

# Lessons learned from stock collapse and recovery of North Sea herring: a review

Mark Dickey-Collas, Richard D. M. Nash, Thomas Brunel, Cindy J. G. van Damme, C. Tara Marshall, Mark R. Payne, Ad Corten, Audrey J. Geffen, Myron A. Peck, Emma M. C. Hatfield, Niels T. Hintzen, Katja Enberg, Laurence T. Kell, and E. John Simmonds

Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., Corten, A., Geffen, A. J., Peck, M. A., Hatfield, E. M. C., Hintzen, N. T., Enberg, K., Kell, L. T., and Simmonds, E. J. 2010. Lessons learned from stock collapse and recovery of North Sea herring: a review. – *ICES Journal of Marine Science*, 67: 1875–1886.

The collapse and recovery of North Sea herring in the latter half of the 20th century had both ecological and economic consequences. We review the effect of the collapse and investigate whether the increased understanding about the biology, ecology, and stock dynamics gained in the past three decades can aid management to prevent further collapses and improve projections of recovery. Recruitment adds the most uncertainty to estimates of future yield and the potential to reach biomass reference points within a specified time-frame. Stock–recruitment relationships must be viewed as being fluid and dependent on ecosystem change. Likewise, predation mortality changes over time. Management aimed at maximum sustainable yield (MSY) fishing mortality targets implies interannual variation in TACs, and variability in supply is therefore unavoidable. Harvest control rules, when adhered to, aid management greatly. We advocate that well-founded science can substantially contribute to management through improved confidence and increased transparency. At present, we cannot predict the effects of collapse or recovery of a single stock on the ecosystem as a whole. Moreover, as managers try to reconcile commitments to single-species MSY targets with the ecosystem-based approach, they must consider the appropriate management objectives for the North Sea ecosystem as a whole.

**Keywords:** demographic, distribution, fisheries management, metapopulation, multispecies, productivity.

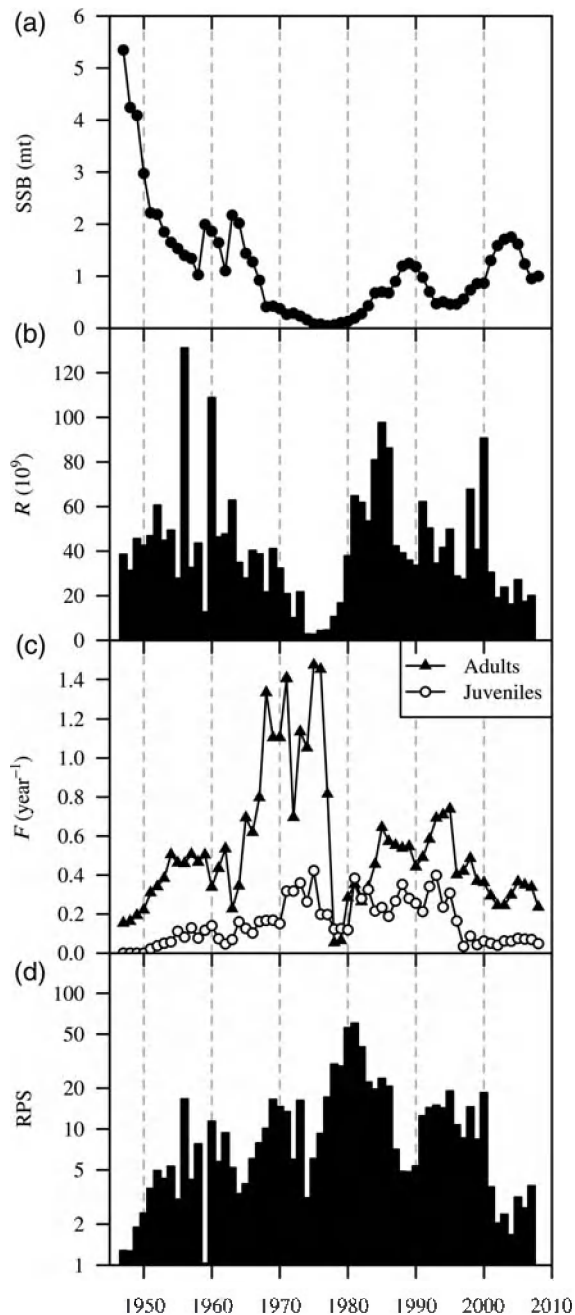
Received 25 October 2009; accepted 2 March 2010; advance access publication 26 April 2010.

M. Dickey-Collas, T. Brunel, C. J. G. van Damme, and N. T. Hintzen: Wageningen Institute for Marine Resources and Ecosystem Studies, PO Box 68, 1970 AB IJmuiden, The Netherlands. R. D. M. Nash: Institute of Marine Research, PO Box 1870, Nordnes, 5817 Bergen, Norway. C. T. Marshall: School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, Scotland, UK. M. R. Payne: National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, 2920 Charlottenlund, Denmark. A. Corten: De Waterdief 52, Uitgeest, The Netherlands. A. J. Geffen and K. Enberg: Department of Biology, University of Bergen, PO Box 7803, 5020 Bergen, Norway. M. A. Peck: Institute of Hydrobiology and Fisheries Science, University of Hamburg, Olbersweg 24, D-22767 Hamburg, Germany. E. M. C. Hatfield: Marine Scotland-Science, PO Box 101, Victoria Road, Aberdeen AB11 9DB, Scotland, UK. L. T. Kell: International Commission for the Conservation of Atlantic Tunas (ICCAT), Corazon de Maria 8, Planta 6, 28002 Madrid, Spain. E. J. Simmonds: European Commission, JRC, ISPC Fish Reg., Via Enrico Fermi, Ispra 21027, Italy. Correspondence to M. Dickey-Collas: tel: +31 317 487166; fax: +31 317 487326; e-mail: mark.dickeycollas@wur.nl.

## Introduction

The development of the North Sea herring (*Clupea harengus*) stock in the 20th century presents a clear example of recruitment overfishing resulting in stock collapse (Saville and Bailey, 1980; Cushing, 1992). Periods of collapse and recovery have been reviewed thoroughly in the light of management and other aspects (Burd, 1991; Corten, 1991; Bailey and Steele, 1992). From  $>2 \times 10^6$  t in the 1960s, the spawning-stock biomass (SSB) declined to  $<50 \times 10^3$  t by the mid-1970s (ICES, 1998a, 2008a; Figure 1a), whereas the maximum age of fish in the catches decreased from 14 to 5 years old. The stock has since recovered and SSB has been estimated to have fluctuated around  $1 \times 10^6$  t during the past 20 years. The spatial distribution is similar to that observed before the collapse (Burd and Howlett, 1974; Schmidt *et al.*, 2009). The stock has experienced

fluctuations in productivity since the recovery, which requires constant management attention to prevent a recurrence of recruitment overfishing (Simmonds, 2007). By considering the collapse and recovery of the North Sea herring, we provide information that might be useful for managing other fisheries or rebuilding other resources. We specifically consider: (i) the distribution and demographic changes in the light of substock structure; (ii) potential changes in genetic diversity and associated changes in life-history traits; (iii) the productivity of the stock and its components; (iv) whether multispecies interactions changed or influenced recovery; (v) consequences of collapse for the fishery; and (vi) the performance of the stock assessment and projections. The effects are considered in the context of the ecosystem as a whole, of the fisheries and suppliers, and of lessons for fisheries management in general.



**Figure 1.** ICES (1998a, 2008a) assessment of stock dynamics of North Sea herring, 1947–2009: (a) SSB, (b) recruitment-at-age 0,  $10^9$  ( $R$ ), (c) fishing mortality rate ( $F$ ) on adults and juveniles, and (d) recruits per spawner (RPS). Two series are concatenated to create complete time-series, because series agree during the period of overlap.

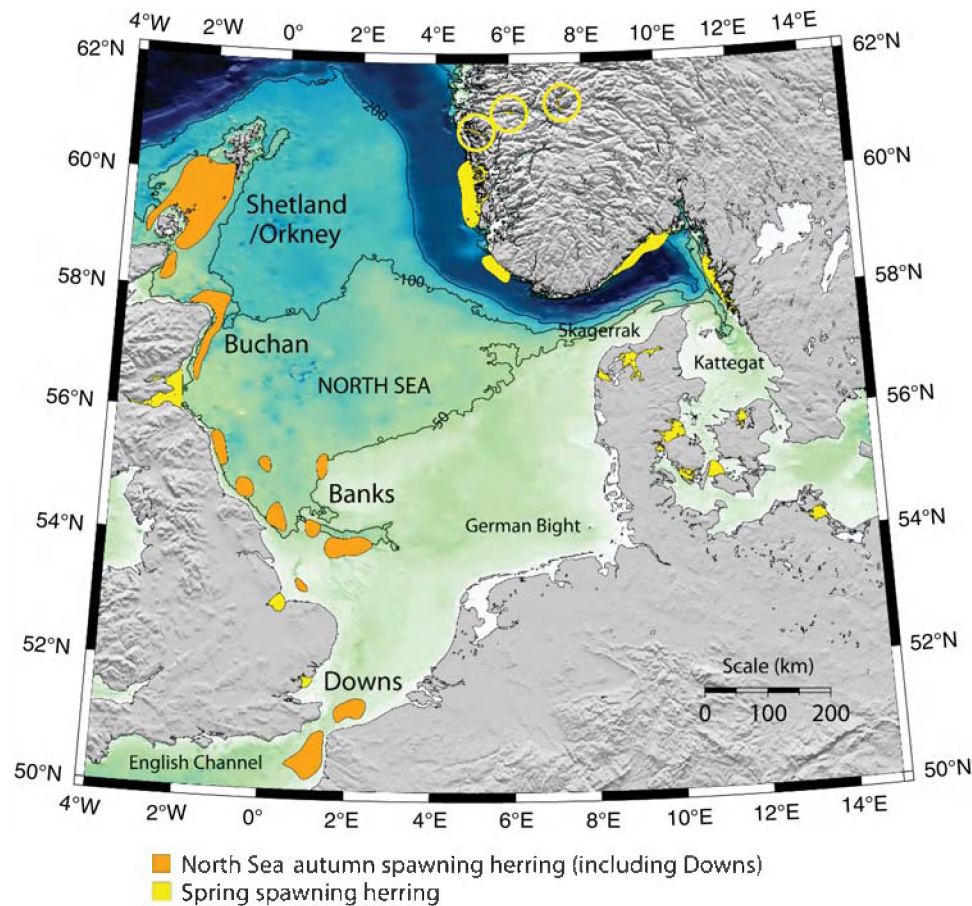
### Distribution and demography

The stock is usually considered to comprise four spawning components (Shetland/Orkney, Buchan, Banks, and Downs; Figure 2) characterized by different growth rates, migration routes, and recruitment patterns (Bjerkkan, 1917; Cushing and Bridger, 1966; Harden Jones, 1968). Within these groups, different spawning grounds might be used. Although the different components mix during part of the year, they experience different

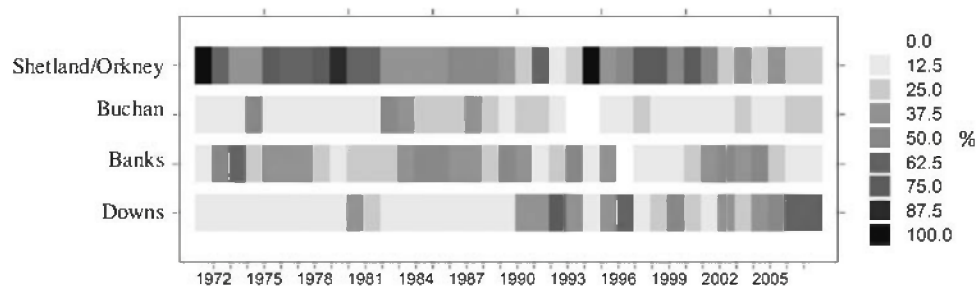
fishing pressures, because they are separate at other times. Surveys of larvae provide information on component dynamics (Payne, 2010). The collapse during the 1970s was spatially heterogeneous, the different components having been depleted consecutively from south to north (Cushing, 1992), in combination with a reduction in the distribution and number of spawning sites (Saville and Bailey, 1980). In addition, the components exhibited different recovery trajectories (Burd, 1985; Corten, 1999) and revealed different patterns in relative abundance (Figure 3). Schmidt *et al.* (2009) emphasized that “full recovery” is not well-defined by merely reaching a biomass threshold: restoring and maintaining spatial diversity might be equally important, because the latter provides resilience to local changes in exploitation, environment, and fish behaviour (McPherson *et al.*, 2001).

The processes involved in recolonization of spawning grounds during the recovery phase have remained unclear, but might have involved subsets of large year classes rediscovering migration routes or joining still-existing remnants of these components (McQuinn, 1997; Corten, 2001). The time required for the rebuilding of the Downs component ( $\sim 25$  years) suggests that the conservation measures taken in terms of specific TACs for this group have not had an immediate effect. If the objective of management is to maintain spatial diversity, clearly, monitoring of all spawning components is crucial. The collapse pattern demonstrates that North Sea herring exhibit the “basin effect” (MacCall, 1990): at low abundance, the population retracted to core spawning areas, whereas the peripheral areas were recolonized during recovery. This feature should be better accounted for in future management. As for the distribution of herring at other times of the year, the collapse seems to have had little effect, because feeding sites and nursery grounds appear to be governed by environmental factors, such as plankton production or physical transport (Bainbridge and Forsyth, 1972; Heath *et al.*, 1997; Maravelias and Reid, 1997; Maravelias, 2001; Dickey-Collas *et al.*, 2009). It is difficult to comment on the effect of collapse on the post-spawning distribution, because there is almost no information on the distribution of overwintering adult North Sea herring since the collapse.

Mixing of North Sea herring with other stocks within the management area affects the quality of the assessment, especially if they exhibit different changes in relative abundance or migration patterns (Kell *et al.*, 2004). At certain life stages and/or certain times of year, North Sea herring do mix with other stocks and these are exploited together (Clausen *et al.*, 2007; Bierman *et al.*, 2010). Although they are predominantly autumn/winter spawners, some small spring-spawning components are included in the assessment and management of North Sea herring, whereas others are not (those spawning in Norwegian fjords and the Thames estuary). The management advice for western Baltic spring spawners is linked to that of North Sea autumn spawners through combined projections of mixed catches by the different fleets. There is a separate sub-TAC for Downs herring. However, this fixed proportion of 11% of the total TAC is not based on robust science (ICES, 2008a). Because of their much larger population size, autumn- and winter-spawning herring dominate the catches in the region and the effect on the assessment of changes in the smaller populations appears to have been relatively minor (Simmonds, 2009). Hence, the current definition of the North Sea stock of autumn and winter spawners as a single management unit appears to operate well (Reiss *et al.*, 2009; Simmonds, 2009), if the dynamics of the major components are also monitored.



**Figure 2.** Spawning grounds of autumn- and spring-spawning herring in the North Sea and adjacent waters. Circles denote locations of spring-spawning herring in fjords. Although spawning in winter, Downs herring are considered an integral part of the autumn-spawning stock.



**Figure 3.** Time-series of the relative importance of the four spawning areas, expressed as the proportion of newly hatched larvae contributing to the total (from Schmidt *et al.*, 2009).

However, reliable monitoring of the dynamics of smaller stocks through collapse and recovery would be extremely difficult, particularly when their relative exploitation rates change in mixed-stock fisheries (Kell *et al.*, 2009). In fact, some of the smaller populations in the North Sea, usually spring spawners (Figure 2), are not monitored at all.

### Genetics and evolution

The genetic composition of large marine fish stocks has long been assumed fundamentally resilient to depletion, because even a collapsed stock might still comprise millions of individuals (Hutchings, 2000). For instance, the lowest recorded size of the

spawning population of North Sea herring was  $\sim 270 \times 10^6$  fish in 1977. However, several studies have demonstrated a loss of genetic diversity in heavily exploited fish populations (Smith *et al.*, 1991; Hauser *et al.*, 2002; Hutchinson *et al.*, 2003; Hoarau *et al.*, 2005), although apparent population sizes remained high. In many marine species, the genetically effective population size ( $N_e$ ), rather than the census population size ( $N$ ), determines whether a large loss of genetic diversity might occur during the periods of sharp population decline. Studies on New Zealand snapper (*Pagrus auratus*; Hauser *et al.*, 2002) and European plaice (*Pleuronectes platessa*; Hoarau *et al.*, 2005) showed the  $N_e$  to be some five orders of magnitude lower than the  $N$  derived



from fisheries data, which at least has the potential to result in a loss of genetic diversity during overexploitation.

Although the population of North Sea herring declined by several orders of magnitude, Mariani *et al.* (2005) could not detect any loss of genetic diversity. The authors hypothesized that compared with other species studied, herring have a larger proportion of the spawning stock contributing to successive generations, and hence a more balanced ratio of  $N_e$  to  $N$ , which reduces the genetic effect of stock decline. Additionally, because herring, like many clupeids, have regularly undergone population depletions independent of fishing pressure, the population might already have suffered natural genetic restriction before a fishery-induced collapse.

Intensive fishing has resulted in life-history changes in other heavily exploited fish stocks that appear to be at least partly of an evolutionary nature (Jørgensen *et al.*, 2007; Kuparinen and Merilä, 2007; Dunlop *et al.*, 2009). The most commonly observed change is earlier maturation (reduced age- and length-at-maturity; Beacham, 1987; Smith, 1994; Trippel, 1995). The driver is assumed to be the elevated mortality, because this favours genotypes associated with early maturation by removing genotypes of fish caught before reproduction (Andersen and Brander, 2009).

The overfishing of North Sea herring resulted in an estimated decline in SSB by 97%. Such a high fishing mortality rate ( $F > 1.2 \text{ year}^{-1}$ ) has the potential to cause evolutionary changes, particularly when fisheries are highly selective (Law and Grey, 1989; Heino, 1998; Ernande *et al.*, 2004). In a preliminary analysis on maturation changes in North Sea herring, Enberg and Heino (2007) found no clear indications to support the hypothesis of a fishery-induced effect on the maturation schedule, similar to the findings obtained for Norwegian spring-spawning herring by Engelhard and Toresen (in press).

## Productivity

Low productivity could be another cause of stock collapse. In fisheries science, productivity tends to be viewed as a combination of growth of the surviving fish and recruitment of new fish (Dutil and Brander, 2003). Mortality affects productivity; this is discussed further in the section on multispecies interactions. Although size-at-age is relatively easy to measure, the factors regulating growth of individual fish and recruitment are difficult to determine. We highlight three effects: changes in density on growth, changes in stock structure on reproductive potential, and changes in the number of recruits per spawner.

## Density-dependent growth

In populations experiencing large changes in abundance, density-dependent regulation of growth might occur, because of reduced competition for food when stock size is smaller (Melvin and Stephenson, 2007). Before and during the collapse (from the late 1940s to the early 1980s), length-at-age increased markedly ( $\sim 2 \text{ cm}$  at age 3) for the Orkney/Shetland, Banks, and Downs components (Burd, 1984; Saville *et al.*, 1984). Although there was no relationship with stock biomass for the Orkney/Shetland component (Saville *et al.*, 1984), the increase in length-at-age was negatively correlated with the changes in stock biomass in the Banks and Downs components, suggesting a density-dependent effect. During the period of stock recovery, weight-at-age decreased (ICES, 2008a) and these declines were correlated significantly and inversely with stock size in Downs herring (Shin and Rochet, 1998). More generally, strong herring

year classes have grown poorly in recent years, suggesting that density-dependent mechanisms are operating (Dickey-Collas *et al.*, 2006; ICES, 2008a).

Whereas most of the variations in size-at-age observed can be explained by density-dependent mechanisms, there are also indications of environmental effects. Modelling the growth of juvenile herring during the period of stock decline (1961–1981), Heath *et al.* (1997) explained the interannual variability in growth rate (superimposed on the main trend of density-dependent growth) by environmental fluctuations (hydrographic conditions and plankton abundance). Shin and Rochet (1998) found that, in addition to effects of stock size, growth in Downs herring was affected by wind-induced turbulence in spring (through its effects on intensity and timing of plankton blooms). For juvenile and adult life stages, a meta-analysis of the effect of temperature and density-dependence on the growth rates of 15 North Atlantic herring stocks by Brunel and Dickey-Collas (2010) established that temperature significantly explained variations in growth between cohorts of North Sea herring from the mid-1980s. Cohorts experiencing warmer conditions throughout their lifetime attained higher growth rates, but had a shorter life expectancy and smaller asymptotic size. There is, however, no current model to disentangle the various causes of variability in historical growth.

## Stock reproductive potential

Consideration of stock reproductive potential (SRP) has provided insight into the dynamics of many stocks (Morgan, 2009; Nash *et al.*, 2009b). Female North Sea herring may mature when  $>25 \text{ cm}$  and the proportion of mature-at-age varies by year and cohort (Davidson, 2009), but first maturation is generally between ages 2 and 3. Fecundity-at-length for different spawning components has not changed significantly (Zijlstra, 1973; Burd and Howlett, 1974; Damme *et al.*, 2009). Similar to Norwegian spring-spawning (Kurita *et al.*, 2003; Kennedy *et al.*, 2010) and Icelandic summer-spawning herring (Óskarsson and Taggart, 2006), fecundity is down-regulated via atresia, depending on available energy reserves (Damme *et al.*, 2009). Because mass atresia has never been recorded, North Sea herring are not thought to skip spawning (Kennedy *et al.*, 2010).

The collapse, however, has influenced overall stock fecundity via changes in the relative abundance of different spawning components, each of which is characterized by different reproductive characteristics. Oocytes mature at a similar rate in autumn (northern) spawners and winter (southern) spawners, but the later spawning season in the latter prolongs gonad development, resulting in larger, but fewer eggs (Blaxter and Hempel, 1963; Damme *et al.*, 2009). Differences in egg size among spawning components have implications not only for reproductive output, as measured by SSB, but also for early survival and growth of larvae, because length-at-hatching, yolk-sac-stage duration, resilience to starvation, and even larval growth rates during early feeding have been positively correlated with egg size (Blaxter and Hempel, 1963; Morley, 1998; Morley *et al.*, 1999). Moreover, egg size in other herring stocks has been shown to be affected by maternal size (particularly among the younger ages; Blaxter and Hempel, 1963), whereas larval quality (in terms of growth rate and biochemical condition indices) is also influenced by paternal size (Panagiotaki and Geffen, 1992; Evans and Geffen, 1998; Høie *et al.*, 1999; Bang *et al.*, 2006). Therefore, variations in spawning-stock composition have the potential to be as important as

variations in SSB. A heterogeneous collapse of the spawning components will not only affect stock fecundity (one unit of SSB of autumn spawners produces 30% more eggs than one unit of SSB of winter spawners does), but might also influence early survival through the quality of progeny produced.

Sex ratio appears to have been relatively static at 50:50 and has not changed throughout the collapse and recovery (as it might in sexually dimorphic species), but age structure might also affect SRP, because demographic changes alter the relative proportions of recruit and repeat spawners. Blaxter and Hempel (1963) found that older and larger females spawn larger (and possibly better-quality) eggs. However, new studies indicate that herring fecundity (numbers of eggs) is regulated to maintain egg size (Almatar and Bailey, 1989; Kurita *et al.*, 2003; Óskarsson and Taggart, 2006). The effect of changes in the relative proportions of recruit to repeat spawners on larval production (and subsequent recruitment), therefore, remains unclear.

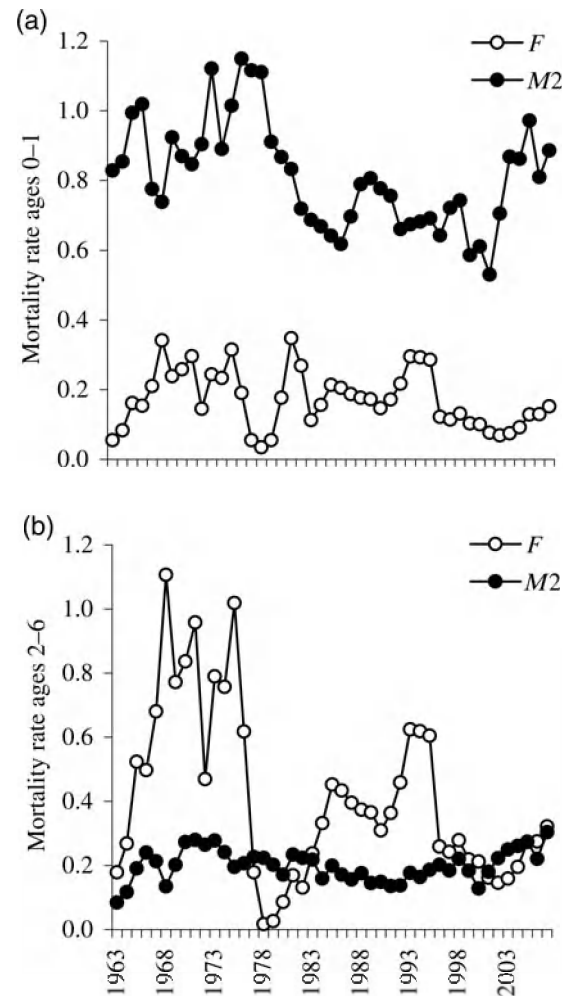
Mean age of the spawners, age diversity of the SSB, and proportion of repeat spawners have been found to correlate positively with the variability in recruitment, but not with recruitment in absolute terms (Brunel, 2010). This might be caused by a more heterogeneous spatial distribution of spawners (and an associated reduction in spawning strategies present) when there are fewer age groups, by compensatory mechanisms or coincident changes in the environment over the period of reduced biomass (Nash *et al.*, 2009a). As yet, SRP has not been shown to be more appropriate than SSB for operational usage in management.

### SSB and recruitment

Recruitment (Figure 1b) has largely preceded the trend in SSB (Figure 1a). Examining these dynamics in detail, Nash *et al.* (2009a) did not find any evidence of depensatory effects (i.e. reduced reproductive capacity at very low population densities). However, compensatory mechanisms (i.e. a negative correlation between number of recruits per spawner and stock size; Figure 1d) were evident. Compensation was stronger during the period of recovery than during the period of collapse, but the question has remained open whether this feature was linked directly to differences in stock dynamics during collapse and recovery or was caused by some environmental factor.

Recent work has also improved our understanding of when year-class strength is determined. Nash and Dickey-Collas (2005) demonstrated that events during the overwintering phase of the larvae (between the early and late stages: 10–30 mm) determine year-class strength. In extending this analysis, Payne *et al.* (2009) found support for this conclusion based on data collected during the recent recruitment failure (2002–2008). However, surveys of late-stage larvae have only been done since 1977, and they do not cover the full period of the collapse.

The complementary questions of how year-class strength is determined, and whether the recruitment for different spawning components is determined by the same processes, remain elusive (Cushing and Bridger, 1966). Recruitment, as measured in stock assessment, is a summation of the survivors of many spawning events across the North Sea. The different spawning grounds experience different environmental variability (Petitgas *et al.*, 2009). Therefore, searching for one environmental driver without accounting for spatial and temporal differences, and discounting the influence of parental factors, might be naïve. Although many hypotheses on environmental drivers have been proposed, there is as yet no explanation for the events that resulted



**Figure 4.** Mean fishing mortality rate ( $F$ ) and predation mortality rate ( $M2$ ) on (a) age groups 0–1 and (b) age groups 2–6; as estimated by the SMS model (ICES, 2008b), 1963–2007.

in the recruitment failures in either the mid-1970s or the 2000s. Variability in advection from the spawning grounds to the nursery grounds has long been thought to be a crucial factor (Corten, 1986; Bartsch *et al.*, 1989; Munk and Christensen, 1990), but unequivocal support for this hypothesis has not been forthcoming (Dickey-Collas *et al.*, 2009). Excessive removal of juveniles by industrial fisheries is thought to have impaired recruitment during the 1970s (Burd, 1978; Simmonds, 2007), but this cannot have been a problem during the recent recruitment failure, because fishing mortality on juveniles was much lower (Figure 4a). Physiological modelling of temperature-specific food requirements suggest that the spawning periods utilized are the most favourable ones for larval growth and survival (Hufnagl *et al.*, 2009). Indeed, changes in the planktonic system have been suggested as critical for recruitment (Cushing, 1992; Payne *et al.*, 2009), but clear evidence is lacking. Variations in bottom temperature near the spawning grounds (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009), predation by jellyfish (Lynam *et al.*, 2005), bottom-up processes (Hufnagl *et al.*, 2009), and competition with other species (Corten, 1986) have been proposed as mechanisms that also affect recruitment. Gröger *et al.* (2010), using only statistical inference, suggested

that recruitment could be predicted reasonably accurately with a forward lag of 2 and 5 years from North Atlantic climatic indices. Their model is not yet operational; it also has not been tested on recruitment data more recent than 2006. Other factors may also affect growth and survival of larval and juvenile herring (disease, storms, contaminants), but with some exceptions (Tjelmeland and Lindström, 2005), it has not been possible to include any environmental factors in recruitment models that can be used in routine assessments.

In terms of designing effective recovery plans, the collapse and subsequent recovery has contributed to a basic shift in thinking about recruitment dynamics. Stock–recruitment relationships are no longer being considered as stationary (Chaput *et al.*, 2005; Stige *et al.*, 2006), and for North Sea herring, a “recruitment–stock relationship” might be more meaningful (Gröger *et al.*, 2010). North Sea herring has provided clear evidence that the paradigm of a single stock–recruitment relationship that has prevailed for the past 60 years (Bailey and Steele, 1992) is clearly invalid. Instead, the interaction of stock and recruitment must be viewed as being more fluid, changing gradually or periodically depending on ecosystem changes (regime shifts). Recent work has begun to reflect this change in mindset (Nash *et al.*, 2009a; Payne *et al.*, 2009), which might help disentangle the multiple roles of climate and fishing in determining recruitment success in exploited stocks (Rijnsdorp *et al.*, 2009). In trying to project the productivity of North Sea herring forward, it is clear that recruitment adds the most uncertainty to the estimates of future yield and of the potential to reach biomass reference points within a specific time-frame (Dickey-Collas *et al.*, 2006; ICES, 2007).

### Multispecies interactions and ecosystem approach

The 100-fold reduction in herring biomass—from  $5 \times 10^6$  to  $<0.05 \times 10^6$  t in 1940s to 1970s—has undoubtedly affected the trophodynamic structure, functioning, and energy flows in the North Sea ecosystem (Jones, 1982). The complex role of herring must have varied accordingly. Essentially, herring forms a prey-to-predator (P2P) loop (Bakun and Weeks, 2006). As a prey, its role has been investigated using multispecies models, such as multispecies virtual population analysis (Vinther, 2001; Kempf *et al.*, 2006), stochastic multispecies (SMS) model (Lewy and Vinther, 2004), and Ecopath with Ecosim (Mackinson and Daskalov, 2007). The last authors estimated that the herring biomass in 1880 must have been  $5 \times 10^6$  t, very similar to the value for the late 1940s. The estimates of stock abundance from different multispecies models agree broadly, but tend to be slightly higher than those derived from single-species assessments are (ICES, 2008b). However, they are sensitive to assumptions about the abundance of mackerel and horse mackerel in the North Sea (ICES, 2007, 2008b), because juvenile herring are mostly eaten by these two predators. The predation mortality ( $M_2$ ) of 0- and 1-group herring has always been substantially higher than the fishing mortality (Figure 4a), but appears to have been highest around the time of the collapse. These  $M_2$  values tend to be lower and exhibit less interannual variability than those estimated for juvenile herring in the western Atlantic ( $M_2$  varies from 0.8 to 3.2; Tyrrell *et al.*, 2008).

Older herring (age 2+) are mainly eaten by gadoids and birds (ICES, 2008b), although historically, herring have also been the main prey of bluefin tuna (Mackinson, 2001), which disappeared from the North Sea in the early 1950s.  $M_2$  has been very stable and only immediately after the collapse and in recent years has

predation removed more 2+ herring than the fishery did (Figure 4b). Kenny *et al.* (2009) suggested that between 1983 and 1993, pelagic components of the ecosystem were predominantly controlled by top-down mechanisms (fishery), whereas thereafter these components mainly responded to bottom-up (environmental) influences.

As implied by the characterization of herring as a P2P loop, herring also play an important role as a predator (though often not included in multispecies models). The prey spectrum varies by size, location (Savage, 1937), season (Hardy, 1924), and year (Last, 1989). Larvae first feed on nauplii and microzooplankton (Checkley, 1982), juveniles subsequently shift to *Pseudocalanus*, *Paracalanus*, and *Temora* copepodites and small meroplankton, and adults feed on *Calanus*, *Temora*, *Oikopleura*, Schizopoda, Amphipoda, juvenile Ammodytidae, and fish eggs and larvae (Garrison *et al.*, 2001; Segers *et al.*, 2007). The effect as a predator on the system, therefore, varies with both stock size and stock distribution. When Daan *et al.* (1985) suggested that herring had little effect as a predator on North Sea cod egg production, the cod SSB was ~32% of the herring SSB. Today, it is ~2% and the interaction is likely to be quite different. There is a significant negative correlation ( $r^2 = 0.45$ ,  $p < 0.002$ ) between the biomass of herring and cod (SMS from 1963 to 2007), suggesting that herring and cod populations do not both exist at high biomass at the same time.

Because herring occupy both prey and predator positions, a collapse will release predation on its prey species and constrain the food resource of its predators, whereas a recovery has the opposite effects. Given its potential numerical dominance, the effect of these trajectories of decline and increase on many other organisms in the system could undoubtedly be large. However, it is questionable whether the outcomes of all of these interactions could be predicted during a collapse or recovery phase (Kempf *et al.*, 2006; ICES, 2008b). Although primary production is variable across the North Sea (Heath and Beare, 2008), the region as a whole can sustain a large herring population (Greenstreet *et al.*, 1997). Recent studies have considered a rebuilding of the stock up to  $1.5 \times 10^6$  t of SSB as a sensible target and yet the stock in the 1880s and 1940s is thought to have been up to  $5 \times 10^6$  t (Mackinson and Daskalov, 2007). Projecting the effect on the ecosystem of a recovery to this size would rely on extrapolations of information gained largely during a period of relatively low abundance. Although current production might support such a large stock in principle, the system would clearly change. Moreover, as managers try to reconcile commitments to single-species maximum sustainable yield (MSY) targets with the ecosystem approach, they must consider the appropriate management objectives for the North Sea ecosystem as a whole (Bakun *et al.*, 2009; Mackinson *et al.*, 2009). Questions arising are for instance: can the North Sea sustain simultaneously huge biomasses of herring and cod, as well as of all other commercially important species; do benthic species and birds benefit from a large herring stock; and what are the consequences for other forage fish and the fisheries exploiting these fish?

### The fishing industry

The recruitment failure in the 1970s has had a profound effect on the herring fishery, not only in the North Sea, but also in adjacent waters. Adequate management action was taken too late to prevent collapse of the spawning stock (Nichols, 2001), so rebuilding required draconian measures (a 5-year closure of all directed



fisheries) that have had a lasting effect on the entire industry (Burd, 1991; Corten, 1991).

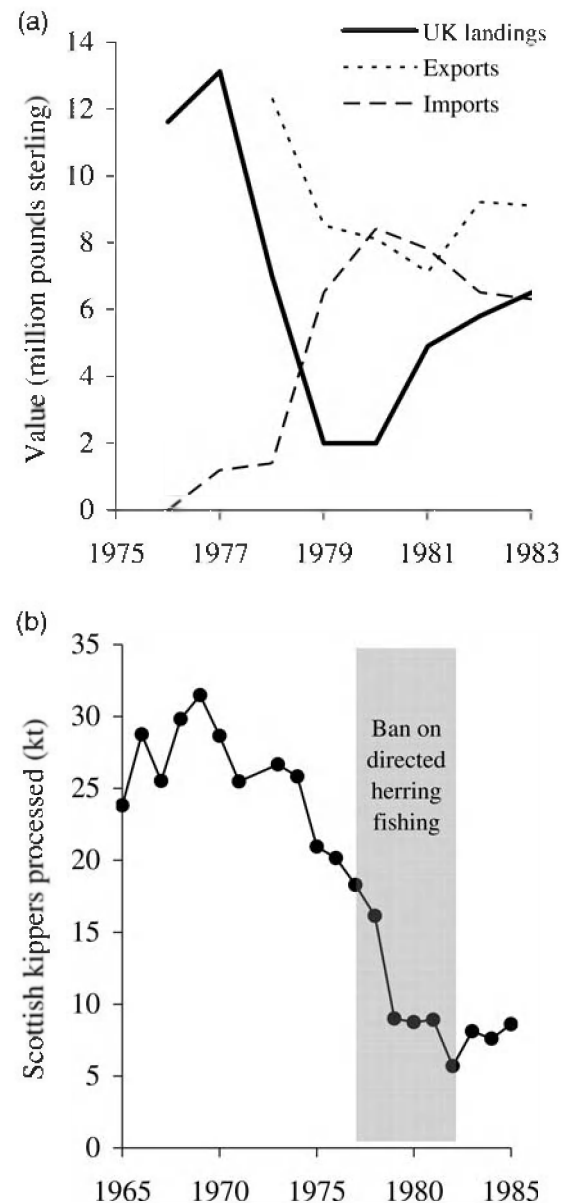
At the time and except the 12-mile coastal zone, the North Sea was still a free fishing area and the stock was exploited by fleets from at least 14 different nations (ICES, 1977). Despite the conclusions of the ICES Herring Assessment Working Group becoming more alarming each year (ICES, 1977), the North East Atlantic Fisheries Commission (NEAFC) had no mandate to impose measures unless they were agreed by all member states (Ackefors, 1977). Consequently, NEAFC could only agree on measures that constituted no real obstacle to any of the national fleets involved (Simmonds, 2007).

The reluctance of member states to agree on substantial catch reductions was fed by several factors. Because no international inspection system was in place, there was a widespread concern that catch restrictions would not be implemented by other states. Furthermore, the economic consequences of catch restrictions would have been severe. Although countries had seen their catches continuously decline, the prices markedly increased, thereby allowing fishing companies to survive. A drastic cut in the catches would have resulted in bankruptcy of many companies, with a consequent loss of employment. The anticipated effect was not only on the fishing fleets, but also on the markets for fish, including animal feeds. The entire industry would have suffered.

The reluctance to accept drastic measures should also be viewed in the historical political context (Bjørndal, 1988; Karlsdóttir, 2005). At the time, the herring fishery was an important economic activity in most countries bordering on the North Sea. Consequently, fisheries organizations had a strong influence on governmental decision-making. This contrasted with the lesser influence carried by the scientific advice in these circles. Uncertainty in the science was used to postpone decisions, and additional studies were initiated more as a device to delay action, rather than to find solutions (Simmonds, 2007).

On 1 January 1977, all countries around the North Sea extended their exclusive economic zones (EEZ) to 200 miles (Coull, 1991). The North Sea was no longer a free fishing area and suddenly national governments could introduce conservation measures within their own areas. Using this opportunity, the British government was the first (1 March 1977) to declare a total ban on all directed herring fisheries in the British EEZ (Coull, 1991). Other governments were slow to follow. The Dutch government objected to the British measure and in June 1977 sanctioned the start of the "maatjes" (the traditional cured herring) season. Dutch vessels entered the British EEZ based on traditional rights to fish and, promptly, two boats were arrested by the British Royal Navy. This resulted in an international confrontation that threatened to escalate. However, the scientific argument that a closure of the fishery was required finally persuaded all other countries to join in. By the end of June 1977, all directed herring fisheries in the North Sea came to a halt.

In general, the fishing ban was well respected, except in the Channel area where local trawlers continued to fish small quantities of spawning herring (ICES, 1982). In addition, herring could still be landed as a bycatch taken in other fisheries, and limited directed fishing did occur on this basis. It was during this time that the European Union agreed on a Common Fisheries Policy and took responsibility for the management in all community waters. Some fleets moved to exploit herring stocks in adjacent areas. Following reports of a recovery of the Downs component, a small TAC for the southern North



**Figure 5.** Economic effect of the ban on directed fishing for herring in the UK: (a) value of the UK herring landings, exports, and imports (1976–1983; Wood and Hopper, 1984); and (b) kipper processing in Scotland (1965–1985; source: Scottish Sea fisheries statistics).

Sea and Channel area was set in 1981 and 1982. The ban on directed fishing in other areas of the North Sea was lifted in June 1983.

Because of the ban, a large number of shipowners went bankrupt. The Dutch fleet had 50 herring trawlers at the time of the closure and only 12 when the ban was lifted. Similar fleet reductions happened in other countries. The German canning industry was hit hard by the ban, and fish processors in Scotland also suffered. The UK started importing herring (Figure 5a). The lack of supply, exacerbated by a closure of the herring fishery west of Scotland in 1979, also resulted in a change in consumer behaviour. In the UK, the kipper (smoked herring) became less popular (Figure 5b). When the fishery was resumed in 1983, a large part of the traditional market for

herring had disappeared. Prices were low, and some of the first catches had to be sent for reduction to fishmeal.

After the closure, Dutch traders sought new suppliers of their traditional “maatjes”. These were found in Denmark and Norway, where fishing in the Skagerrak and Kattegat was allowed to continue, because of the mixed catch with spring spawners. Scandinavian fishers soon learned how to serve the Dutch market and after the North Sea fishery was reopened, the Dutch suppliers had permanently lost the market. In the early 1980s, more than 50% of the UK herring catch was sold to “Klondikers” (factory processing vessels from eastern Europe), because no local buyers could be found (Wood and Hopper, 1984).

In other aspects, however, the herring ban also had favourable effects. When the vessels could no longer fish for North Sea herring, some switched to mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) west of the British Isles. These species could not be preserved in brine (as was done traditionally with herring), but had to be frozen on board. Therefore, ship owners started to convert their vessels into freezer trawlers. These vessels turned out to be very successful, not only for mackerel and for horse mackerel, but later also for herring. In this way, the herring ban paved the way for a contemporary pelagic fishing fleet.

### Assessment, projections, and predictions

North Sea autumn-spawning herring have been assessed by ICES since the 1960s. Although registration of landings started around the beginning of the 20th century (Saville and Bailey, 1980), data collection among countries remained inconsistent up to the 1980s, and methods for analytical assessments were still under development (Simmonds, 2009). Nevertheless, the lack of analytical assessments did not impede scientists from warning of stock collapse. From the 1980s on, the basic data needed were routinely compiled and analytical assessments were done annually, resulting in gradually more sophisticated advice (ICES, 2008a). There is always a degree of uncertainty associated with such advice. This arises from the input data, as well as from the assumptions, choice, and fitting of the assessment and projection model used. Therefore, addressing uncertainty explicitly has become part of the assessment process.

Over the past 5 years, projections of SSB for 1 year ahead have been, on average, within 4% of the biomass estimate in the assessment 1 year later, without a directional bias. An example of uncertainty caused by assumptions can be highlighted by the influence of the 2000-year class in the projections. This year class grew slowly and matured at a later age than usual and this had not been foreseen. The assumption of business as usual resulted in a subsequent actual decline of 25% in SSB compared with the projected value, 1 year ahead. Although the short-term projection of SSB was affected, the estimates of numbers of herring were not, and the year class fully matured in the medium term. Therefore, the discrepancy was much less.

Over the time-series of providing advice, projections for 2 years ahead have been, on average, 25% different from the assessment estimates 2 years later (when accounting for deviations between advised and actual TACs). Large deviations generally arose from differences between projected (average) and actual recruitment. Therefore, assumptions about future recruitment are important (ICES, 2007). The projections incorporate a 0-group recruitment index, which has allowed warnings of forthcoming years of poor

recruitment (Payne et al., 2009), but does not provide information for the expected SSB more than 2 or 3 years ahead. Nevertheless, the medium-term projections have conformed overall to the actual recovery trajectory (Simmonds, 2007), and SSB recovery has been within the 95% confidence intervals of the projections.

Since the early 1990s, the agreed TAC has broadly followed the trends in advice. Until 1996, however, the TAC overshoot—the difference between the estimated catch and the TAC—averaged approximately +30%. This TAC overshoot, in combination with reduced recruitment, resulted in an increase in fishing mortality in the mid-1990s (Figure 1c). In 1996, a management plan that incorporated a harvest control rule was put in place (Simmonds, 2007). Operational versions have varied, because the plan is reviewed and adapted approximately every 3 years, but since its introduction, the TAC overshoot has been reduced to approximately +10%. The different versions of the plan have always been founded on the precautionary approach (ICES, 1998b) and yet the stock again declined below the biomass threshold in the mid-2000s. This was primarily caused by a series of poor recruitments, but also by a failure to comply with the management plan. Despite warnings that substantial reductions in TAC were required to maintain compliance, smaller cuts were enacted. Consequently, even larger reductions had to be imposed in subsequent years to comply with the target fishing mortalities of the management rule.

Overall, the stock appears to be assessed and managed reasonably well. However, it is questionable whether the current management plan is the most effective one in the longer term, in either maximizing yield or maintaining biomass targets, because it does not consider interactions with other species or stock structure. This again emphasizes the need to understand better the dynamics of the wider ecosystem and to monitor the variability among stock components (Schmidt et al., 2009; Bierman et al., 2010) and mixing with other stocks (Kell et al., 2009).

However, breaking up a consistent assessment and management approach carries many dangers. Any move to more spatially resolved management should be carefully evaluated beforehand, because it requires more process knowledge and/or the ability to identify adequately the diverse components in mixed catches, as well as an understanding of how inclusion of that knowledge is going to affect the entire management strategy (De Oliveira et al., 2006).

### Lessons learned

The lessons learned for management from the collapse and recovery can be split in three main topics: (i) the underlying biology as it affects management and exploitation; (ii) the effects of exploitation on stock structure; and (iii) the role of herring in the North Sea ecosystem.

- (i) Recruitment is intrinsically variable and, in combination with variability in predation mortality on adults, can yield natural variation in stock abundance by at least a factor of 4. Management aimed at MSY fishing mortality targets implies interannual variation in TACs and managers and fishers must accept this variability in supply and restrain the catches accordingly. Setting TACs appears to be a suitable mechanism for doing so (if catches are closely monitored). Greater understanding of the properties and causes of recruitment variability should increase predictability, which would help taking appropriate management decisions. It might also allow simulations of management scenarios that



account for longer-term environmental change, thus aiding the development of more robust management plans.

- (ii) So far, SSB appears to have operated well as a proxy for SRP and the evidence obtained during the collapse (learning by mistakes) clearly indicates that recruitment is impaired if SSB is not maintained above some critical threshold. Nevertheless, series of poor year classes may still occur, even when SSB is relatively large. Maintaining sufficient SSB can be accomplished by either reducing TACs as the biomass declines or setting a fixed TAC that is sufficiently low. From a precautionary point of view, there is a need to ensure spatial diversity of spawning components. Although past experience suggests that this spatial aspect of stock structure has not been critical to reproductive potential of the stock as a whole, this issue would become relevant if the fisheries would target specific components or if strong spatial patterns in recruitment success were observed. Given a limit reference level of SSB, density-dependent effects on growth, maturation schedules and genetic diversity will be relatively unimportant in management terms. However, spatially explicit monitoring of the development of different spawning components remains a priority for the science.
- (iii) The role of herring in the North Sea ecosystem is difficult to evaluate quantitatively. Fisheries science cannot at present provide management advice and predictions of herring that account for this role, especially when extrapolating beyond the range of recent observations. At the ecosystem level, the behaviour and interactions of species are adaptive and complex. However, management should always endeavour to maintain recruitment, a certain biomass of spawning adults and spatial diversity, to sustain the ecosystem services of herring.

In conclusion, monitoring spawning biomass (total and by component), compliance with a simple harvest control rule, and an enforced quota regime should deliver most of the management requirements for preventing future collapse. However, this is only valid as long as the environment maintains the fluctuations in productivity at levels observed during the past 100 years. This condition of long-term stationarity in the North Sea system is—in contrast to the situation for Norwegian spring-spawning herring for instance (Torensen and Østvedt, 2000)—supported by the apparent match between the projections of stock development in the 1980s and the observed recovery of the stock.

We can infer from this review that hypothesis-driven research could contribute meaningfully to management through improved confidence in and increased transparency of the advice. At present, we cannot predict the effects of collapse or recovery of a single stock on the ecosystem as a whole, nor can we predict the direct and indirect effects of large environmental change, such as global warming, on a single stock. Therefore, North Sea herring is likely to remain a continuing source of both inspiration and frustration to researchers for many years to come.

## Acknowledgements

This review was only possible because of the hard work and labour of the ICES Herring Assessment Working Group for the Area South of 62°N; all its members over the past 50 years are thanked for their contribution. The study was partly funded through the EC research, technological and demonstration

(RTD) programme “Specific Support to Policies” (SSP-4-FISH-Area 8.1. B.1.3: Task 2. Understanding the mechanisms of stock recovery). It does not necessarily reflect the views of the EC and in no way anticipates its future policy. The manuscript was greatly improved through reviews by Niels Daan and Steve Cadrin.

## References

- Ackefors, H. 1977. Production of fish and other animals in the sea. *Ambio*, 6: 192–200.
- Almatar, S. M., and Bailey, R. S. 1989. Variation in the fecundity and egg weight of herring (*Clupea harengus* L.) Part I. Studies in the Firth of Clyde and northern North Sea. *Journal du Conseil International pour l'Exploration de la Mer*, 45: 113–124.
- Andersen, K. H., and Brander, K. 2009. Expected rate of fisheries-induced evolution is slow. *Proceedings of the National Academy of Sciences of the USA*, 106: 11657–11660.
- Bailey, R. S., and Steele, J. H. 1992. North Sea herring fluctuations. In *Climate Change, Climate Variability and Fisheries*, pp. 213–230. Ed. by M. Glantz. Cambridge University Press, Cambridge.
- 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. *Bulletin of Marine Ecology*, 8: 21–52.
- Bakun, A., Babcock, E. A., and Santora, C. 2009. Regulating a complex adaptive system via its wasp-waist: grappling with ecosystem-based management of the New England herring fishery. *ICES Journal of Marine Science*, 66: 1768–1775.
- 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.
- Bang, A., Grønkjær, P., Clemmesen, C., and Høie, H. 2006. Parental effects on early life history traits of Atlantic herring (*Clupea harengus* L.) larvae. *Journal of Experimental Marine Biology and Ecology*, 334: 51–63.
- Bartsch, J., Brander, K., Heath, M., Munk, P., Richardson, K., and Svendsen, E. 1989. Modelling the advection of herring larvae in the North Sea. *Nature*, 340: 632–636.
- Beacham, T. D. 1987. Variation in length and age at sexual maturity of Atlantic groundfish—a reply. *Environmental Biology of Fishes*, 19: 149–153.
- Bierman, S. M., Dickey-Collas, M., van Damme, C. J. C., van Overzee, H. M. 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.
- Bjerkas, P. 1917. Age, maturity and quality of North Sea herrings during the years 1910–13. Report of Norwegian Fisheries and Marine Investigations, III(1). 119 pp.
- Bjørndal, T. 1988. The optimal management of North Sea herring. *Journal of Environmental Economics and Management*, 15: 9–29.
- Blaxter, J. H. S., and Hempel, G. 1963. The influence of egg size on herring larvae, *Clupea harengus* L. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, 28: 211–240.
- Brunel, T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. *ICES Journal of Marine Science*, 67: 1921–1930.
- Brunel, T., and Dickey-Collas, M. 2010. Effects of temperature and population density on Atlantic herring von Bertalanffy growth parameters: a macro-ecological analysis. *Marine Ecology Progress Series*, 405. doi:10.3354/meps08491.
- 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: 04.
- 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. 1991. The North Sea herring fishery: an abrogation of management. In *Proceedings of the International Herring Symposium*, Anchorage, Alaska, 23–25 October 1990, pp. 1–22. Ed. by V. Wespestad, J. Collie, and E. Collie. 9th Lowell Wakefield Fisheries Symposium. University of Alaska Sea Grant, AK-SG-91-01, Fairbanks. 672 pp.
- 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.
- Chaput, G., Legault, C. M., Reddin, D. G., Caron, F., and Amiro, P. G. 2005. Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. *ICES Journal of Marine Science*, 62: 131–143.
- Checkley, D. M. 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. *Marine Ecology Progress Series*, 9: 245–253.
- Clausen, L. A. W., Bekkevold, D., Hatfield, E. M. C., and Mosegaard, H. 2007. Application and validation of otolith microstructure as a stock identification method in mixed Atlantic herring (*Clupea harengus*) stocks in the North Sea and western Baltic. *ICES Journal of Marine Science*, 64: 377–385.
- Corten, A. 1986. On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972–1978. *Journal du Conseil International pour l'Exploration de la Mer*, 42: 281–294.
- Corten, A. 1991. Management of North Sea herring in the 1980s. In *Proceedings of the International Herring Symposium*, Anchorage, Alaska, 23–25 October 1990, pp. 477–490. Ed. by V. Wespestad, J. Collie, and E. Collie. 9th Lowell Wakefield Fisheries Symposium. University of Alaska Sea Grant, AK-SG-91-01, Fairbanks. 672 pp.
- Corten, A. 1999. The reappearance of spawning Atlantic herring (*Clupea harengus*) on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2051–2061.
- Corten, A. 2001. Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. *Fisheries Research*, 50: 189–204.
- Coull, J. R. 1991. The North Sea herring fishery in the twentieth century. In *The Development of Integrated Sea Use Management*, pp. 122–138. Ed. by H. D. Smith, and A. Vallega. Routledge, New York.
- Cushing, D. H. 1992. A short history of the Downs stock of herring. *ICES Journal of Marine Science*, 49: 437–443.
- Cushing, D. H., and Bridger, J. P. 1966. The stock of herring in the North Sea, and changes due to fishing. *Fishery Investigations*, London, Series II, 25: 1–123.
- Daan, N., Rijnsdorp, A. D., and Overbeek, 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.
- Damme, C. J. G., van Dickey-Collas, M., Rijnsdorp, A. D., and Kjesbu, O. S. 2009. Fecundity, atresia and spawning strategies in Atlantic herring. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 2130–2141.
- Davidson, D. 2009. Spatial and temporal variability in fat content and maturation of North Sea herring, *Clupea harengus* L. PhD thesis, University of Aberdeen.
- De Oliveira, J. A. A., Roel, B. A., and Dickey-Collas, M. 2006. Investigating the use of proxies for fecundity to improve management advice for western horse mackerel *Trachurus trachurus*. *ICES Journal of Marine Science*, 63: 25–35.
- Dickey-Collas, M., Bolle, L. J., van Beek, J. K. L., and Erftemeijer, P. L. A. 2009. 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., Skagen, D., and Simmonds, J. 2006. Harvest control rules and changing productivity: the working example of North Sea herring. ICES Document CM 2006/R: 05. 8 pp.
- Dunlop, E. S., Enberg, K., Jørgensen, C., and Heino, M. 2009. Toward Darwinian fisheries management. *Evolutionary Applications*, 2: 245–259.
- Dutil, J. D., and Brander, K. 2003. Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production. *Fisheries Oceanography*, 12: 502–512.
- Enberg, K., and Heino, M. 2007. Fisheries-induced life history changes in herring. ICES Document CM 2007/E: 23. 12 pp.
- Engelhard, G. H., and Toresen, R. in press. Case study on fisheries-induced adaptive change in Norwegian spring-spawning herring. In *Fisheries-Induced Adaptive Change*. Ed. by U. Dieckmann, O. R. Godø, M. Heino, and J. Mork. Cambridge University Press, Cambridge, UK.
- Ernande, B., Dieckmann, U., and Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271: 415–423.
- Evans, J. P., and Geffen, A. J. 1998. Male characteristics, sperm traits, and reproductive success in winter-spawning Celtic Sea Atlantic herring *Clupea harengus*. *Marine Biology*, 132: 179–186.
- Garrison, L. P., Micheals, W., Link, J. S., and Fogarty, M. J. 2001. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 2455–2469.
- Greenstreet, S. P. R., Bryant, A. D., Broekhuizen, N., Hall, S. J., and Heath, M. R. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES Journal of Marine Science*, 54: 243–266.
- Gröger, J. P., Kruse, G. H., and Rohlf, N. 2010. Slave to the rhythm: how large-scale climate cycles trigger herring (*Clupea harengus*) regeneration in the North Sea. *ICES Journal of Marine Science*, 67: 454–465.
- 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. *Fishery Investigations*, Series 2, 7(3). 140 pp.
- Hauser, L., Adcock, G. J., Smith, P. J., Ramirez, J. H. B., and Carvalho, G. R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences of the USA*, 99: 11742–11747.
- Heath, M. R., and Beare, D. J. 2008. New primary production in north-west European shelf seas, 1960–2003. *Marine Ecology Progress Series*, 363: 183–203.
- 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.
- Heino, M. 1998. Management of evolving fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1971–1982.
- Hoarau, G., Boon, E., Jongma, D. N., Ferber, S., Pálsson, J., van der Veer, H. W., Rijnsdorp, A. D., et al. 2005. Low effective population size and evidence for inbreeding in an overexploited flatfish, plaice (*Pleuronectes platessa* L.). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 272: 497–503.
- Høie, H., Folkvord, A., and Johannessen, A. 1999. The influence of different parental combinations and incubation temperature on the RNA and DNA content of herring larvae at hatching: a pilot study. *Journal of Fish Biology*, 55 (Suppl. A): 110–118.

- Hufnagl, M., Peck, M. A., Dickey-Collas, M., Nash, R. D. M., and Pohlmann, T. 2009. Climate-driven changes in the recruitment of North Sea herring: bottom-up control on the survival of early life stages identified using a biophysical individual-based model. ICES Document CM 2009/E: 09. 15 pp.
- Hutchings, J. A. 2000. Collapse and recovery of marine fishes. *Nature*, 406: 882–885.
- Hutchinson, W. F., van Oosterhout, C., Rogers, S. I., and Carvalho, G. R. 2003. Temporal analysis of archived samples indicates marked genetic changes in declining North Sea cod (*Gadus morhua*). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270: 2125–2132.
- ICES. 1977. Assessment of herring stocks south of 62°N, 1973–1975. ICES Cooperative Report Series, 60. 117 pp.
- ICES. 1982. Report of the Herring Assessment Working Group South of 62°N (HAWG). ICES Document CM 1982/Assess: 17. 127 pp.
- ICES. 1998a. Report of the Study Group on Stock–Recruitment Relationships for North Sea Autumn-spawning Herring. ICES Document CM 1998/D: 02. 60 pp.
- ICES. 1998b. Report of the Study Group on the Precautionary Approach to Fisheries Management, 3–6 February 1998, Copenhagen. ICES Document CM 1998/Assess: 10, ref D.
- ICES. 2007. Report of the Workshop on the Integration of Environmental Information into Fisheries Management Strategies and Advice (WKEFA). ICES Document CM 2007/ACFM: 25. 182 pp.
- ICES. 2008a. Report of the Herring Assessment Working Group South of 62°N (HAWG). ICES Document CM 2008/ACOM: 02. 601 pp.
- ICES. 2008b. Report of the Working Group on Multispecies Assessment Methods (WGSAM). ICES Document CM 2008/RMC: 06. 113 pp.
- Jones, R. 1982. Species interactions in the North Sea. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 59: 48–63.
- Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., *et al.* 2007. Managing evolving fish stocks. *Science*, 318: 1247–1248.
- Karlsdóttir, H. 2005. Fishing on common grounds: the consequences of unregulated fisheries of North Sea herring in the postwar period. PhD thesis, Göteborg University. 221 pp.
- Kell, L. T., Scott, R., and Hunter, E. 2004. Implications for current management advice for North Sea plaice: part I. Migration between the North Sea and English Channel. *Journal of Sea Research*, 51: 287–299.
- Kell, L. T., Nash, R. D. M., Dickey-Collas, M., Pilling, G. M., Hintzen, N. H., and Roel, B. A. 2009. Lumpers or splitters? Evaluating recovery and management plans for metapopulations of herring. *ICES Journal of Marine Science*, 66: 1776–1783.
- Kempf, A., Floeter, J., and Temming, A. 2006. Decadal changes in the North Sea food web between 1981 and 1991—implications for fish stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 2586–2602.
- Kennedy, J., Skjæraasen, J. E., Nash, R. D. M., Thorsen, A., Slotte, A., Hansen, T., and Kjesbu, O. S. 2010. Do capital breeders like Atlantic herring (*Clupea harengus* L.) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation? *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 16–27.
- 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.
- Kuparinen, A., and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution*, 22: 652–659.
- Kurita, Y., Meier, S., and Kjesbu, O. S. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturity cycle. *Journal of Sea Research*, 49: 203–219.
- Last, J. M. 1989. The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. *Journal of Fish Biology*, 34: 489–501.
- Law, R., and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology*, 3: 343–359.
- Lewy, P., and Vinther, M. 2004. A stochastic age–length-structured multispecies model applied to North Sea stocks. ICES Document CM 2004/FF: 20. 33 pp.
- Lynam, C. P., Heath, M. R., Hay, S. J., and Brierley, A. S. 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series*, 298: 157–167.
- MacCall, A. D. 1990. *Dynamic Geography of Marine Fish Populations*. Washington Sea Grant, University of Washington Press, Washington. 153 pp.
- Mackinson, S. 2001. Representing trophic interactions in the North Sea in the 1880s, using the Ecopath mass-balance approach. In *Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses*, pp. 35–98. Ed. by S. Guenette, V. Christensen, and D. Pauly. Fisheries Centre Research Reports, 9 (4).
- Mackinson, S., and Daskalov, G. 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. Science Series Technical Report, Cefas Lowestoft, 142. 196 pp.
- Mackinson, S., Deas, B., Beveridge, D., and Casey, J. 2009. Mixed-fishery or ecosystem conundrum? Multispecies considerations inform thinking on long-term management of North Sea demersal stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 1107–1129.
- 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.
- Mariani, S., Hutchinson, W. F., Hatfield, E. M. C., Ruzzante, D. E., Simmonds, E. J., Dahlgren, T. G., Andre, C., *et al.* 2005. North Sea herring population structure revealed by microsatellite analysis. *Marine Ecology Progress Series*, 303: 245–257.
- McPherson, A. A., Stephenson, R. L., O'Reilly, P. T., Jones, M. W., and Taggart, C. T. 2001. Genetic diversity of coastal Northwest Atlantic herring populations: implications for management. *Journal of Fish Biology*, 59(Suppl. A): 356–370.
- McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries*, 7: 297–329.
- 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.
- Morgan, M. J. 2009. Integrating reproductive biology into scientific advice for fisheries management. *Journal of Northwest Atlantic Fishery Science*, 41: 37–51.
- Morley, S. A. 1998. Environmental and parental influences on the body size of N.E. Atlantic herring, *Clupea harengus*, larvae. PhD thesis, University of Liverpool. 140 pp.
- Morley, S. A., Batty, R. S., Geffen, A. J., and Tytler, P. 1999. Egg size manipulation: a technique for investigating maternal effects on the hatching characteristics of herring. *Journal of Fish Biology*, 55(Suppl. A): 233–238.
- Munk, P., and Christensen, V. 1990. Larval growth and drift pattern and the separation of herring spawning groups in the North Sea. *Journal of Fish Biology*, 37: 135–148.
- 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. 2009a. Stock and recruitment in North Sea herring (*Clupea harengus*); compensation and depensation in the population dynamics. *Fisheries Research*, 95: 88–97.
- Nash, R. D. M., Kjesbu, O. S., Trippel, E. A., Finden, H., and Geffen, A. J. 2009b. Potential variability in the paternal contribution to stock reproductive potential of Northeast Arctic cod (*Gadus morhua*). *Journal of Northwest Atlantic Fishery Science*, 41: 71–83.
- Nichols, J. H. 2001. Management of North Sea herring and prospects for the new millennium. In *Herring 2000: Expectations for a New Millennium*, pp. 645–665. Ed. by F. Funk, J. Blackburn, D. Hay, A. J. Paul, R. Stephenson, R. Toresen, and D. Witherell. 18th Lowell Wakefield Fisheries Symposium, Anchorage, Alaska, 23–26 February 2000. University of Alaska Sea Grant, AK-SG-01-04, Fairbanks. 800 pp.
- Óskarsson, G. J., and Taggart, C. T. 2006. Fecundity variation in Icelandic summer-spawning herring and implications for reproductive potential. *ICES Journal of Marine Science*, 63: 493–503.
- Panagiotaki, P., and Geffen, A. J. 1992. Parental effects on size variation in fish larvae. *Journal of Fish Biology*, 41: 37–42.
- Payne, M. R. 2010. Mind the gaps: a new analysis gives insight into the dynamics of the North Sea herring spawning components. *ICES Journal of Marine Science*, 67: 1939–1948.
- Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaus, 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.
- 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. 12 pp.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. G. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361–395.
- Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, 66: 1570–1583.
- Savage, R. E. 1937. The food of North Sea herring 1930–1934. MAFF Fisheries Investigations, London, Series II, 15(5). 60 pp.
- Saville, A., and Bailey, R. S. 1980. The assessment and management of the herring stocks in the North Sea and to the west of Scotland. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 177: 112–142.
- Saville, A., Bailey, R. S., and Black, M. 1984. Variations in growth of herring in the Shetland area and to the west of Scotland in relation to population abundance. *ICES Document CM 1984/H*: 61.
- 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.
- Segers, F. H. I. D., Dickey-Collas, M., and Rijnsdorp, A. D. 2007. Prey selection by North Sea herring (*Clupea harengus*), with special reference to fish eggs. *ICES Journal of Marine Science*, 64: 60–68.
- Shin, Y. J., and Rochet, M.-J. 1998. A model for the phenotypic plasticity of North Sea herring growth in relation to trophic conditions. *Aquatic Living Resources*, 11: 315–324.
- 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.
- Simmonds, E. J. 2009. Evaluation of the quality of the North Sea herring assessment. *ICES Journal of Marine Science*, 66: 1814–1822.
- Smith, P. J. 1994. Genetic diversity of marine fisheries resources: possible impacts of fishing. *FAO Fisheries Technical Paper*. 53 pp.
- Smith, P. J., Francis, R. I. C. C., and McVeagh, M. 1991. Loss of genetic diversity due to fishing pressure. *Fisheries Research*, 10: 309–316.
- Stige, L. C., Ottersen, G., Brander, K., Chan, K.-S., and Stenseth, N. C. 2006. Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Marine Ecology Progress Series*, 325: 227–241.
- Tjelmeland, S., and Lindstrøm, U. 2005. An ecosystem element added to the assessment of Norwegian spring-spawning herring: implementing predation by minke whales. *ICES Journal of Marine Science*, 62: 285–294.
- 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.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *Bioscience*, 45: 759–771.
- Tyrrell, M. C., Link, J. S., Moustahfid, H., and Overholtz, W. J. 2008. Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem using multispecies virtual population analysis. *ICES Journal of Marine Science*, 65: 1689–1700.
- Vinther, M. 2001. *Ad hoc* multispecies VPA tuning applied for the Baltic and North Sea fish stocks. *ICES Journal of Marine Science*, 58: 311–320.
- Wood, J. D., and Hopper, A. G. 1984. A report on the UK herring fisheries in the 1980s. Sea Fish Industry Authority Technical Report, 245. 50 pp.
- Zijlstra, J. J. 1973. Egg weight and fecundity in the North Sea herring (*Clupea harengus*). *Netherlands Journal of Sea Research*, 6: 173–204.

doi:10.1093/icesjms/fsq033