

## V. Variability at all scales and its effect on the ecosystem

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### Variability at all scales and its effect on the ecosystem – an overview

Robert R. Dickson

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In many ways, ICES was founded to explore the link between environmental change and ecosystem response. As early as 1890, Otto Pettersson and Gustav Ekman began the process of applied hydrographic monitoring in the Baltic and North Seas, and it was the utility of Pettersson's scheme that prompted the founding of ICES in 1902. Though these early initiatives were invaluable in establishing a basis for the long-term detection of "change", it required something more for this to develop into the wealth of decade-to-century time-series that today form so much of the focus, interest, and expertise of ICES. That extra stimulus was provided by the large-scale, long-period shifts in ocean climate that have successively worked their way through ICES waters during much of the present century: the "Warming in the North", the "Russell Cycle", the "Great Salinity Anomaly", and the varied effects of the North Atlantic Oscillation (NAO). This paper is built around four case studies which describe the growth of our understanding in contrasting aspects of biophysical change. In the first, we are concerned with the *vertical circulation* in the sea and the key developments in critical depth theory by which Gran and Braarud and Sverdrup were able to postulate and then demonstrate the seasonal changes which control the spring phytoplankton bloom, before we go on to discuss the "match-mismatch" theory of Cushing by which the interannual variability of "production" is related to the success of fish stocks. The second pair of cases illustrates the dramatic dislocation of ecological distributions that can result when the effects of climatic change spread through the *large-scale ocean circulation*. Two contrasting examples are discussed: 1) the rise and spread of the West Greenland cod stock and fishery as a wave of warming passed through the Northern Gyre in the middle decades of the 20th century, and 2) the equally dramatic dislocation of the traditional pattern of herring migration in the Nordic Seas in the 1960s–1990s as extremes of NAO activity forced fundamental changes in the position of the Oceanic Polar Front. The third case study concerns ways in which perturbations of the *intermediate-scale flow field* might contribute to the success of fish stocks through space–time variations in the loss or retention of larvae. The fourth and final example is reserved for a description of *ocean temperature* and its variability, both as a key control variable on the success of fish stocks and as a proxy for others. Subtle shifts in the marine climate may have important effects on the ecosystem. To mitigate these or even to be aware of them, our prime requirement is the continuation of our long hydrobiological time-series, and the need to continue these series is the main conclusion of this paper.

Keywords: climate change, cod, ecosystem, Great Salinity Anomaly, herring, hydrography, larval drift, North Atlantic Oscillation, phytoplankton bloom, time-series.

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## Long time-series and the detection of change

Arguably, the pioneering efforts to describe ocean variability, its causes, and effects on the ecosystem, began in European waters, and the standing committees of ICES have long taken responsibility for maintaining these initiatives and developing them into a science. While there will be space below to identify certain officers of ICES who have led particular advances, we cannot hope to capture in detail the interplay between individual scientists and the work and structures of ICES. A glance at our bibliography, however, should confirm that the preponderance of scientists mentioned were active participants in ICES fora, and that this was where the science of ocean variability was debated, published, and progressed.

As early as 1890, Otto Pettersson and Gustav Ekman began the process of hydrographic monitoring in the Baltic and North Seas, working agreed routes and stations on a quarterly basis. In 1892, this was developed into an international scheme of investigations at the request of a meeting of Scandinavian naturalists held in Copenhagen, and in 1893, this international effort got under way with scientists from Sweden, Norway, Denmark, Germany, and Scotland taking part. From the outset, these studies had a multidisciplinary "applied" aim with plankton observations included and with Pettersson attempting to show the influence on the Bohuslän herring fishery of changes in hydrography. It was the utility of Pettersson's scheme that prompted recommendations that the Swedish government should initiate broader international actions based on it, and the founding of ICES in 1902 was one direct result.

It may well have been change itself that kept the process going, since as our time-series lengthened into the middle decades of the 20th century, they began to capture evidence of one of the largest and most widespread regime shifts that has ever affected our waters. For these were the decades of "the warming in the north", when the salinity of North Atlantic water passing through the Faroe-Shetland Channel reached a century-long high (Dooley *et al.*, 1984), when salinities were so high off Cape Farewell that they were thrown out as erroneous (Harvey, 1962), when a precipitous warming of more than 2°C in the 5-year mean pervaded the West Greenland banks (all in Figure 1), and when the northward dislocations of biogeographical boundaries for a wide range of species from plankton to commercially important fish, terrestrial mammals, and birds were at their most extreme in the 20th century. The astonishing nature of these radical events is vivid in the contemporary scientific literature, most notably in the classic accounts by A. S. Jensen (1939), Å. Vedel Tåning (1943, 1949), B. Sæmundsson (1934), P. M. Hansen *et al.* (1935), A. Fridriksson (1949), N. M. Knipowitsch (1931), A. C. Stephen (1938), and many others summa-

rized in a comprehensive bibliography by Arthur Lee (1949) and reviewed in an ICES special scientific meeting on "Climatic Changes in the Arctic in Relation to Plants and Animals" in 1948.

There seems little doubt that these riveting events were a lasting stimulus to the direction and thinking of ICES. Even in wartime, under the Presidency of Johan Hjort (1938–1948), Martin Knudsen's<sup>1</sup> Sub-committee on Hydrographical and Biological Investigations continued to plan the data collection that would be needed to meet Hjort's aim of fish stock prediction, the *Annales Biologiques* series was begun (1939–1943) to collate and keep pace with these changes, and in 1939, Jens Smed started to develop the Service Hydrographique into an effective regional data centre and to piece together the accumulated records into reliable long time-series. We retain that legacy in the wealth of decade-to-century hydrographic time-series that today enable us to compile an annual summary of the changing hydrographic status of ICES waters and that have provided insight into the way the marine ecosystem responds to its changing environment.

## Vertical mixing and the spring bloom

There can be few better or more fundamental case studies of interaction between physical variability and the marine ecosystem than that of physical controls on the spring phytoplankton bloom in temperate waters. While it will have been known or assumed in the early decades of the 20th century that the growth of plants in the sea was some function of the seasonal availability of light and nutrients, the early model was an agricultural one, based on Liebig's Law of the Minimum which asserted that the quantity of algae produced depended solely on the quantity of available nutrients and was limited by the nutrient in least supply (e.g., Cushing, 1975). In Cushing's words, "Algae were simply produced to the nutrient limit and were then eaten by herbivores." However, in the same year that Harvey, Cooper, Lebour, and Russell (1935) were providing their irresistible evidence for the restraint of algal production by grazers, so in the West Atlantic Gran and Braarud (1935) were showing in their "critical depth" theory how the changing physical environment might drive the process. Photosynthesis decreases logarithmically with depth (following light intensity), while respiration is more or less uniform in the wind-mixed layer (because so is the algal concentration). There is, therefore, a depth *above which* the destruction of organic matter by respiration will equal its production by photosynthesis, and the

<sup>1</sup> Martin Knudsen acted as ICES *Chef du Service Hydrographique* under various titles from 1928 to 1948. Jens Smed succeeded him as Hydrographer from 1946 to 1984, and the top panel in Figure 1 is built from "Smed's anomalies" (see Smed, 1965).



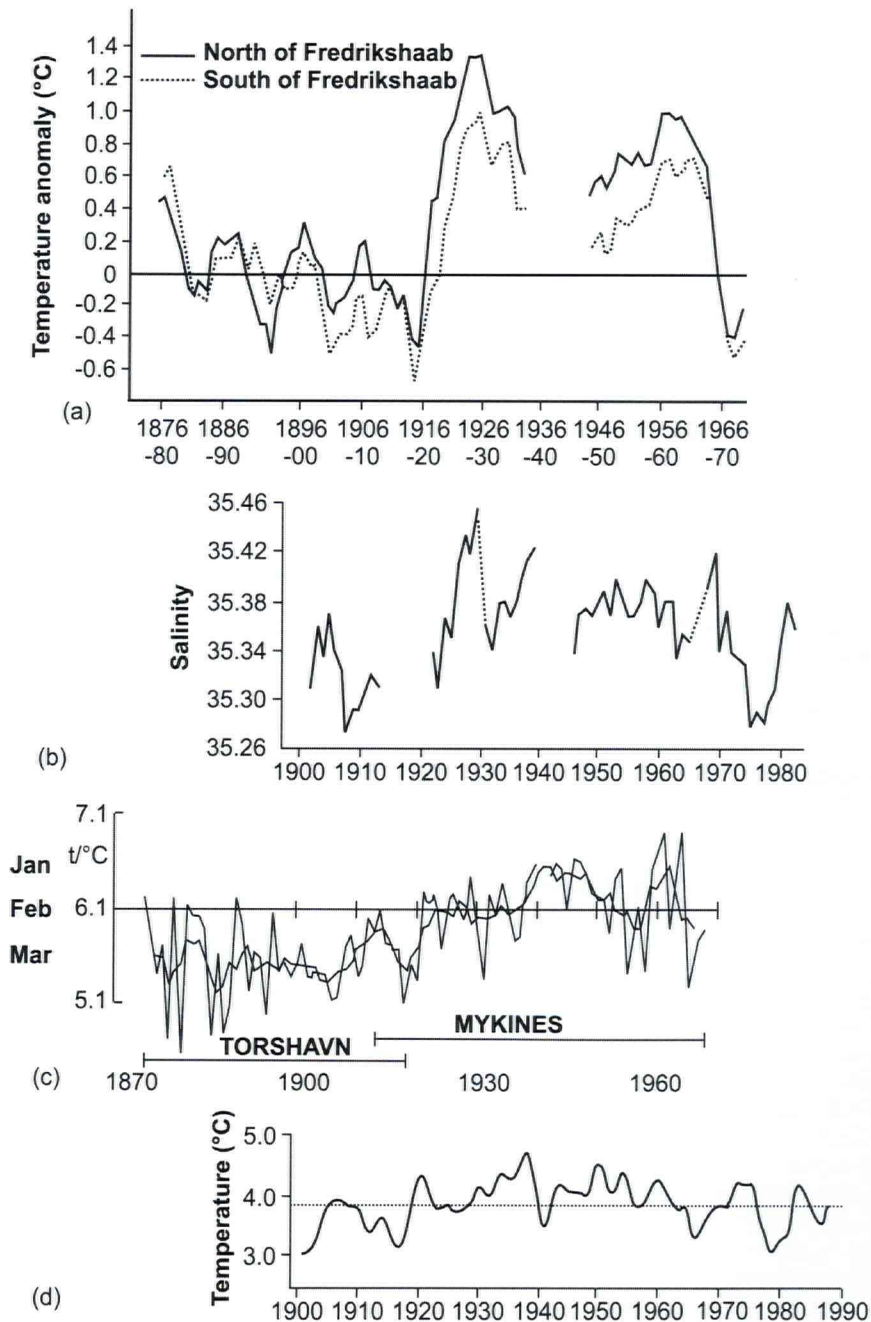


Figure 1. Records of the warm salty wave that passed through the Subpolar Gyre of the North Atlantic in the middle decades of the 20th century: (a) surface temperature anomalies for West Greenland, 1876–1974 (Smed's data, from Buch and Hansen, 1988), (b) the salinity of the North Atlantic water in the Faroe–Shetland Channel, 1902–1982 (from Dooley *et al.*, 1984), (c) winter surface temperature at Faroes, 1875–1969 (from Hansen and Meincke, 1984), (d) 3-year running averages of yearly temperature along the Kola Section of the Barents Sea, 1900–1990 (from Loeng, 1991) plotted to a common time base. From Dickson and Brander (1993).

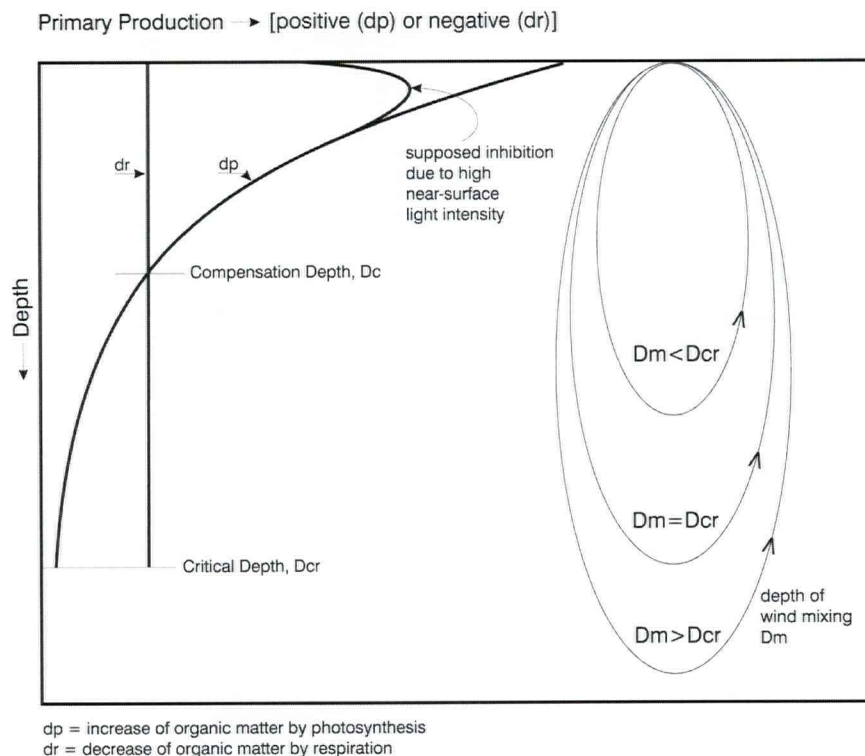


Figure 2. Schematic description of the Gran and Braarud (1935) "critical depth" hypothesis for the vernal blooming of phytoplankton in temperate waters. For explanation, see text.

condition for the vernal blooming of phytoplankton is simply that the depth of mixing ( $D_m$ ) should rise above this critical depth ( $D_{cr}$ ), as Gran and Braarud pointed out (Figure 2).

Though G. A. Riley (1942) had obtained some partial confirmation of the concept on Georges Bank in 1941, showing a relation between plankton and stability, the validation of this theory awaited Sverdrup's (1953) classic analysis of observations made aboard Ocean Weather Station (OWS) MIKE in the spring of 1949. As a seasonal strengthening of insolation and a seasonal weakening of wind speeds provided the necessary crossover of  $D_{cr}$  and  $D_m$ , so the diatoms, coccoliths, dinoflagellates, and copepods appeared on cue in the surface layers (Figure 3) [This land-mark experiment can certainly be described as an ICES achievement. Sverdrup, at that time, was the third Chair of its Hydrography Committee (1950–1955), and Odd Sælen, who made the physical measurements, was later to be its ninth (1970–1973).] Though theorists later modified the critical-depth argument to allow for inhibition of photosynthesis at high near-surface light levels, this proved to be inappropriate. By the simple, but ingenious, expedient of cycling incubation flasks over a mixed layer which varied with the wind speed, Lenz and

Moigis (1984) were able to complete the validation of the critical-depth theory by showing that cells spend insufficient time in the surface layers for significant inhibition to occur.

The critical-depth theory plainly bore implications for long-term as well as seasonal changes in production. Since the main factors which determine  $D_{cr}$  and  $D_m$  (insolation and windspeed) are unrelated or not obviously so, it follows that the timing and development rate of the spring bloom may differ greatly from one year to the next. Colebrook (1965) showed from Continuous Plankton Recorder (CPR) survey records that onset can vary by six weeks or more in British waters. In contrast, Cushing (1969) noted that the spawning time of herring, plaice, sockeye salmon, and cod took place at the same time each year, with a standard error of about one week in the time of peak spawning. This difference famously formed the basis of Cushing's "match-mismatch" hypothesis (Figure 4; from Cushing, 1982), which holds that the production of fish larvae is either matched or mismatched to the production of their food in a given year, with fish spawning at that fixed season which, on average, will maximize larval survival in the face of a highly variable onset of production. Coupled with the auxiliary hypothesis that recruitment is largely gov-

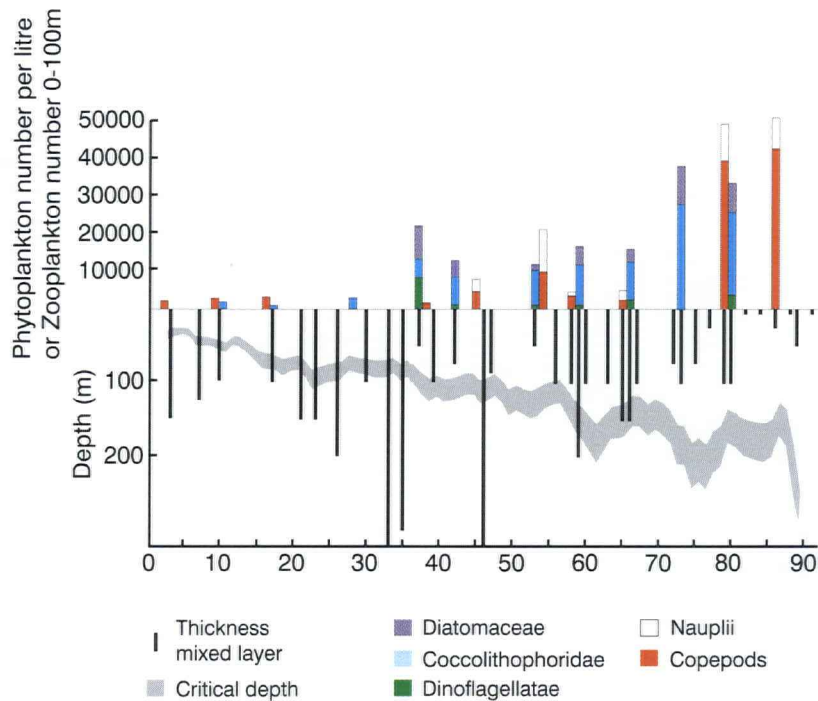


Figure 3. Sverdrup's (1953) classic demonstration of the critical depth hypothesis, using observations made aboard OWS MIKE in the spring of 1949.

erned by survival in the late larval stage, the match-mismatch hypothesis does appear to provide an explanation of how recruitment variability may be generated. However, the idea that the timing of plankton production is related to the recruitment of fish will always be difficult to test for a number of reasons, not least of which is the lack of adequately resolved spatial and seasonal data for matching fish larvae and their food (Brander, Dickson, and Shepherd, 2001). Cases can certainly be found in which the evidence seems *consistent with* match-mismatch, including the case which Brander *et al.* describe; but whether it makes sense to talk about hypothesis testing for open biological systems remains questionable (Taylor *et al.*, 1996).

## Climatic effects on the large-scale ocean circulation

Long-term measurements of the ocean circulation are still rare. However, in a few extreme cases, when climatic change spreads through the semi-permanent current system, the nature of the ecosystem response may be so dramatic as to be unmissable. Four main, large-

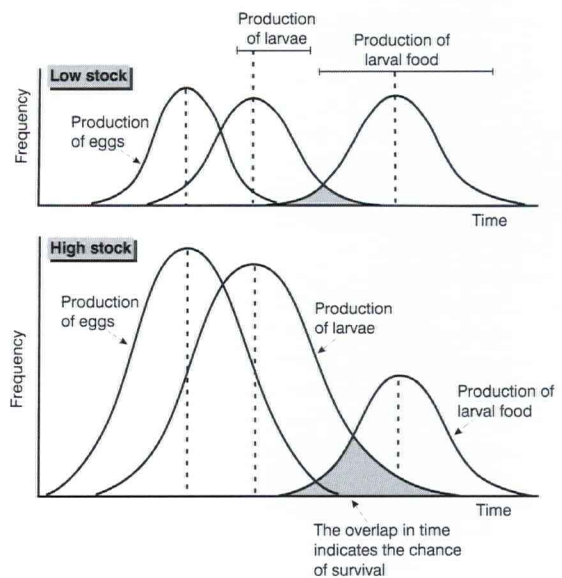


Figure 4. Principle of Cushing's match-mismatch hypothesis. From Cushing (1982).



scale and long-term shifts in ocean climate successively worked their way through ICES waters during the 20th century: the "Warming in the North", a warm, salty wave which passed through the Northern Gyre between the 1920s and 1950s, the "Russell Cycle" which affected the ecosystem of the Western Channel at about the same time and perhaps for related reasons (e.g., Cushing, 1982), the "Great Salinity Anomaly" of 1968–1982 (Dickson *et al.*, 1988), and the varied effects of the North Atlantic Oscillation (NAO), particularly those associated with its largest recorded low-frequency shift between the 1960s and 1990s. In each case, the committees of ICES were instrumental in piecing together the physical evidence of change and matching it to the ecosystem response. Two of these cases, a demersal and a pelagic example, are illustrated here.

During the middle decades of the 20th century as the circulation and hydrography of the Subpolar Gyre underwent its slow evolution, the rise and spread of the West Greenland cod fishery was one spectacular result, apparently reflecting a change in the effectiveness of egg and larval drift in the Irminger/West Greenland Current system. The body of evidence is circumstantial, but appears to be self-consistent. As Buch and Hansen (1988) indicated, the warming on the West Greenland banks was accompanied by an explosive development of the West Greenland cod fishery, which, from a negligible tonnage in the early 1920s, rose to over 300 000 t yr<sup>-1</sup> in the 1950s and 1960s, and a maximum of >450 000 t yr<sup>-1</sup> before abruptly declining once again between the late 1960s and the present as cooler conditions returned (Figure 5; from Dickson and Brander, 1993). Such "cod periods" have been documented in the past at West Greenland, in the 1820s and 1840s (Hansen, 1949) and perhaps much earlier (Fabricius, 1780), but this change represented a return of cod to West Greenland after an absence of at least 50–70 years (Buch and Hansen, 1988; Dickson *et al.*, 1994).

The hypothesis is that this change was both initiated and maintained by an increased exchange of cod larvae from the spawning grounds off southwest Iceland during the warm decades compared with the cold periods which preceded and succeeded them (Schopka, 1993, 1994). Two items of evidence sustain this theory (Dickson and Brander, 1993). The first is based on the use of haddock as a tracer of larval exchange (Hovgård and Messtorff, 1987). Unlike cod, haddock do not spawn successfully at West Greenland, so if adult haddock are caught there, they must have drifted there as larvae. The closest known spawning site for haddock lies upstream near the cod spawning grounds off southwest Iceland. When the (small) international catch of haddock at West Greenland is compared with the (large) international catch of cod, essentially similar trends of change are observed in both species since 1952, when annual haddock catch statistics first became available and a qualitative similarity before that (Figure 5). Thus, while it is possible that the first cod colonizing the West

Greenland banks established a self-sustaining stock there, purely through the amelioration of the marine climate, the parallelism between cod and haddock catches along the western banks seems to argue that recruitment to the West Greenland cod stock was fed to a significant extent by a time-varying larval drift from Iceland. Kushnir (1994) confirmed that during the period of warming off West Greenland, the North Atlantic wind field was configured in such a way to boost the warm Irminger Current through the establishment of an increased easterly airflow over the west-going Irminger Current.

As the NAO minimum of the mid-1960s brought polar conditions and a record sea ice extent to North Icelandic waters (Malmberg, 1969), and as these cold, fresh conditions passed out through the Denmark Strait to form the Great Salinity Anomaly (Dickson *et al.*, 1988), so the cod fishery at West Greenland and the warmth which sustained it both came to an abrupt end. By 1992, Jakobsson was able to report in his keynote review of "Recent Variability in Fisheries of the North Atlantic" that the Greenland fishery had not been self-sustaining for 35 years, and that despite occasional years (e.g., 1984) with a heavier drift of larvae from Iceland, it was unavailing. "By 1990, the cod had disappeared from Greenlandic waters."

The 14-year propagation of the Great Salinity Anomaly through the Northern Gyre was a quite exceptional event. Jakobsson (1992) concluded that "the 'Great Salinity Anomaly' has probably generated more variability in fisheries during the last quarter of a century than any other hydrographic event in recent years". During its passage, Cushing (1995) found a significant reduction in recruitment in 11 out of 15 deepwater fish stocks examined. And, as its harsh conditions closed down the excursion loop of cod to West Greenland, they also set in train a change in the migration pattern of Norwegian spring-spawning herring in the Nordic Seas that has taken 35 years to unfold. The pelagic example is thus a story of the amplifying NAO.

During the NAO minimum of the 1960s, a record northerly airflow swept the Norwegian–Greenland Sea bringing an increasing proportion of polar water south to the seas north of Iceland in a swollen East Greenland Current. The East Icelandic Current, which had been an ice-free, Arctic current in 1948–1963, became a Polar Current in 1965–1971, transporting drift ice and preserving it (Malmberg, 1969). Aided by active ice formation in these polar conditions, sea ice extended to the north and east coasts of Iceland. Jakobsson (1992) and Vilhjálmsson (1997) summarized the ecological upheaval that resulted from this southeasterly shift of the Oceanic Polar Front. With extensive freshening in the surface layers, suppressed vertical mixing is held responsible for a poor renewal of nutrients and for a much-reduced primary production (Thórhartóttir, 1977). Only partly as a result, the species composition of the zooplankton community north of Iceland changed in character from boreal to Arctic (Jakobsson, 1980;



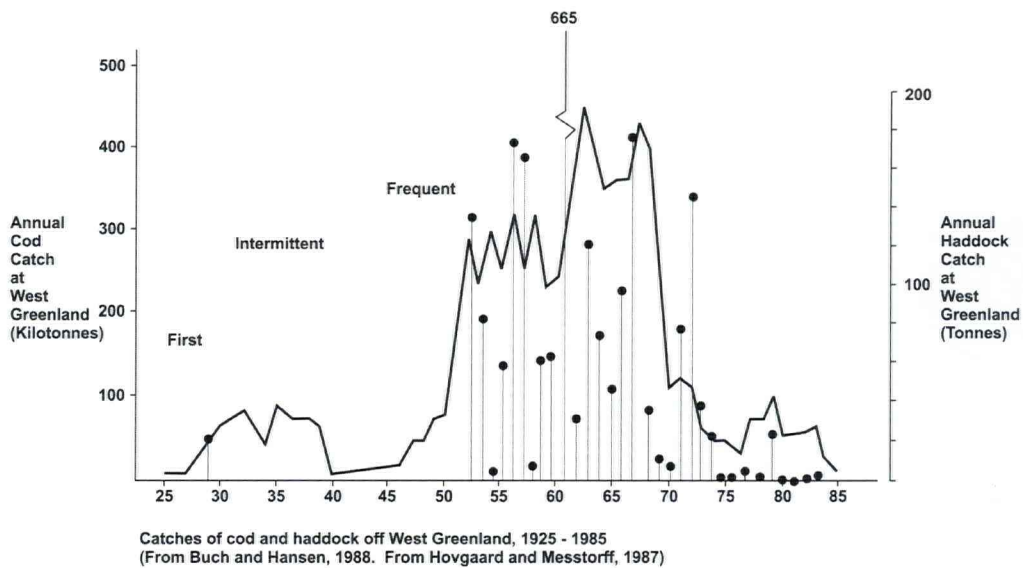


Figure 5. Comparison between the international annual catch of cod at West Greenland, 1925–1985 (solid line; from Buch and Hansen, 1988) and the corresponding annual catch of haddock, 1952–1983 (dots; data from Hovgård and Messtorff, 1987).

Ástthórsson *et al.*, 1983), so that by the late 1960s, North Icelandic waters had become a "veritable desert" for *Calanus finmarchicus*, one of the main food items of herring in the Nordic Seas. Since herring are plankton feeders and are close to their limits of range in Icelandic waters, it is not surprising that they should have suffered more than other fish species from this severe deterioration in the marine climate (Jakobsson, 1980; Dragesund *et al.*, 1980).

Vilhjálmsson (1997) chronicled the resulting progressive dislocation in the traditional migration pattern of the Norwegian spring-spawning herring in a series of five maps, reproduced here as Figure 6. In the mid-1960s, the traditional feeding migration to North Icelandic waters stopped completely (cf. Figures 6a and c), with the older fish foraging in the Norwegian Sea east of the East Icelandic Current in 1965–1966 (Figure 6b) and right along the Ocean Polar Front to Spitsbergen in 1967–1968 and 1969 (Figure 6c). In 1969, their overwintering grounds also retracted eastwards, shifting from east of Iceland to the west coast of Norway. Thereafter, reinforced by a stock collapse in the late 1960s through heavy overfishing, the stock conducted its spawning, feeding, and overwintering movements close in along the Norwegian coast between 1972 and 1986 (Figure 6d), and westward feeding migrations into the Norwegian Sea stopped altogether.

Gradually, however, as the winter NAO index underwent its long amplification through the 1970s and 1980s to record positive values in the early 1990s, and a deepening Icelandic Low directed a strengthened southerly airflow across the eastern Norwegian Sea, a warmer,

stronger, if narrower Norwegian Atlantic Current has brought climatic amelioration back to the Norwegian Sea (Dickson *et al.*, 2000; Blindheim *et al.*, 2000). Further west, although conditions remain cool and very fresh in the surface layers, the amplifying NAO has been accompanied by a steady, large-scale reduction in the late-winter extent of sea ice (Deser *et al.*, 2000). We may, therefore, perhaps be justified in interpreting recent signs of renewed westward foraging by the Norwegian spring spawners (Figure 6e and Aure, 2000) as a sign that a cycle in the migration pattern of this great herring stock is about to be closed. If Alheit and Hagen (1997) are correct in linking the great herring fluctuations of northwestern Europe with NAO forcing, it is a cycle which will have been played out before.

### Variability in the intermediate-scale circulation: drift and retention

Though it has been apparent for decades that large-scale changes in the flow field can affect the distribution and survival of stocks, it is only in relatively recent years that we have begun to recognize the ways in which smaller-scale physics can modulate the process; and, in most cases, we have still to determine how the variability of such processes might contribute to the varying success of fish stocks.

For example, it has long been realized that oceanic banks may have a circulation that isolates them from surrounding waters, and more recently that a closed

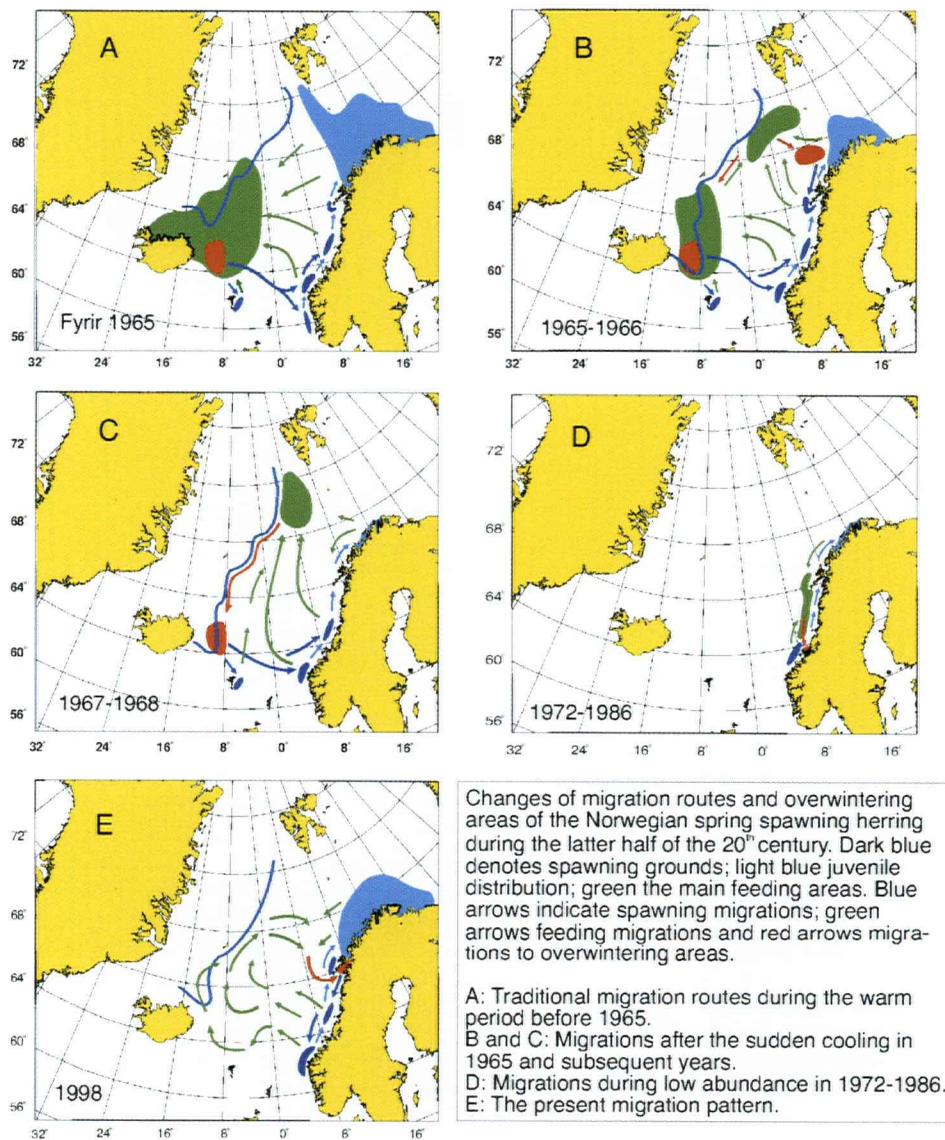


Figure 6. Changes in migration routes and overwintering areas of the Norwegian spring-spawning herring during the latter half of the 20th century. From Vilhjálmsson (1997).

anticyclonic circulation is a common feature (see Hansen *et al.*, 1986, for a succinct review). The apparent isolation of Faroe Bank, for example, was known and debated by Nielsen (1907), Knudsen (1911), Nansen (1913), and Jacobsen (1915), but a physical mechanism was not apparent until Taylor column theory became available to provide an explanation (Proudman, 1916; Taylor, 1917); even then, its applicability to the large topographic scale of the Northeast Atlantic banks awaited the reworking of the theory by Bannon (1980) using shallow-water assumptions, and

the practical application of Bannon's theory by Dooley<sup>2</sup> (1984). The essentials are these (Figure 7): as an open-ocean flow bumps up and over a submerged bank, it changes its relative vorticity by squashing, so to conserve potential vorticity, it must add negative vorticity (turn to the right). Since it loses energy against stratifi-

<sup>2</sup> Harry Dooley has served as ICES Hydrographer (now Oceanographer) since 1984, the third long-standing *Chef du Service Hydrographique* to occupy this post after Knudsen and Smed.



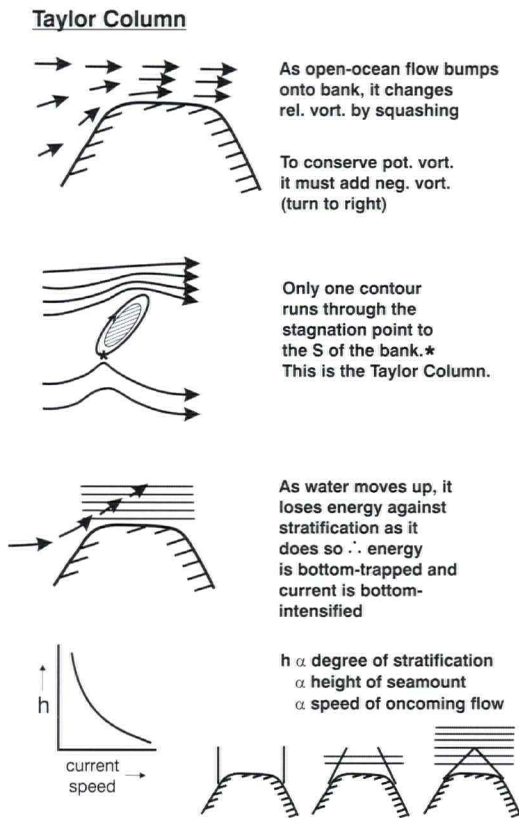


Figure 7. The Taylor column circulation around banks: cause and characteristics.

cation as it does so, the resulting current around the bank will tend to be bottom-intensified. As Bannon also concluded, the speed of this clockwise circulation and the residence time of water over the bank will be inversely proportional to the speed of the oncoming flow (Figure 8a).

In his fieldwork at Rockall in 1979–1983, Dooley (1984) was among the first to seek and find direct evidence of such a circulation and to show, in the only full year of current measurements recovered, a large-scale, coherent, quasi-seasonal variation in the strength of the flow around the bank (Figure 8b). In common with Shomura and Barkley (1980), Dooley was quick to recognize the importance of a Taylor column circulation in maintaining the isolation of the Rockall haddock stock (since confirmed genetically by Jamieson and Birley, 1989), and to suggest that long-term changes in the strength of the circum-bank flow, including episodes of total breakdown, might control haddock recruitment through a variable loss or retention of larvae. Though the pattern of haddock recruitment at Rockall is strikingly variable, typified by major spikes at 10–15 year intervals, and though a similar circulation and control mechanism has since been claimed for Porcupine Bank (Kloppmann *et al.*, 1996; White *et al.*, 1998), these ideas have never been properly tested.

A wide range of other physical mechanisms have been claimed to affect the success of fish stocks through the variable retention or spillage of larvae (e.g., Iles and Sinclair, 1982; Sinclair and Iles, 1989; Skreslet, 1976). Brown *et al.* (1995; see also Hill, Brown, and Fernand, 1996) suggest just such a role for the density-driven circulation of the western Irish Sea where, in summer, a retentive system of full-depth, jet-like flows develop along the flanks of a cold, dense core of bottom water remaining from the previous winter. The distribution of *Nephrops*, cod, herring, and whiting larvae appear to reflect this current structure (Dickey-Collas *et al.*, 1997), and since the intensity of this circulation will be the net result of variable climatic conditions in summer, the previous winter, and the intervening spring, the potential for year-to-year variability of retention would appear to be high. However, as with most other studies which derive some plausible physical basis for the time-dependent distribution of young fish, we are unlikely to have observations of the system over a sufficiently long period to quantify this variability and convert a potential control into a demonstrable one.

## Temperature: the vital control

Around the beginning of the 20th century, as Ottersen (1996) made clear in his recent review, little was known about the reasons for fluctuations in fish stock abundance. Around that time also, as the yield, weight, liver weight, and roe weight of *skrei* descended to what would prove to be a 100-year minimum (Figure 9; from ICES, 1996), there was much cause to debate the issue. Helland-Hansen and Nansen (1909) were among the first to formulate a clear environmental or climatic connection, and from the information they advanced – highlighting the contemporary minima in the extent of open water in the Barents Sea and in the sea temperatures at Kola, Lofoten, and Stat – it seems clear that they had their focus correctly set on the long-term, large-scale variations in environmental temperature. Since then, a long literature has underscored just how all-pervasive the influence of temperature can be on the life cycle of fish. The effect of temperature change on the survival and distribution of a stock near its limits of range has already been described for the Greenland cod. Other specific and remarkable examples might be these: 1) off Labrador and Northeast Newfoundland, cold ocean temperatures drive cod off the "right site" for the retention and survival of their larvae into more southerly locations where larval retention will be poor (de Young and Rose, 1993); 2) "the temperature dependent spawning of the copepod *Calanus finmarchicus* may be the most important process to cause variability in cod larval survival for the Arcto-Norwegian cod stock" (Ellertsen *et al.*, 1989); 3) for every 1°C warming of the Barents Sea, the food consumption by the Arcto-Norwegian cod

### **Taylor-column flow around Rockall Bank**

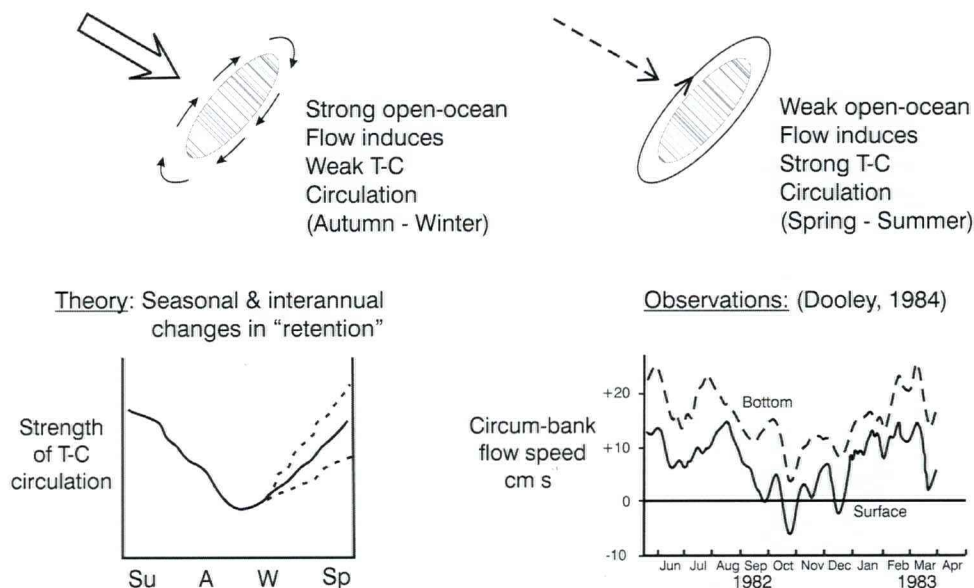


Figure 8. The Taylor column circulation around banks: schematic of seasonal and interannual variability in the strength of the circum-bank flow.

stock increases by up to 800 000 t (Bogstad and Gjøsæter, 1994 and pers. comm.); 4) at 9°C, a 1°C drop in temperature during vitellogenesis will delay cod spawning by 8–10 days (Kjesbu, 1994); 5) for Nova Scotian haddock, "thermal stratification intensity was a better predictor of larval condition ...than any other variable examined including food abundance" (Frank and McRuer, 1989); 6) for a 1°C cooling, annual recruitment to the Irish Sea cod stock will double (Planque and Fox, 1998); and 7) for every 1°C increase in temperature, the weight of a 4-year-old Atlantic cod will increase by almost 30% (Brander<sup>3</sup>, 1994).

Despite a diverse, century-long literature on "temperature and fisheries", it is only since 1995 that three key relationships have been described for most or all of the 17 Atlantic cod stocks. Since establishing these relationships for a single stock might be the product of decades of observations, it is perhaps not surprising that these pan-Atlantic, cross-stock, cod-temperature relations should have emerged so recently.

Brander (1995) was the first to describe the *growth* of Atlantic cod in all 17 stocks as a simple function of temperature and age (Figure 10). The results are dramatic. The mean weight-at-age of cod was found to differ by an

order of magnitude or more between stocks, so that a 4-year-old at Labrador/Grand Banks would weigh 610 g, while one from the Celtic Sea would weigh 7.3 kg. From the growth model provided, Brander suggested that (averaged over ages 2–9) the mean weight of the population would be expected to increase by nearly 1 kg for every 1°C increase in temperature. *Within* a stock also, he shows from observations of the Faroese cod that the mean weight-at-age can almost halve in 5 years through environmental cooling.

The second of the three key relationships which connect the Atlantic cod with temperature variability was established in 1999 when Planque and Frédou pieced together a number of weakly- (or non-) significant, single-stock relationships to form a unifying, significant, Atlantic-wide link between temperature change and *recruitment* for nine Atlantic cod stocks. Their main conclusion (Figure 11b) was that for stocks located in warm (cold) water, the relationship is negative (positive), while for stocks in the mid-range of temperature, there is no relationship. In Figure 11a, the individual regressions of recruitment on temperature for each stock are assembled into a schematic that is more directly comparable with the temperature-growth relationship just described (Figure 10).

In attempting to assess the response of a cod stock to temperature variability, age of maturity is a third key factor. Figure 12 is a first attempt to illustrate the

<sup>3</sup> After serving as the first Chair of the ICES Working Group on Cod and Climate Change, Keith Brander has served as ICES GLOBEC Secretary since 1996.



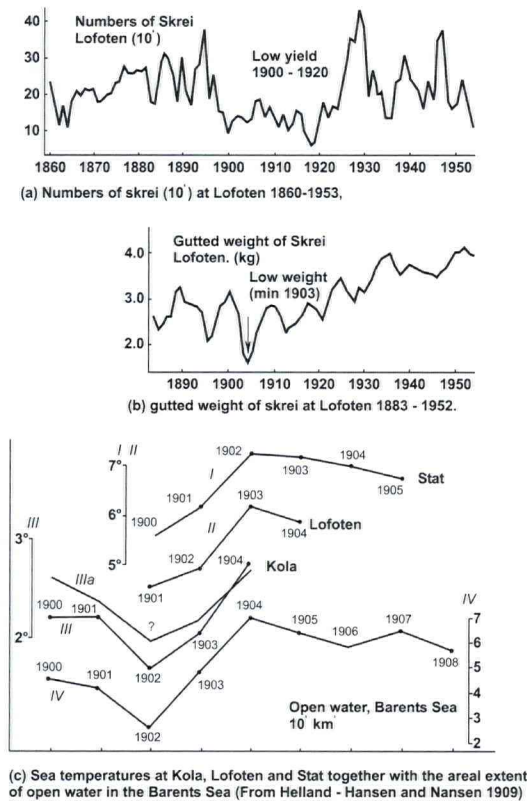


Figure 9. Extreme climatic deterioration off northern Norway in the early years of the 20th century. Panels show (a, b) minima in the yield and weight of *skrei* at Lofoten (Anon., 1996) coincident with long-term minima in sea temperatures from Stat to Kola and in the extent of open water in the Barents Sea (Helland-Hansen and Nansen, 1909).

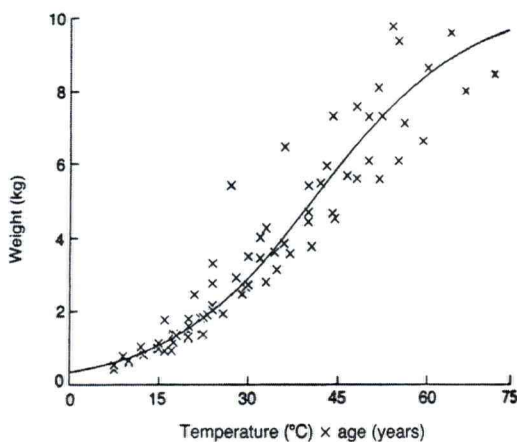


Figure 10. Weight of Atlantic cod in all 17 stocks as a function of temperature and age. From Brander (1995).

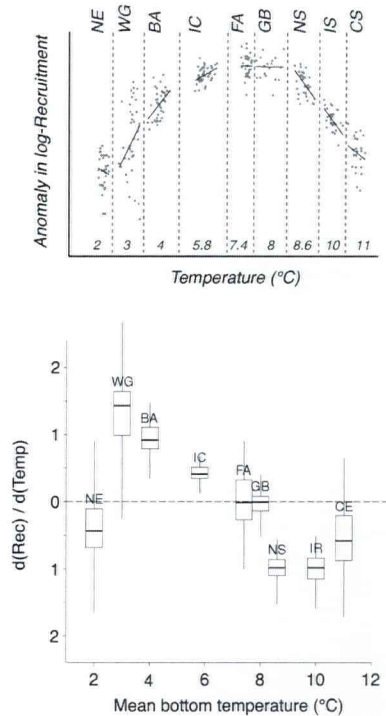


Figure 11. (lower panel) Relationship between temperature change and recruitment for nine Atlantic cod stocks, from Planque and Frédou (1999). In the upper panel, the individual regressions of recruitment on temperature for each stock are assembled into a schematic that is more directly comparable with the temperature–growth relationship described in Figure 10 (Planque, pers. comm.). For further explanation, see text.

Atlantic-wide nature of the relationship, kindly constructed for this paper by Keith Brander using data from 10 stocks (Baltic, North Sea, Celtic Sea, Northeast Arctic, Faroe Plateau, Iceland, Irish Sea, Kattegat, West Scotland, and NAFO 2J3KL; data from the 1999 ICES ACFM report).

These three pan-Atlantic figures are appropriately the culmination of this paper, forged as they are from so much of the available record of multi-decadal hydrographic variability in the ICES area. And as Brander (1994) suggested, "the comparative method is a powerful tool both for identifying factors which shape life history patterns and for investigating them thoroughly". Although temperature is plainly not the only parameter affecting the growth or maturity or recruitment or distribution of a stock, it is one which will, nevertheless, have significant effects on stock assessment, catch forecasting and in evaluating the effects of climate change. Although exploiting this fact will require more detailed information than is currently available on the *ambient* temperature experienced by different ages of cod in dif-

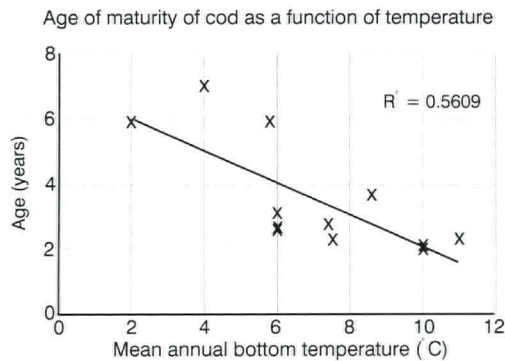


Figure 12. Relationship between age of maturity and temperature for ten Atlantic cod stocks (constructed by Keith Brander).

ferent years (Brander, 1995; Ottersen *et al.*, 1998), there are now three potential aids to doing so: 1) the use of micro mass spectrometry to derive high-resolution, ambient temperature, and salinity records from cod otoliths (Weidman in ICES, 1996, pp. 7–8), 2) the use of data storage tags to record ambient data in the field (Metcalf and Arnold, 1997; Metcalfe *et al.*, 1999), and 3) a limited, but improving, ability to model and predict sea temperature for important areas of shelf (e.g., Ottersen *et al.*, 2000). Even so, the research problem will not end with the building of realistic predictive models; the ecosystem response may move beyond the range of our past experience. To give just one apposite example, if the NAO continues to amplify under greenhouse gas forcing (see Gillett *et al.*, 2002), will *continued* warming of the Barents Sea necessarily be to the benefit of its ecosystem and fishery?

ICES was founded to explore the link between environmental change and ecosystem response. As NAO forcing passes beyond the range of our past experience and as an anthropogenic contribution to climate change becomes more probable (Houghton *et al.*, 1996), it would seem vital that ICES continues to keep pace with both forcing and response through the maintenance of its long hydrographic and ecological time-series. The need to continue these series is the main conclusion and recommendation of this paper.

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