

Recruitment in a changing environment: the 2000s North Sea herring recruitment failure

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Environmentally induced change appears to be impacting the recruitment of North Sea herring (*Clupea harengus*). Despite simultaneously having a large adult population, historically low exploitation, and Marine Stewardship Council accreditation (implying sustainability), there have been an unprecedented 6 sequential years of poor juvenile production (recruitment). Analysis suggests that the poor recruitment arises during the larval overwintering phase, with recent survival rates greatly reduced. Contemporary warming of the North Sea has caused significant changes in the plankton community, and a recently identified regime shift around 2000 shows close temporal agreement with the reduced larval survival. It is, therefore, possible that we are observing the first consequences of this planktonic change for higher trophic levels. There is no indication of a recovery in recruitment in the short term. Fishing mortality is currently outside the agreed management plan, and forecasts show a high risk of the stock moving outside safe biological limits soon, potentially precipitating another collapse of the stock. However, bringing the realized fishing mortality back in line with the management plan would likely alleviate the problem. This illustrates again that recruitment is influenced by more than just spawning-stock biomass, and that changes in other factors can be of equal, or even greater, importance. In such dynamically changing environments, recent management success does not necessarily guarantee future sustainability.

Keywords: environmental change, North Sea herring, recruitment, regime shift, sustainability.

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Introduction

The size of an exploited fish population is determined by the balance of losses from natural mortality, predation, and fishing, and the gains from the addition of new individuals to the population. The management of most fish species is centred on the concept of a stock, where the exchange of individuals with other stocks is negligible, so the only source of new individuals is through the reproductive process (recruitment). Therefore, recruitment places a firm constraint on the number of individuals that can potentially grow to maturity, and hence on the number of individuals (or biomass) that can be removed from the stock in a sustainable manner. Large interannual variations in recruitment are common, especially in pelagic fish, but longer term directional changes lasting for decades or more are also well documented, e.g. the Russell cycle (Cushing, 1995) and Pacific sardine, *Sardinops*

sagax, fluctuations (Watanabe, 2007). Short-term variability can mask such long-term changes, often making it impossible to identify such a change until well after the event. Furthermore, management structures are commonly based around the assumption that the system is stationary, i.e. the assumption that the past is representative of the future. The consequences of undetected reductions in stock productivity, along with sustained heavy exploitation, can therefore be severe, causing a healthy stock to collapse within a few years (Torensen and Østvedt, 2000). Here, we report evidence that a directional change in recruitment recently occurred in North Sea autumn-spawning herring (*Clupea harengus*).

The autumn-spawning herring stock in the North Sea is often considered a classic model fish stock because of its long history of exploitation, collapse, and recovery, and the close scrutiny with which these changes have been studied. Historical records

show that fishing for herring has been carried out in the North Sea since the first century A.D. It was the largest European sea fishery at the beginning of the 20th century, and one of the first to be studied across the whole North Sea community under the auspices of the newly created International Council for the Exploration of the Sea (ICES). Catch data have been compiled since the 1940s, giving insight into past population sizes and dynamics, and the stock has been the subject of scrutiny for formal assessment and management under ICES since the 1970s. The spawning-stock biomass (SSB) has ranged from a high of 5 million tonnes in the late 1940s (ICES, 1998) to <50 000 t following the stock collapse in the late 1970s (ICES, 2008a). Recently, the stock reached a 40-year high SSB of 1.8 million tonnes, a result of successful management from the mid-1990s (Simmonds, 2007; ICES, 2008a). Recognition of this success came with the awarding of Marine Stewardship Council (MSC) accreditation in 2006, implying that the stock is well managed and exploited in a sustainable manner. However, the past six year classes (2002–2007) have been consistently poor despite high biomass levels, an unprecedented occurrence for North Sea herring. Consequently, the SSB in recent years (2005–2007) has begun to decline. Here, we examine the sequence of poor recruitment in detail, comparing recent and historical patterns, and analyse where, in the life cycle, the poor recruitment is determined. We then consider candidate mechanisms that could be driving the phenomenon, and implications for the future exploitation of this stock. Finally, we discuss the implications of such changes in a broader context.

Material and methods

Estimates of SSB, number of recruits (at 6 months old), and fishing mortality were obtained from the most recent stock assessment (ICES, 2008a). The Ricker, Beverton–Holt, and hockey-stick (segmented regression) stock–recruitment relationships (SRRs) were fitted to the estimates of SSB and recruitment using the Fisheries library in *R* (Kell *et al.*, 2007), assuming a lognormal error structure. The hockey-stick relationship gave the most meaningful fit, as judged by the Akaike Information Criterion (Quinn and Deriso, 1999). Natural logarithm (ln) residuals were then calculated from the fitted model and used in the analysis. However, the trends in the residuals were similar for all three models, and the choice of stock–recruitment model does not greatly influence the conclusions. This approach assumes that recruitment is driven by stock size (an SRR) and not the inverse, where stock size is driven primarily by recruitment (a recruitment–stock relationship), as one would expect with short-lived species.

A Paulik diagram (Paulik, 1973) was used to examine the relative importance of each life stage in determining recruitment strength. The method plots observations of year-class strength at different points in the life cycle in a single figure, visually distinguishing inter-annual differences in survival. North Sea herring is a stock that is particularly amenable to such analysis, because multiple surveys cover its early life stages. The adults spawn along the east coast of Great Britain, and around Orkney and Shetland, from August to December, and the early larval stages, i.e. <10–11 mm long, are characterized by the multiplicative larvae abundance index (MLAI; Gröger *et al.*, 2001; ICES, 2008a), based on a series of larval surveys performed in the area throughout the spawning period. The late stages of the larval phase are observed in February by a survey covering the entire North Sea, and are characterized by the MIK 0-group index (ICES, 2008a). The International Bottom Trawl Survey (IBTS), performed concurrently with the MIK

survey, gives an index of cohort strength at age 1-winter ring (wr) juveniles (ICES, 2008a). A Paulik diagram analysis based on these datasets has been used previously with North Sea autumn-spawning herring (Nash and Dickey-Collas, 2005): here we update this analysis by adding an additional 7 years of data covering the period of reduced recruitment.

Results

The residuals to an SRR provide a measure of the productivity of a fish stock relative to some expected recruitment at a given stock size. Insight into the factors influencing the reproductive dynamics of a stock can therefore be gained by comparison of the time-series of SSB (Figure 1a), recruitment (Figure 1b), and fishing mortality (Figure 1c) with the relative productivity (SRR residuals; Figure 1d). Four distinct phases in the history of this stock are visually apparent. From 1965 to 1977, fishing mortality was high and recruitment declined markedly, leading to the stock collapse of the late 1970s. The role of overfishing, especially of juveniles, in this collapse is well documented (Simmonds, 2007) and clearly apparent as the high fishing pressure on juveniles (Figure 1c) at that time; its impact on recruitment is reflected in the sequence of declining residuals (Figure 1d). Total closure of the fishery between 1977 and 1980 and reduced quotas in subsequent years initiated a recovery phase associated with high stock productivity (positive residuals) until the mid-1980s. Then, recruitment residuals suddenly dropped in the mid- to late 1980s, with residuals randomly distributed around zero until 2001 (the “normal” fishery). In the mid-1990s, heavy fishing pressure was brought under control, and fishing on the 0–1 age groups was virtually eliminated. The aforementioned poor recruitment of the 2002–2007 year classes is apparent in the recent phase as a series of negative residuals: this sequence is significantly different from both the normal fishery period (*t*-test for difference of two means: $t = 4.92$, d.f. = 19, $p < 0.001$), and also all three previous periods combined ($t = 3.53$, d.f. = 46, $p = 0.001$). Fishing mortality during the recent phase of poor recruitment has been, by historical standards, relatively low on adults and virtually absent on juveniles, whereas stock biomass has been at high levels. It appears that neither reduced SSB nor fishery-induced effects can explain the recent sequence of recruitment failures. An alternative mechanism needs to be sought.

Recruitment to a fish stock is the consequence of the number of eggs produced by the adult population and a large number of other, often unknown, processes, each of which involves a distinct but variable mortality of the offspring during the development cycle. The updated Paulik diagram (Figure 2) shows that, in the recent phase of poor recruitment, the abundance of early larvae (MLAI) is high and in line with expectations, given the concomitant high adult biomass. However, during the development phase from early stage to late stage larvae (MLAI to MIK), survival rates appear dramatically lower in the recent years of poor recruitment than in most other years. The subsequent survival to juveniles (MIK to IBTS) is comparable with other years. Similar trends are also seen for the year classes 1988–1990, which also showed reduced recruitment from a relatively high SSB, but noting the gap of 11 years between the two periods, the causative factors may not necessarily be the same. Nevertheless, it appears that mechanisms acting during the overwinter larval development period can determine the year-class strength of this stock. The association of overwinter larval survival rates and poor year classes agrees with and extends the analysis of Nash and Dickey-Collas (2005).

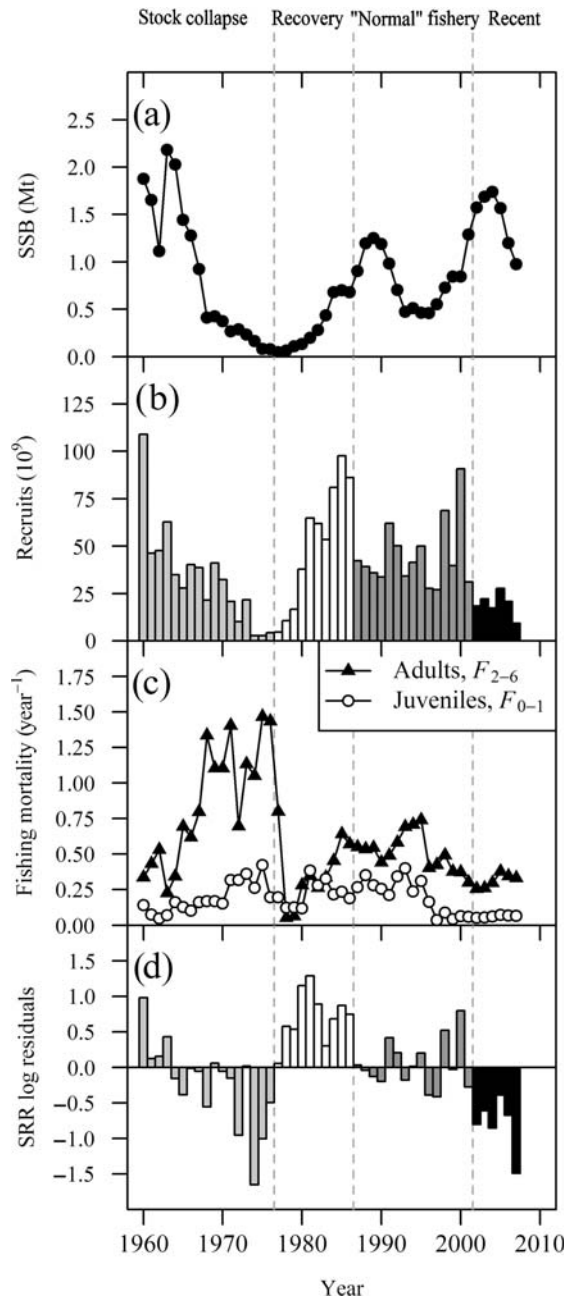


Figure 1. North Sea herring stock history from the stock assessment: (a) annual changes in SSB; (b) time-series of recruitment at 6 months old; (c) mean annual fishing mortality (F) on the stock for ages 2–6 winter rings (wr; closed triangles) and ages 0–1 wr (open circles) from the stock assessment; and (d) the stock residuals [$\ln(\text{observed}/\text{fitted})$] from the segmented-regression (hockey-stick) model. Negative values indicate a lower than expected level of recruitment for a given stock size. Bars in (b) and (d) are shaded according to classification in the stock collapse phase (light grey), recovery phase (no fill), normal fishery (dark grey), and recent years with poor recruitment (black).

Discussion

Our analysis suggests that the sequence of poor recruitment cannot be attributed to the fishery, and instead is more likely determined during the larval overwintering period. There are

several candidate mechanisms that may be responsible for these reduced rates of survival.

In the central and northern North Sea, a prolonged structural shift in the planktonic community has taken place over time (Figure 3a), most likely in response to oceanic climate changes. Two major regime shifts, the first in the mid- to late 1980s and the second around 2000, have resulted in a significant change in the structure of this community. The contemporary regime is now 25% different from that observed during the 1960s and consists of a more diversified warmer water community (Beaugrand, 2004; Edwards *et al.*, 2007; PL, unpublished data). It is widely recognized that larval development is strongly influenced by the quantity, suitability, and timing of planktonic prey available and that a change in one, some, or all of these factors can reduce survival rates: indeed, such a mechanism has been suggested for reduced recruitment in North Sea cod (*Gadus morhua*) in response to the 1980s regime shift (Beaugrand *et al.*, 2003).

The 2000 regime shift shows close temporal agreement with the observed reduction in survival rates of herring larvae. The event has been associated with changes in the prey of herring larvae, in particular with the decrease of small copepods such as *Paracalanus* spp. and *Pseudocalanus* spp. that were typically very abundant in autumn (PL, unpublished data). Discrepancies in the timing of events (the first year of the recent poor recruitment phase is 2002) can be attributed to the fact that the meta-analysis underpinning Figure 3a is based on a broad cross section of the North Sea plankton community and therefore may not be completely representative of the species of direct relevance to herring larvae. Moreover, it is unclear whether the year 2001 should be classified as part of the normal fishery or the recent phase: whereas the recruitment (Figure 1b) and SRR residuals (Figure 1d) match the recent phase, the Paulik diagram has the overwinter survival of the 2001 year class (bottom left quadrant of Figure 2) lying closer to the main body of values than the highlighted group containing the recent phase. It may therefore be more appropriate to consider the 2001 year class as an intermediate year between the two phases, bringing the temporal correlation into even tighter agreement.

Changes in the North Sea plankton community appear also to have impacted this stock in the past. The transition from the recovery phase to the normal fishery phase, marked by a sudden reduction in recruitment residuals (Figure 1d), agrees closely in timing with the well documented late 1980s regime shift (Beaugrand, 2004; Figure 3a) and also with previous occurrences of the reduced overwinter survival phenomenon (bottom left quadrant of Figure 2). It remains unclear, however, why after three sequential years of reduced survival (1988–1990) the system reverted to a normal fishery again after 1991, and whether the actual mechanism underpinning the phenomenon is the same as that observed more recently. Nevertheless, the close temporal agreement between changes in the North Sea planktonic community and in North Sea herring productivity and survival, while not being conclusive evidence in and of itself, suggests that the proposed mechanism is consistent with observations. We may therefore be documenting the first response to the 2000 regime shift at higher tropic levels.

Alternatively, changes in the physical environment may also have contributed to, or indeed been the major driving force behind, the recent reduced larval survival. Significant hydrographic changes, including an increase in bottom-water temperature, have been observed near the main herring spawning areas in recent years (ICES, 2007; Figure 3d). Hydrographic processes

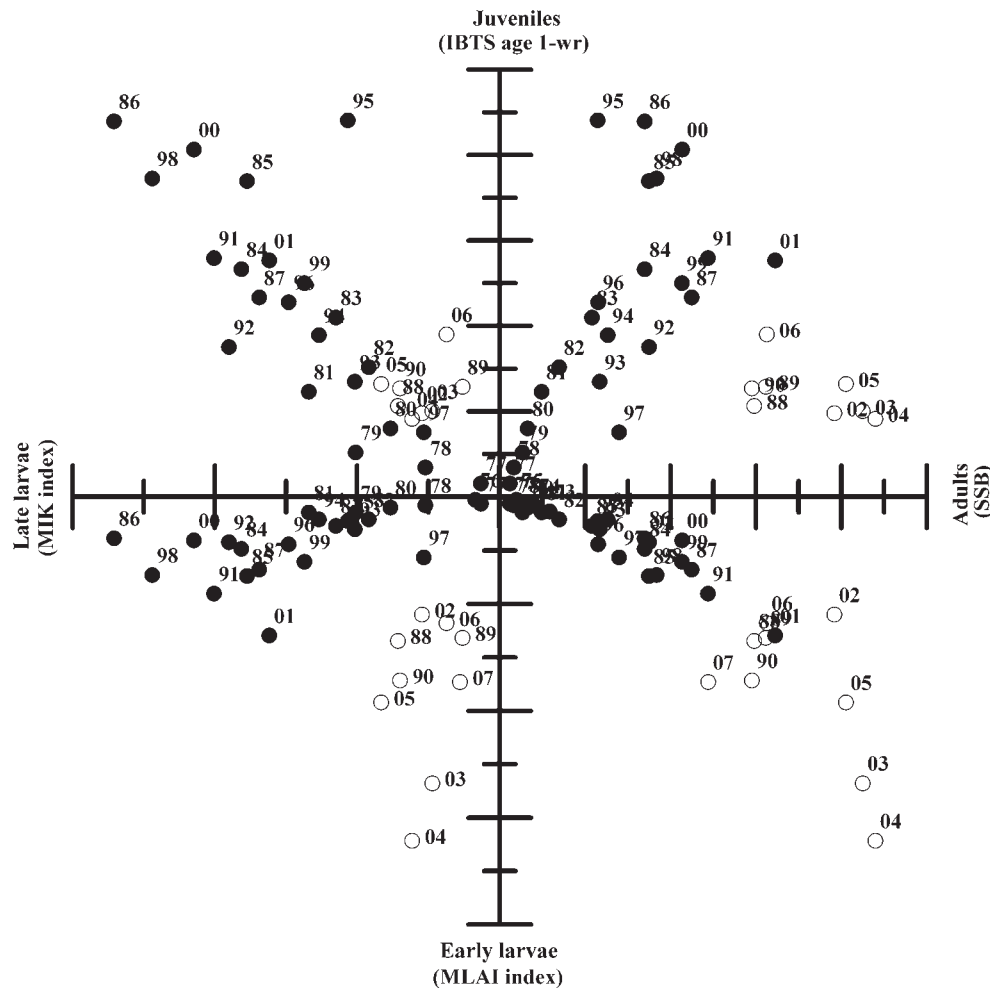


Figure 2. Paulik diagram for North Sea herring showing the observed relative abundance of each stage in the life cycle, with the data source identified in parenthesis (an updated Figure 7 of Nash and Dickey-Collas, 2005). The diagram should be read in a clockwise manner, starting from the adults, hence following the development life cycle. Data labels denote the cohort. Points plotted with open circles mark years of unusually poor recruitment in the adult–juveniles plot (top right). SSB, spawning-stock biomass (1973–2007) from the stock assessment; MLAI (1973–2007) characterizing early stage larvae abundance; MIK 0-age, MIK age 0 index (1976–2007), characterizing the abundance of late larvae; IBTS age 1-winter ring (wr), International Bottom Trawl Survey index (1973–2007), characterizing the number of juveniles at age 1-wr. Axis values are indices and are for illustrative purposes only, so no numbers are indicated. The juveniles are the observed numbers of age 1-wr, differing from recruitment at 6 months old plotted in Figure 1.

determine the position, structure, and productivity of the marine frontal zones in which herring larvae feed and reside (Kiørboe *et al.*, 1988). Warming temperatures in the North Sea have also been linked to changes in the distribution of many fish species, including the recent invasion of warmer water species such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*; Beare *et al.*, 2004). The presence of these non-endemic species may have increased the rates of predation on herring larvae and reduced survival.

A third potential mechanism is that of effects caused by high population density: the top right quadrant of Figure 2, adults vs. juveniles, could suggest Ricker-like density-dependent reductions in survival at high stock sizes (i.e. overcompensation). However, the life history model showing the relationship between production of larvae (MLAI) and abundance at age 0 (MIK), the bottom left quadrant of Figure 2, is poorly described by a single relationship, with impaired recruitment at high density (i.e. Ricker-like), so does not suggest a classic overcompensatory

response. Instead, the link between MLAI and MIK is readily described by two separate linear relationships, implying two unique regimes of survival rates. Furthermore, no evidence of overcompensation in recruitment has been observed in this stock during previous periods of high biomass, e.g. before the 1970s collapse (ICES, 1998, 2008a). Overcompensation does not, therefore, appear a likely explanation for the phenomenon we are investigating here.

At the moment, it is not possible to identify which, if any, of these candidate mechanisms is responsible for the reduced recruitment, although it appears unlikely that overcompensation is to blame. Although the regime-shift hypothesis appears most probable, it is primarily based on the temporal correlation between events and requires a more detailed examination to test its validity. There have been hydrographic changes, but it is unclear why gradual changes in temperature have caused a sudden reduction in overwintering survival. Further work is required, therefore, to identify the underlying mechanism.

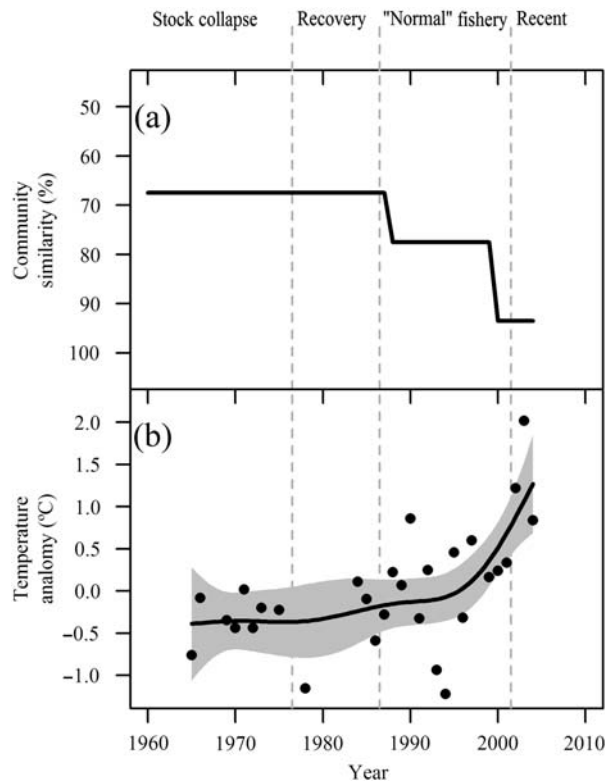


Figure 3. Recent changes in the North Sea environment: (a) regime shift index of the plankton community giving community-level similarity between 2005 and earlier years, from a 50-species meta-analysis of central North Sea plankton (after Edwards *et al.*, 2007); (b) spawning (September–October) bottom temperatures around the Orkney spawning area, with a GAM regression (line) and \pm 2s.e. confidence intervals (shaded area; after ICES, 2007). For comparison, the periods defined in Figure 1 are marked.

The high natural variability of stock–recruitment processes often makes it difficult to identify a long-term directional shift against the background of short-term random fluctuations. Appropriate management decisions within such apparent randomness are often hampered by the natural human tendency towards optimism, even though the costs of inaction can be significant (Simmonds, 2007). Sequences of poor recruitment have been observed in the stock in the past, only for it to recover at the point where they appeared to have become permanent (e.g. the three poor year classes of 1988–1990). However, the current sequence is already 6 years long, and is statistically different from both the immediately prior normal fishery period, and also the entire time-series leading up to that point. The sequence of poor annual recruitments cannot, therefore, be attributed solely to random variation: there has been a significant shift in recruitment.

This stock is subjected to a management framework agreed between the EU and Norway in 2004. However, a combination of management and enforcement issues has meant that it has not been fully implemented, resulting in recent exploitation rates (2005–2007) some 40% above the value considered sustainable by the management plan. Moreover, the current reduced recruitment has started to impact on the stock size in recent years, with the SSB decreasing from 1.8 million tonnes in 2004 to 1 million tonnes in 2007 (Figure 1a). Medium-term forecasts

that assume continued poor recruitment, but a strict implementation of the management rule, show that the stock biomass will level off near the accepted safe biological limits (ICES, 2008a, b). However, forecasts made with continued poor implementation of the management rule show that the stock will continue to decline, and that there is a high probability of moving outside safe biological limits (ICES, 2008a, b). This poses a subsequent risk of further impaired recruitment attributable to low stock levels, and hence the possibility of a stock collapse. Strict implementation of the existing harvest rule is therefore key to the continued sustainable exploitation of the stock.

More generally, this case study serves as a good example of the inherent dangers associated with assumptions of stationarity in marine ecosystems. For example, medium-term projections made in 2000 would have assumed a continuation of the normal recruitment regime, leading to severe overestimation of the development of the stock. Such projections and forecasts are driven, primarily, by the assumption of a unique relationship between SSB and recruitment. However, as we illustrate here, adult biomass is just one axis of a very high-dimensional surface that determines recruitment to the stock: given our lack of understanding regarding the other dimensions, and our distinct inability to characterize them, it is therefore not surprising that two similar SSBs can give rise to such widely different levels of recruitment. Instead of talking about a single SRR, it is crucial that forecasts recognize the existence of multiple relationships between stock and subsequent recruitment, each corresponding to a different combination of key variables (e.g. regimes). Although it may not be possible to treat these relationships explicitly at the moment, or perhaps ever, recognizing their existence will help improve the reliability and the robustness of future management decisions.

Conclusions

Although the proximate causes of the current sequence of poor recruitment in North Sea herring are uncertain, it appears that the ultimate cause most probably lies with changes in the North Sea environment, and not overfishing. Survival rates through the winter larval development phase have been greatly reduced. The recently identified 2000 planktonic regime shift in the North Sea appears to be the leading candidate mechanism, especially considering the close temporal correlation between the events and evidence that such changes have impacted upon the stock previously: we may therefore be describing the first consequences of this shift at higher trophic levels. However, identifying the underlying responsible mechanism is challenging, especially considering the strong coupling between many of the proposed factors, e.g. warming of the ocean affects the timing and the composition of plankton populations, influences larval development rates, and facilitates the invasion of foreign predatory species. However, although the precise mechanism remains uncertain, the productivity of the stock has clearly been reduced. It is not possible to say when, or whether, the sequence of poor recruitment will abate. Despite fishing pressure unlikely being to blame for the decline in recruitment, current exploitation rates are above those considered sustainable. Therefore, reducing the fishing mortality back in line with the management plan gives a good chance of the stock remaining within safe biological limits. In dynamically changing environments, recent management success does not necessarily guarantee future sustainability.

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References

- Beare, D. J., Burns, F., Greig, A., Jones, E. G., Peach, K., Kienzle, M., McKenzie, E., *et al.* 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Marine Ecology Progress Series*, 284: 269–278.
- Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245–262.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661–664.
- Cushing, D. H. 1995. The long-term relationship between zooplankton and fish. *ICES Journal of Marine Science*, 52: 611–626.
- Edwards, M., Johns, D. G., Licandro, P., John, A. W. G., and Stevens, D. P. 2007. Ecological Status Report: results from the CPR survey 2005/2006. SAHFOS Plymouth Technical Report, 4. 8 pp.
- Gröger, J., Schnack, D., and Rohlf, N. 2001. Optimisation of survey design and calculation procedure for the international herring larvae survey in the North Sea. *Archive of Fishery and Marine Research*, 49: 103–116.
- ICES. 1998. Report of the Study Group on Stock–Recruitment Relationships for North Sea Autumn-spawning Herring. ICES Document CM 1998/D: 2. 60 pp.
- ICES. 2007. Report of the Study Group on Recruitment Variability in North Sea Planktivorous Fish (SGRECVAP). ICES Document CM 2007/LRC: 07. 69 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 ICES Workshop on Herring Management Plans (WKHMP). ICES Document CM 2008/ACOM: 27. 102 pp.
- Kell, L. T., Mosqueira, I., Grosjean, P., Fromentin, J.-M., Garcia, D., Hillary, R., Jardim, E., *et al.* 2007. FLR: an open-source framework for the evaluation and development of management strategies. *ICES Journal of Marine Science*, 64: 640–646.
- Kjørboe, T., Munk, P., Richardson, K., Christensen, V., and Paulsen, H. 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Marine Ecology Progress Series*, 44: 205–219.
- 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.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York. 542 pp.
- Paulik, G. J. 1973. Studies of the possible form of the stock–recruitment curve. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 164: 302–315.
- 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.
- 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.
- Watanabe, Y. 2007. Latitudinal variation in the recruitment dynamics of small pelagic fishes in the western North Pacific. *Journal of Sea Research*, 58: 46–58.

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