler).

Their model indicated that survival of larvae in the North Sea declined rapidly at temperatures >11°C due to a conflict between the higher food requirement of the larvae (because of a higher metabolic rate) and the lower food availability.

Oceanic changes after 2000

Following the line of thought presented in the Introduction, one of the potential causes of a sustained recruitment depression is a hydrographic change that originates from the adjacent ocean. For the post-2000 recruitment depression, such an oceanic cause is a distinct possibility. The persistent high temperatures experienced by the larvae of the central and northwestern North Sea since 2002 (Fässler *et al.*, 2011) were probably not merely the result of local meteorological conditions but must have originated partly from the ocean. The temperature of the inflowing Atlantic water in the northwestern North Sea shows the same upward trend since the late 1990 as the oceanic water in the Rockall Trough between 0 and 800 m (Hughes *et al.*, 2010). Therefore, this warming of the North Atlantic must have contributed to the persistent warming of spawning grounds in the central and northwestern North Sea since the late 1990s.

Apart from the increased temperature, however, there are few indications of a profound ecological change in the North Sea around 2000 that originated from the North Atlantic. The regime shift in the plankton of the central North Sea around 2000, proposed by Payne *et al.* (2009) as a possible cause of the herring recruitment depression, was not very pronounced, and the time of its occurrence is generally put several years before the appearance of the first poor year class in 2002. Weyerman *et al.* (2005) indicated a possible regime shift in the plankton in 1998, but they state that this regime shift was less clear-cut than those in 1979 and 1988. Alvarez-Fernandez *et al.* (2012) also date the latest regime shift in the North Sea in 1998, and they describe this shift as an increase in the relative contribution of warm-water copepod species and a decrease in the total number of copepods. The regime shift in 1998, if one may call it by this name, was therefore mainly the result of the rise in water temperature.

In order to investigate whether, in addition to the temperature increase, there was also a change in oceanic inflow around the year 2000 similar to the one that presumably occurred in the 1970s, one may consider the time-series of the two Atlantic plankton species *C. armata* and *M. lucens* that showed a pronounced reduction during the earlier recruitment depression (Figure 5). It is seen that these two species did not exhibit a similar depression after 2000; therefore, a major change of Atlantic inflow in this period is not supported by these data.

Changes in predators after 2000

An alternative explanation for the post-2000 recruitment depression in herring is a sustained increase in predation on the larvae by an organism that maintained its abundance over a series of years, and that occurred over a large part of the distribution area of the larvae. Planktonic predators generally do not fulfil these criteria, but planktivorous fish could be suitable candidates. Blaxter and Hunter (1982) mentioned already that perhaps the most important group of predators on pelagic eggs and larvae of clupeoids are the pelagic fish themselves.

The most likely candidates would be the main pelagic species in the North Sea, i.e. the mackerel, horse mackerel, and herring. The first two of these migrate out of the North Sea during autumn and they return to the North Sea in spring. They are absent from the North Sea during winter, at the time when the herring larvae sustain their critical mortality. The only species that does not leave the North Sea during winter is the herring, so this species could well be a predator on its own larvae. The recruitment failure coincided with the period when the herring stock reached its maximum level in recent years (Figure 1), and the distribution of adult herring during winter partly overlaps with that of the herring larvae (Figure 7). Cannibalism by adult herring on its own larvae, therefore, is also a possible explanation for the post-2000 recruitment depression.

Evidence for cannibalism in herring

Cannibalism occurs widely in fish (Smith and Reay, 1991), and herring is no exception to the rule. In this species, cannibalism can be easily demonstrated under laboratory conditions (Hourston *et al*., 1981; Fuiman and Gamble, 1988; Fuiman, 1989; Wespestad and Moksness, 1990). The laboratory experiments by Hourston *et al*. (1981) showed that juvenile herring of 8–10 cm had a clear preference for larvae of their own kind. As soon as the larvae were introduced into the tank, the juveniles stopped schooling and immediately began to feed on the larvae. They even had a preference for the larvae since they actually selected herring larvae from a mixed supply of food items. Hungry juveniles could eat up to 17 larvae per minute. If herring larvae are attractive as food to juvenile herring, one may assume that the same applies to adult herring.

Cannibalism in herring is more difficult to demonstrate in the field, due to the fact that larvae quickly disintegrate after ingestion (Balfoort, 1984; Daan *et al*., 1985). However, despite this problem, there are numerous records of cannibalism in herring from field observations (Hourston *et al*., 1981; Daan *et al*., 1985; Last, 1989; Holst, 1992; Skaret *et al*., 2002; Gröger *et al*., 2010).

In North Sea herring, the larvae born in the northwestern and central North Sea in September–October drift during winter towards the nursery areas in the southeastern North Sea. At the same time, the adult herring after spawning migrate to the overwintering areas along the northeastern edge of the North Sea. The precise migration path of the adult herring is not known; presumably the fish migrate in a dispersed manner. Whichever their precise migration route is in a particular year, they are likely to pass through concentrations of herring larvae (Figure 8). Results from the IBTS show a partial overlap between the distribution of adult herring and larvae in February (Figure 7). The herring larvae at that time have a length of 15–25 mm, which is a suitable prey size for adult herring (Last, 1989; Gröger *et al*., 2010). One may assume, therefore, that adult herring will eat at least some of the larvae that they come across, and that cannibalism is one of the causes of natural mortality in herring larvae during winter.

A plot of herring recruitment on spawning stock size for the most recent 40 years (Figure 9a) shows a declining recruitment at stock sizes >1 Mt. This could be an effect of increased cannibalism at this level of stock size. However, the density-dependent effect is virtually absent when the series is extended backward to include the years starting from 1947 (Figure 9b).

If the density-dependent effect in recent decades was due to cannibalism, this effect was apparently less pronounced in the years prior to 1970 A possible explanation for this phenomenon could be that the stock structure of North Sea herring in recent years was different from the one that existed in historic times. Until about 1955, the herring populations spawning in the English Channel, Straits of Dover, and central North Sea constituted the main part of the total North Sea stock (Burd, 1978). The larvae from these spawning grounds had a shorter distance to cover to their nursery areas than the larvae from the more northern spawning grounds (Figure 3). After a period of heavy exploitation in the 1950s and early 1960s, the southern and central populations were severely reduced and some of their spawning grounds were completely abandoned (Figure 10, based partly on data from Postuma *et al*., 1977). As a result, the North Sea herring stock after 1970 was mainly composed of the northern populations. These are the populations that will be most vulnerable to cannibalism, due to the fact that their larvae have to cross an area where overwintering adults occur. The profound change in stock structure of North Sea herring after 1970 could thus explain why the stock in recent times might have become more sensitive to cannibalism.

Discussion

The two recruitment depressions in North Sea herring observed in recent decades were most probably caused by different factors. The first depression (1971–1979) was caused primarily by a depletion of the parent stock, but there are indications that the effects of the low egg production were exacerbated by adverse environmental conditions. Many observations on hydrography, plankton, and fish stocks indicate a profound ecological change in the northern North Sea in the 1970s, presumably due to a reduction of the Atlantic inflow. When the Atlantic inflow returned to normal after 1979, the remaining herring stock was suddenly capable of producing much stronger year classes than in the preceding years. The fact that the oceanic disturbance coincided with the period of stock depletion, however, makes it difficult to quantify the contribution of each factor to the recruitment depression.

For the second period (2002–2010) too, there are also several causes that may have contributed to the recruitment depression. The two potential causes discussed above, the warming of the northwestern North Sea and the increased stock size of adult herring, also occurred at the same time, and again it is difficult to separate the effects of each of them.

The temperature hypothesis is supported by modelling studies that suggest a negative effect of high temperatures on survival of the larvae (Fässler *et al*., 2011; Hufnagl and Peck, 2011). Interestingly, a negative effect of high spawning temperatures on recruitment success was already shown several decades before by Postuma (1971) for Dogger bank herring. The negative effect that he found, however, occurred at temperatures $>12^{\circ}$C,

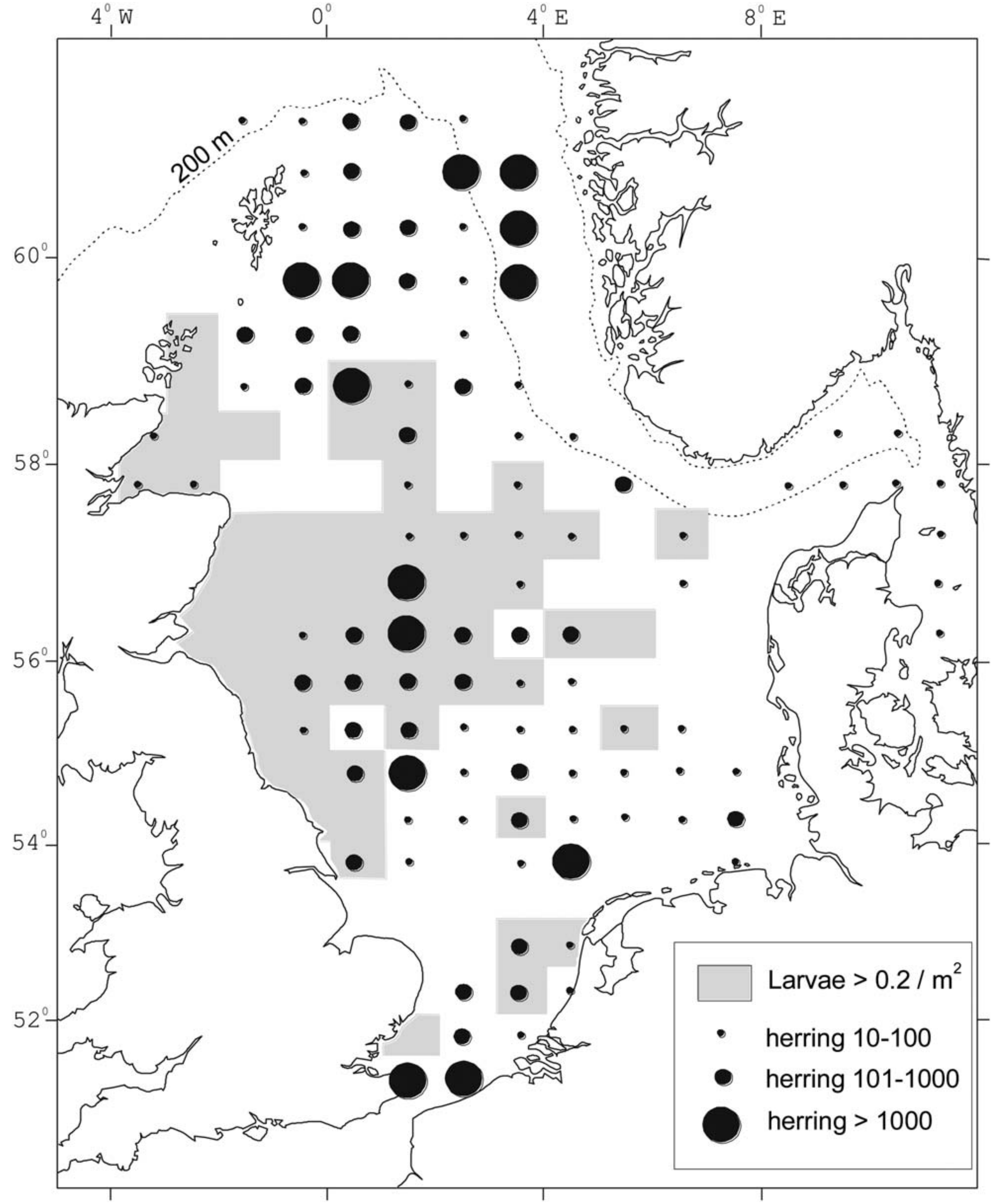

Figure 7. Distribution of herring larvae and adult herring in February. Mean values for 2002–2004 from the ICES Fishmap database (http://www.ices.dk/marineworld/ices-fishmap.asp).

whereas the study by Fässler *et al.* (2011) suggests a low survival for larvae in the central and northern North Sea already at temperatures between 11.5 and 12.0°C.

While the temperature hypothesis may partly explain the recent recruitment depression, the question remains whether a variable parameter such as temperature can explain the persistent nature

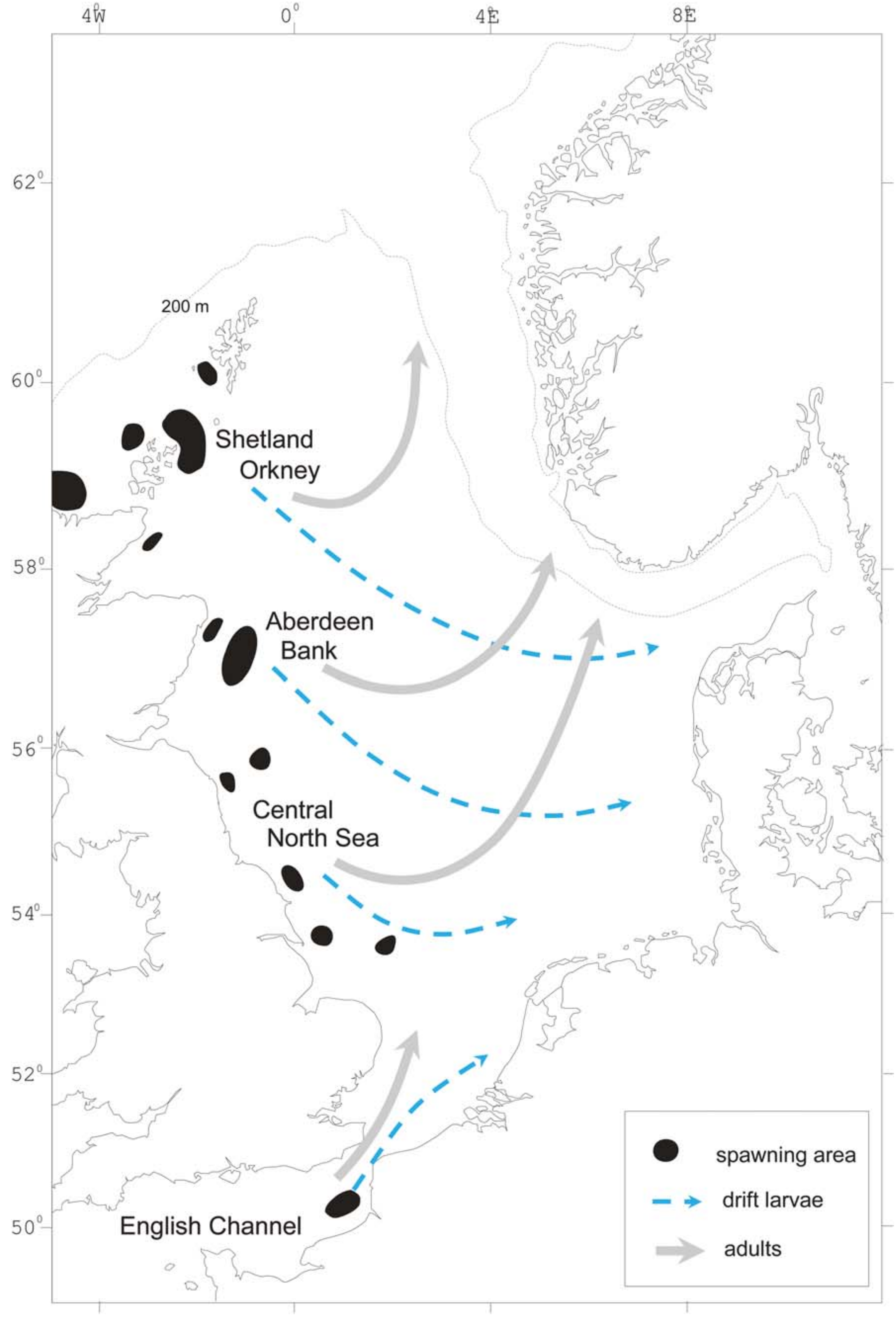

Figure 8. Drift routes of herring larvae and migration of adults after spawning.

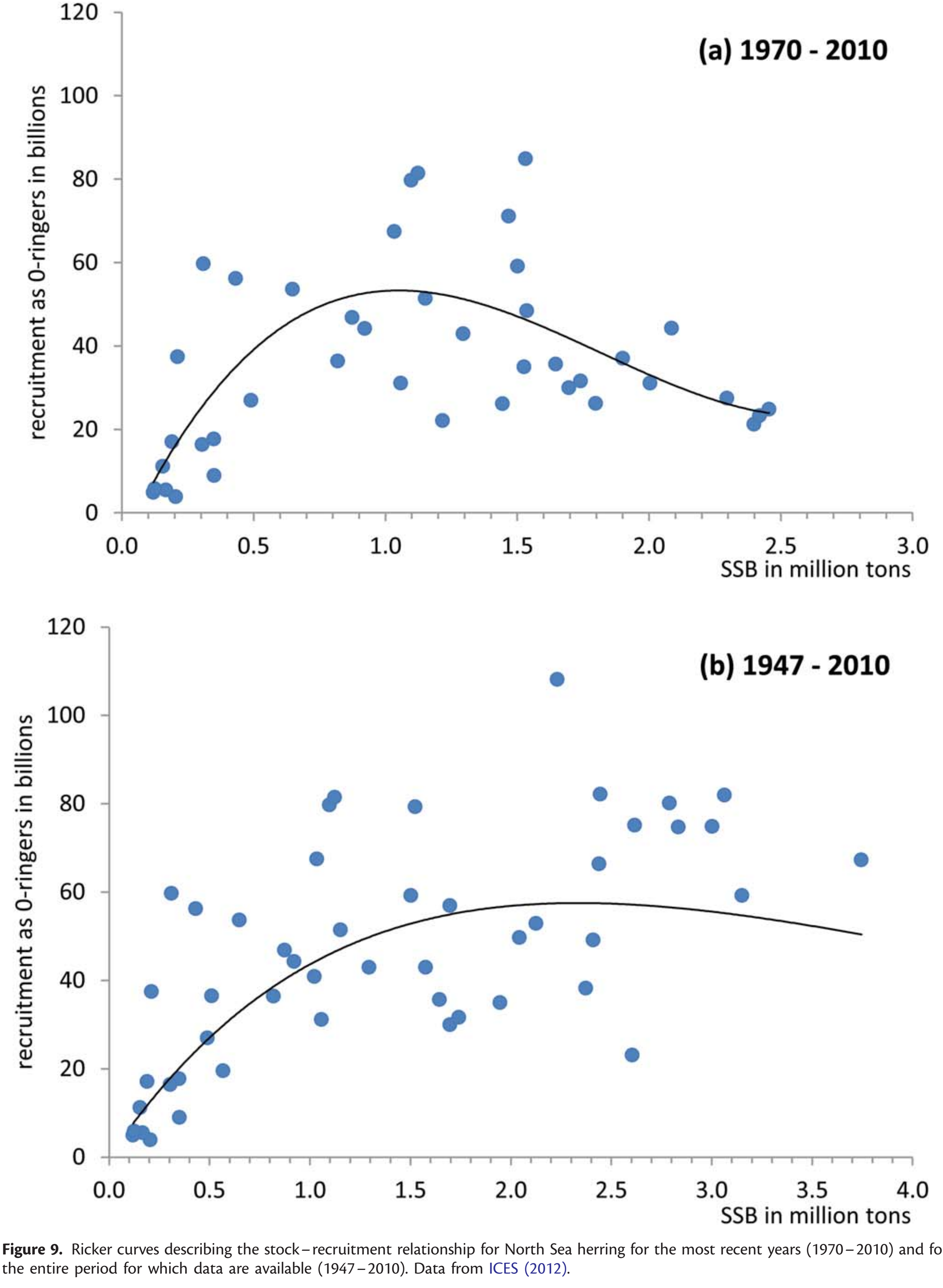

Figure 9. Ricker curves describing the stock–recruitment relationship for North Sea herring for the most recent years (1970–2010) and for the entire period for which data are available (1947–2010). Data from ICES (2012).

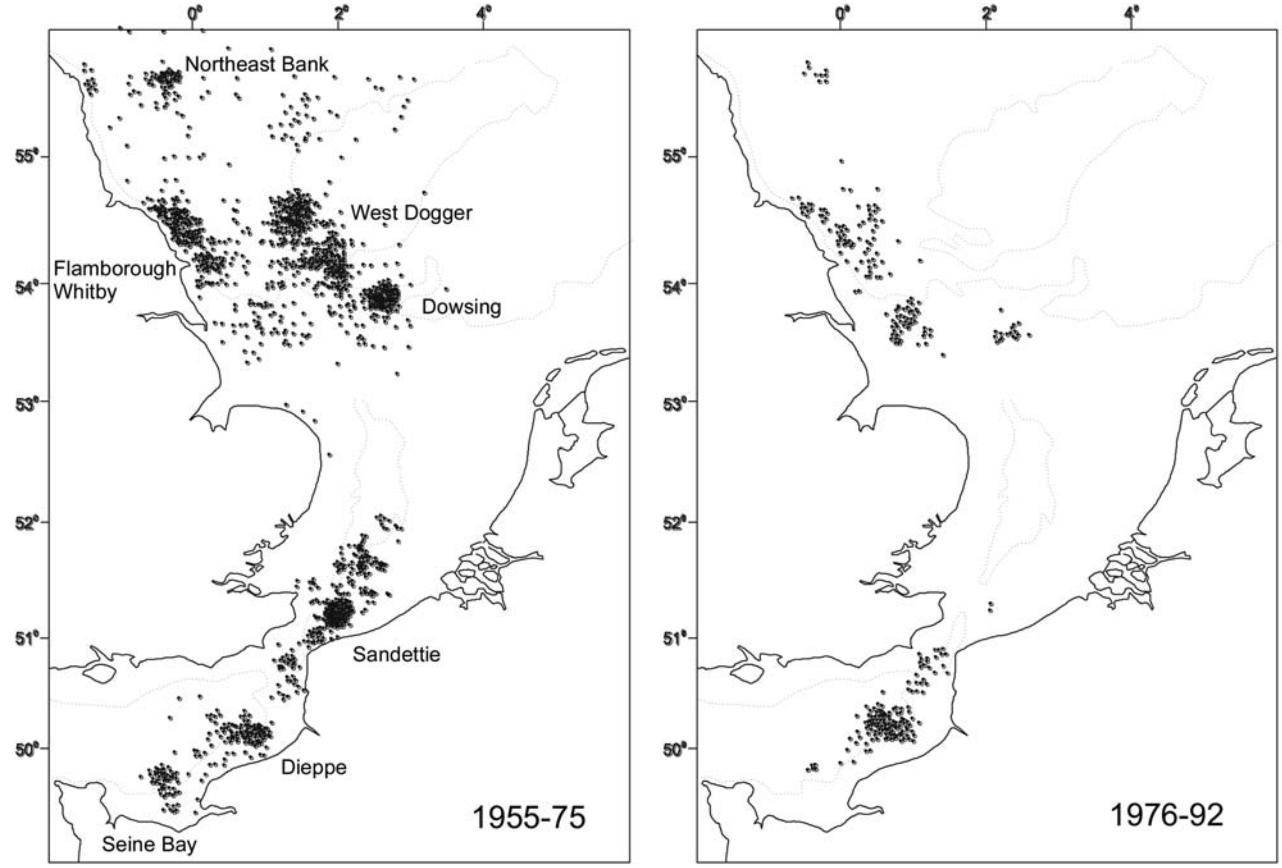

Figure 10. Spawning grounds (as indicated by catches of spawning herring) in the central and southern North Sea before and after the stock collapse in the mid 1970s. Based on results published by Postuma *et al.* (1977) and sampling of commercial fisheries in later years by RIVO, The Netherlands.

of the recruitment depression. Although the annual temperatures in the northwestern North Sea were all high from 2002 onwards (Figure 6), they still showed more interannual variability than the recruitment (Figure 1). A second question is why the herring stock in earlier times (1981–1984) could produce strong year classes at hatching temperatures that were not very different from those in recent years. It seems, therefore, that temperature may not have been the only factor that reduced year-class strength in recent years.

The cannibalism hypothesis described above offers a different explanation for the recent period of low recruitment. Although the stock sizes of 1.5–2.5 Mt that occurred since 2002 are not extremely large in a historic perspective (Figure 1), the stock in recent decades consisted mainly of the northern and central populations (Payne, 2010); the larvae of which have to cross the North Sea and thereby may be exposed to cannibalism (Figure 8).

In herring, and in particular North Sea herring, the possibility of cannibalism has so far received little attention. Fox (2001) mentions cannibalism as one of many possibilities for the density-dependent recruitment in Blackwater herring. The Blackwater herring, however, is a small local herring stock with no connection to the main stock of North Sea autumn spawners. In their exhaustive review of possible causes of the recent low recruitment of North Sea herring, the ICES SGRECVAP did not consider cannibalism as a likely cause. Their argument was that the IBTS data on adult herring distribution for recent years seemed to indicate a slight shift to the east, away from the centre of larval distribution (ICES, 2007). This is not a strong argument against the cannibalism hypothesis. The IBTS provides only a snapshot picture of the distribution of larvae and adults in February. It is generally accepted that year-class strength by this time has already been largely determined (Nash and Dickey-Collas, 2005; ICES, 2006; Payne *et al*., 2009), which means that the critical mortality has taken place before February. The IBTS does not provide information on the spatial overlap between adults and larvae in the preceding months. However, considering the fact that the adult herring during the preceding months have migrated from the spawning areas in the western North Sea to the eastern North Sea, they must have passed through some of the areas where larvae were distributed.

The question, therefore, is not whether cannibalism occurs, but to what extent it occurs. If cannibalism is responsible for a substantial fraction of the total mortality sustained by the larvae, the ultimate size of the year class will be affected by the total stock size of adult herring. A large adult stock will reduce recruitment, and, conversely, a small adult stock will result in higher recruitment than normal. This could be an explanation for the high recruitment during the recovery phase of the herring stock after 1979. During the 1970s, the adult stock was reduced for some years to $< 10\%$ of its long-term mean (Figure 1). Larval mortality due to cannibalism must have been very low in this period. Up until 1979, the larvae did not benefit from this reduced

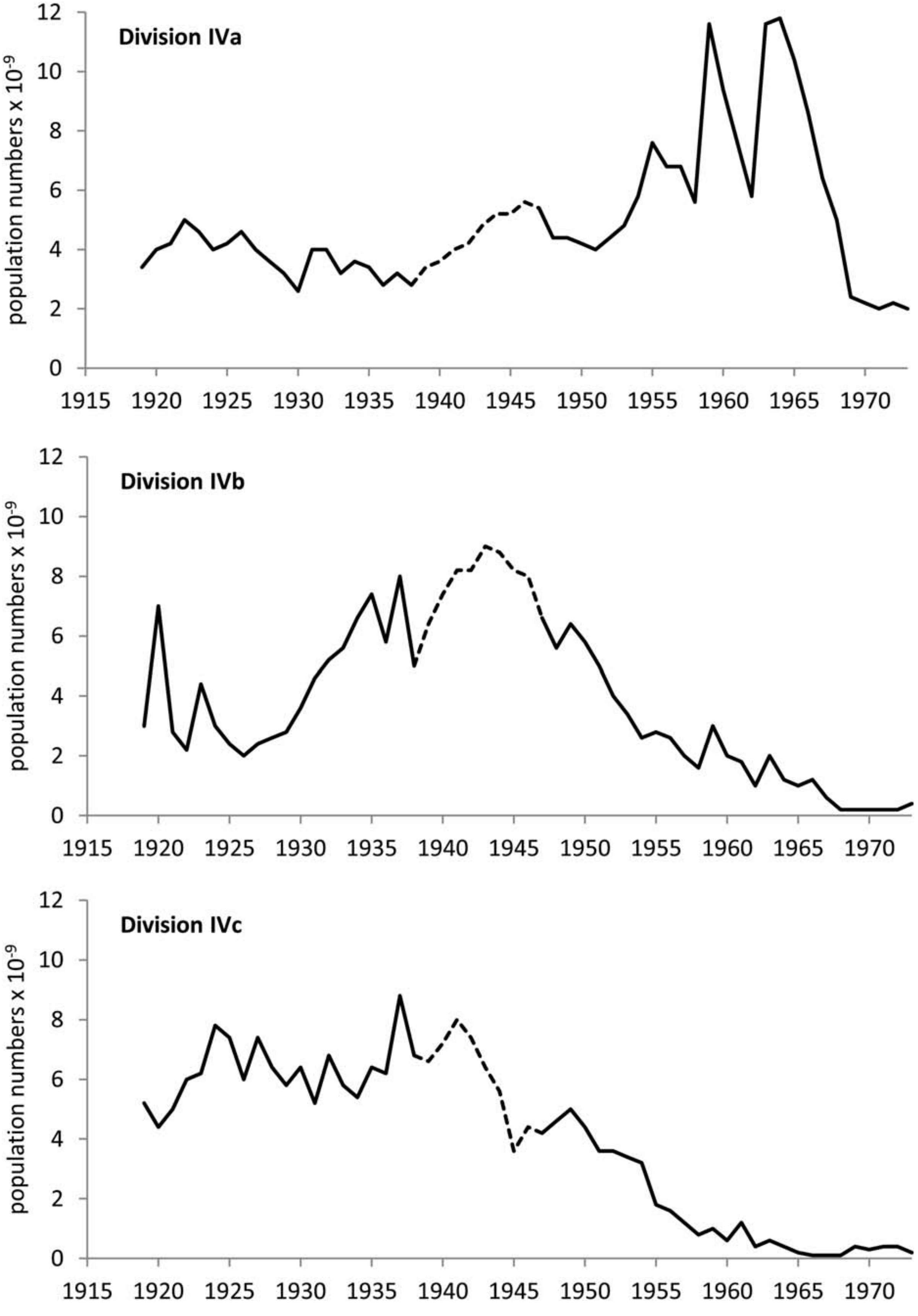

Figure 11. Historical trends of populations in different North Sea divisions. Adapted from Burd (1978). Boundaries of North Sea divisions are shown in Figure 12.

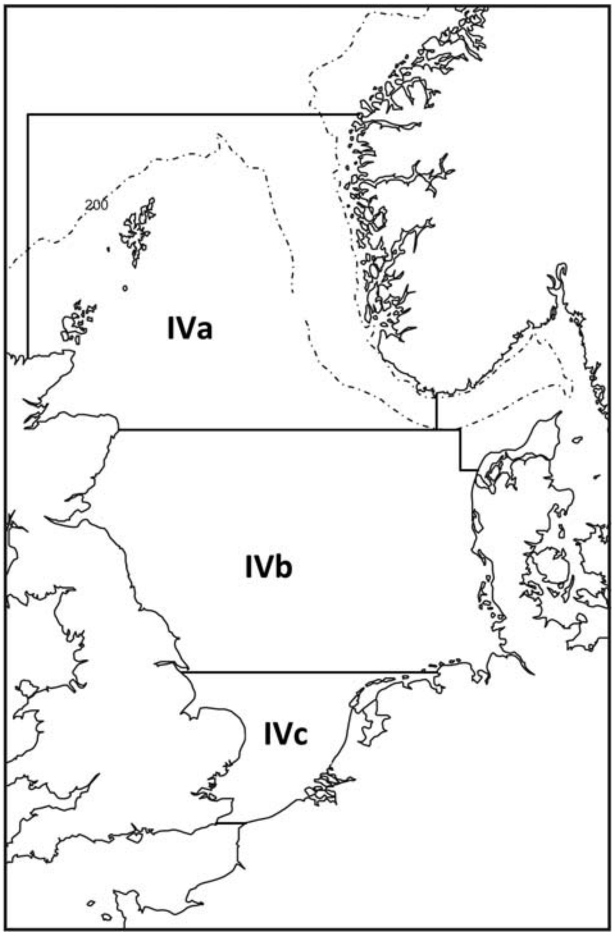

Figure 12. ICES North Sea Divisions referred to in Figure 11.

cannibalism because their survival was probably affected by the reduced Atlantic inflow in the northwestern North Sea. However, when this negative environmental condition disappeared after 1979, the larvae suddenly had better chances of survival than normal, due to the lower exposure to cannibalism. This could explain the unusually strong year classes 1981–1984, produced by a relatively small spawning stock.

It was mentioned earlier that the North Sea herring stock in recent decades may have been more sensitive to cannibalism than in earlier periods, due to the dominance of the northern population. Prior to 1955, the spawning populations of the central and southern North Sea were much larger, and larvae from these populations were probably less exposed to cannibalism because of the shorter distance to their nurseries. It is interesting to note that during this period the northern population was smaller than either the southern or the central population. Burd (1978) estimated stock sizes in each of the North Sea divisions during the period 1919–1973 by cohort analysis, in which he assumed that the catches in each division corresponded to the population in that division. The author was well aware of the fact that members of the spawning population in each division were also caught in other divisions, and that the population estimates for each division, therefore, would not correspond exactly to the spawning stocks in that division. Nevertheless, the results of his exercise provide an interesting picture of the evolution of the populations in the different parts of the North Sea over a long period (Figure 11). It is seen that the population in the northern North Sea (Division IVa) started to increase only around 1955, at the same time as when the populations in the central and southern North Sea (Divisions IVb and IVc) were severely reduced. This suggests that the populations in the North Sea are in competition with one another, and that not all populations can attain their maximum size at the same time. The competition occurs prior to recruitment, and it could be caused either by cannibalism of one population on the other, or by competition among larvae in the common nursery areas (Fox, 2001). Cannibalism on larvae from the northern population would be expected, particularly when the central population was large (Figure 8).

The revival of the southern North Sea population in recent years (Payne, 2010; ICES, 2012), at the same time as when recruitment to the northern and central populations was reduced, appears to be another example of interaction between the various North Sea stocks. Since the larvae of the southern population share part of their nursery area with larvae from the central and northern populations, a direct competition between these larvae is a distinct possibility. In periods when the northern and central larvae are abundant, the larvae from the southern population will be at a disadvantage because of their smaller size and later arrival in the nursery area (Corten and Van der Kamp, 1979). A reduced survival of larvae from the northern and central populations, regardless of its cause, would therefore leave more food for the southern larvae and increase their chances of survival.

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