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Understanding environmental controls on fish stocks and progress towards their inclusion in fish stock assessment

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The need to understand the impact of the environment on the fluctuations in fisheries yield in the Northeast Atlantic was a major motivation for the creation of ICES. From the very beginning, two main research tasks were taken on: 1) the establishment of relationships between the distribution and behaviour of fish and environmental characteristics for the purpose of real-time and short-term predictions and advice about where and when the fishing fleets could increase their catches, and 2) the influence of environmental factors on fish stock parameters/variables such as recruitment, growth, maturation, and mortality in order to advise on optimum yields and forecast yield fluctuations. While the purpose of the first of these tasks was rendered unnecessary some decades ago by developments in fish finding and communication systems in the commercial fleets, the second task remains a major topic for study. Until a few decades ago, knowledge of the relationship between fish and environmental conditions was largely qualitative and based almost exclusively on field studies which provided information on "associated phenomena", in some instances quantified by correlations where the underlying mechanisms were hypothesized. During the 1960s and 1970s, efforts to describe "cause and effect" and to quantify the relationships increased considerably. These efforts included studies of species and stock interactions, ecosystem modelling, and field and laboratory experiments with instrumentation enabling observations of fish and their offspring as well as environmental variables over wide ranges of size, space, and time scales. The results of such process-related investigations, coupled with observations from long time series of environmental data and life history tables for fish stocks form the basis for our present understanding of how environmental conditions influence stocks and yields. For some stocks, such knowledge has been included in the regular stock assessments carried out by ICES in recent years.

Keywords: environment, fish, fluctuations, history, stock assessment.

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Introduction

In a report to one of the early ICES meetings, Otto Pettersson (1905) wrote: "Up to the present time the migrations of the fishes have been ascribed solely to tendencies of food seeking and propagation. The discovery of fish migration with hydrographic conditions is in no way inconsistent with this theory." Pettersson had long been aware that environmental conditions would affect migrations (Pettersson and Ekman, 1891). A few years later, Johan Hjort, in his summary of the first five years of ICES cooperation, stated: "That we can thus from the Arctic Ocean and even down to the North Sea, trace a connection between the growth and production of fishes and climatic conditions, seems to show that the productiveness of fish is subject to such mighty influences that it may be regarded as independent of the interference of man." The hypothetical conclusion in this statement regarding the independence of interference of man has later been experienced to be wrong for exploited species and stocks. However, the general observation, i.e., "a connection between the growth and production of fishes and climatic conditions" was elucidated in Hjort's classic work a few years later (Hjort, 1914) and became a major topic of study throughout the history of ICES. The immediate outcome of such studies was often to explain all fluctuations in fish populations in terms of environmentally related variability in recruitment. Some decades later, when marine scientists acquired the tools for studying the effect of fisheries on the populations, they tended to forget about effects of changing environmental conditions and to explain all stock fluctuations as effects of fishing (Jakobsson, 1992). The concept of maximum sustainable yield (MSY), together with the tools Jakobsson (1992) referred to, led scientists into a "trap" where they struggled to provide a value for MSY; i.e., an estimate of long-term mean yield that the stock can sustain. Because of the great natural fluctuations many stocks experience, the level of MSY will fluctuate between wide limits depending on which period of a data time-series is used for computation. Today, there seems to be general agreement that "the role of stock assessment is not to make best possible guesses at MSY, but rather to help design a management system that can respond to the types of variability we see in nature" (Hilborn and Walters, 1992).

The expectations among the founders of ICES as to the future results of the cooperation they had initiated were great: "Undoubtedly we shall derive therefrom splendid discoveries of both practical and theoretic interest, and these discoveries await the attention of International Fishery Research," to quote Johan Hjort (1908). However, apparent discoveries to some scientists have often been mistakes in the opinion of others owing to the difficulties involved in separating causes and quantifying their influence on the great fluctuations in fisheries yields. The Thompson-Burkenroad debate about the cause of the decline in the abundance of Pacific halibut is a classic example (Hilborn and Walters, 1992). Another example is the Devold-Høglund debate on the Bohuslän herring fishery. Devold claimed that the appearance of rich fisheries for herring at the Swedish west coast in previous centuries was due to "periodic" shifts in spawning grounds and spawning time of Norwegian spring-spawning herring, and he attempted to justify this through a temperature-related shift in maturation which, year by year, caused the herring to migrate farther south in order to find suitable spawning conditions. Høglund, who had sampled and analysed the remains of herring left from previous production, simply stated that the herring fisheries at the Swedish west coast were based on North Sea herring. At the 1964 ICES meeting, Hela, the Chair of the Hydrography Committee, closed the meeting of the Committee so that we could attend the Devold-Høglund debate in the Herring Committee.

Clearly, our understanding of how environmental factors affect fish stocks is closely related to our understanding of how fishing affects fish stocks. The separation and quantification of these effects is the main challenge and task in fish stock assessment.

Existing knowledge in about 1950

In 1948 and 1951, ICES arranged two special meetings on fish in relation to their environment: "Climate Changes in the Arctic in Relation to Plants and Animals" (ICES, 1948) and "Fisheries Hydrography" (ICES, 1952).

In their invitation to the 1948 meeting, the Conveners, Rollefsen and Tåning (1948), wrote: "Thus it is clear that some of the largest fisheries in the northern hemisphere – e.g., some cod fisheries – during the coming years will be completely dependent on the course of the present mild period in northern waters." The mild period they referred to was the northward penetration of warm and saline water masses in the North Atlantic since 1920, particularly pronounced during the 1930s and accompanied by northward displacements of distribution boundaries for a wide range of species as well as increased yields in many fisheries (see Dickson *et al.*, 1992 for references). Obviously, Rollefsen and Tåning held the opinion that the increased yields of cod during the previous decades were, at least partly, the result of increased biomass production due to favourable environmental conditions. This opinion was based on a large number of studies on changes in the North Atlantic ecosystem and their causes (Lee, 1948) as well as on experimental and field work showing a positive correlation between fish growth and temperature (Fulton, 1904; Johansen and Krogh, 1914; Tåning, 1929; and others). They also knew that the results of studies carried out over several decades on the survival of larvae and young fish in relation to plankton indicated the importance of the timing of plankton production for larval survival in several species. In addition, they had long been aware of the dependency of plankton feeders (sardines and herring) on sufficient amounts of suitable plankton for growth, and plankton investigations were established for the purpose of advising fishermen about herring concentrations (Russell, 1952).

Both the 1948 and 1951 meetings may be seen as follow-ups to the thoughts behind the creation of *Annales Biologiques* (first published in 1943) a decade earlier, i.e., to provide time series of hydrographic and biological data that could easily and directly be compared. At both meetings, papers were presented showing correlations between environmental factors (temperature, salinity, and wind) and biological variables (distribution, recruitment, and growth). In particular, it was mentioned that salinity seemed to have a great influence on year classes of cod in the Baltic (Alander, 1952) as "they have been strong when the salinity has been high".

So, what was known about fish and the environment in about 1950? A brief and schematic answer might be:

1) Associations between changes in environmental variables (mainly temperature and salinity and plankton) and changes in the availability, distribution, recruitment (i.e., survival of larvae and young fish), and growth were demonstrated by time-series from field studies and were subjected to attempts at quantification by correlations for several species and stocks in various regions.
2) The large year-to-year variations in mortality at early stages were well documented in several stocks and were hypothesized to be caused by starvation, mechanical disturbances, predation, etc.
3) The mechanisms involved in the relationships were also, to a large extent, hypothetical because of the

lack of both experimental studies and appropriate field data. (In particular, the two World Wars had interrupted most of the time-series of such data).

These points were commented on by Lucas, who was the Convener of the 1951 meeting, as follows: "Whilst these various observations point as yet only to associated phenomena, it may be difficult to resist the view that, in some instances, the workers have been discussing relationships which may come to be seen as cause and effect" (Lucas, 1952). At the same meeting, Russell, in his review of plankton research in relation to fisheries hydrography, stated: "There are now correlations known to fit wind and water movements, but the success of any one year-class of a fish has not yet been pinned down to the abundance of the right food at the right moment or even the recorded destruction of eggs and larvae by storm action." Russell (1952) asked for more and longer time-series of observations of appropriate plankton organisms for larvae survival studies.

Spatial and temporal distribution – where and when to fish?

The study by Pettersson and Ekman (1891) showing that herring at the west coast of Sweden avoided the cold, low-salinity Baltic water is perhaps one of the earliest demonstrations that changes in the environment largely affected the availability of fish to the fisheries. The promising immediate economic benefit of such investigation, i.e., advice on where and when to fish, made them attractive to industry and scientists, and throughout the main part of the history of ICES, efforts have been made relating harvestable concentrations of fish to environmental characteristics (hydrography and plankton) for purposes of direct fishery use. The importance ICES placed on this matter is evident in the recommendations from the 1951 special meeting on "Fisheries Hydrography" (ICES, 1952) where it was explicitly said that the results for cod near Bear Island (Lee, 1952) and for herring in the Norwegian Sea (Devold, 1952) should be brought to the attention of fishermen in all countries.

In their book *Fisheries Hydrography*, Hela and Laevastu (1961) summarized the information gathered prior to 1960 on the influence of the environment on fish (distribution, migration, behaviour, growth, and mortality). The book focused on how to use observations of physical and chemical variables and plankton as guidance for where and when to fish, i.e., "relations which can be used directly or indirectly for the benefit of fisheries operations", in the words of the authors.

Prior to the introduction of acoustics, nearly all information on the spatial distribution of fish was from catches (commercial and scientific) and tagging experiments. The improved resolution and sampling speed offered by echosounders and sonars initiated an era of thorough mapping of the oceans and their inhabitants. In order to advise fishing fleets, large-scale echo surveys were carried out in many regions during the 1950s and 1960s with the aim of mapping fish concentrations and studying migrations in relation to environmental factors, including prey organisms. Examples of such surveys and their results are given in Hela and Laevastu (1961), Kristjonsson (1971), and Cushing (1973). Jakobsson (1971) listed the information that had to be obtained before bulletins were broadcasted to the fleet:

1) position, extent, depth, average size and number of schools, as well as their movements; and
2) the state of environmental factors (hydrography and plankton) that were likely to influence movements and behaviour of the concentrations in near future.

The increasing survey activity during the first 2–3 decades after World War II combined with information from increasing and more wide-ranging commercial fishing activities contributed greatly to the detailed knowledge on fish distribution, migration, and behaviour in relation to environmental factors in many fish stocks (Cushing, 1973), knowledge that has become useful both in the planning of surveys for stock assessment purposes as well as in the processing of data and interpretation of results from such surveys. The development of fish-finding equipment, capture technology, and communications systems in the fishing fleets in the period 1950–1970 rendered, to a large extent, unnecessary the need for direct advice to the fishermen, and the main objectives of this type of survey gradually shifted towards obtaining estimates of abundance for stock assessment purposes (Sætersdal, 1978). Also, field survey activities directed towards basic oceanographic studies (transport, sea-atmosphere energy exchange, etc.) as well as process-oriented investigations in ecology, including survival studies of eggs and larvae, increased substantially during these years (see ICNAF, 1965; Blaxter, 1974; Sherman and Lasker, 1981). Along with the accelerating development in observation, data-processing capacity, and modelling, and the rapidly growing number of scientists with backgrounds from a wide range of disciplines, the angle of attack of the old problem – when and why do the offspring from a spawning die? – also became wider.

Fluctuations in yield and stock size – fishing or/and environment?

How many offspring from a spawning reach the size (age) of recruitment to the fishery and how are these numbers reduced as fish become larger (older)?

At the time ICES was created, some scientists were convinced that fishing in addition to the environment affected the future yield. They were mainly concerned with growth overfishing, i.e., where fisheries removed small and young fish of no commercial value to an extent that reduced future stock numbers and yields of

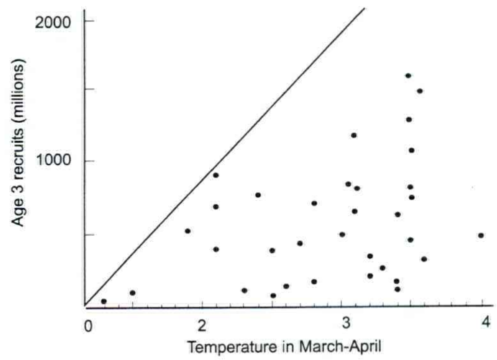

Figure 1. Year-class strength in Northeast Arctic cod and temperature on the spawning grounds. Redrawn from Ellertsen *et al.* (1989).

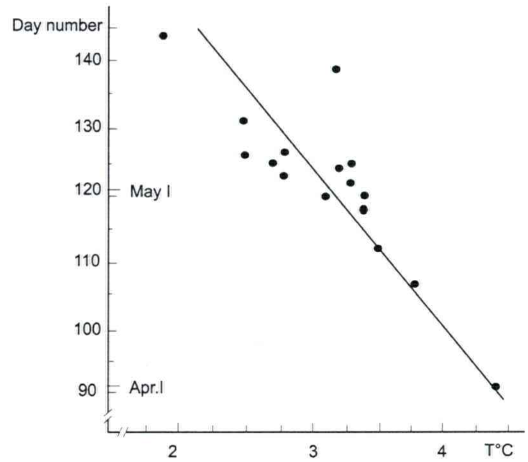

Figure 2. Time of maximum occurrence of *Calanus finmarchicus*, stage 1, versus temperature. Redrawn from Ellertsen *et al.* (1989).

large-sized valuable fish. Less attention was paid to the problem of recruitment overfishing, i.e., where the fishery reduces the spawning stock so much that recruitment is negatively affected, although the Danish scientist Johannes Petersen had made the distinction between these two types of overfishing as early as 1903 (Jakobsson, 1999). Prior to World War II, neither the available observations nor the analytical tools were convenient for analysing stock-recruitment relationships and determining possible recruitment overfishing. The development of the theory of fish population dynamics (Graham, 1939; Beverton and Holt, 1957) and its implementation using catch-at-age data (Fry, 1949; Gulland, 1965) changed that situation: from the late 1960s, it became possible routinely to generate life history tables for exploited stocks, i.e., observations of catch-at-age were used to generate annual time-series of stock numbers-at-age. Although the new technique was developed and used to analyse the impact of fishing on stocks, the results of the analyses, i.e., the time-series of stock numbers at age which included estimates of recruitment, provided valuable basic data for studies of how recruitment was related to environmental factors and parent stock size.

The extension of the Beverton and Holt theory to take account of prey–predator relationships (Andersen and Ursin, 1977) was another major breakthrough in the establishment of more realistic life history tables, particularly for typical prey species and the younger age groups of large-sized fish for which the natural mortality usually is large and variable. The practical applications of Andersen and Ursin's work required quantitative knowledge of the energy budget in fish, knowledge that had been gathered from increasing efforts in the study of fish physiology, metabolism, and growth since World War II, particularly since 1970 (see Brett and Groves, 1979; Jobling, 1994). From information on predator stomach contents and stomach evacuation rates, the effect of predation could now be estimated and incorporated when life history tables were generated from catch-at-age data. Important results of these achievements are that we have had access to time series of recruitment during the past few decades for most exploited stocks, i.e., the number of fish which recruit to the fishery, based on commercial catches. In more recent years, the effect of predation is also, to a large degree, accounted for in the recruitment estimates given for some stocks.

However, long before it became possible to quantify prey–predator relationships, scientists were well aware of the effects of such relationships on stocks. This is evident from Graham's discussion of the theoretical results obtained during the 1930s for detecting overfishing (Graham 1939): "As the stock of food fishes is reduced these other species probably increase." The stock of "food fishes" was cod and haddock, while "these other species" were their prey, and Graham continued: "For this reason the case is probably more complicated than has been assumed here." In present-day ICES language, Graham would probably have said: "The inclusion of stock interactions in the analysis will affect the results obtained from this single-species assessment model."

The usefulness for fish-environment-related studies of the theories and techniques developed is that we now have long time-series of stock numbers-at-age, dating back to the beginning of the 20th century for some stocks (Hylen, 2002; Toresen and Østvedt, 2002).

Enclosure studies – recruitment studies – cause and effects

When and why do prerecruits die?

Ever since the great variations in year-class strength of fish were discovered – actually, it was the variations in number of fish caught from each year class (Hjort, 1914) – the major question has been, "When do the offspring from a spawning die and what are the causes of the mortality?" Hjort (1914) hypothesized that the most critical period in Norwegian spring-spawning herring was the "very earliest larvae and young fry stages", and he suggested that lack of food could be a major cause of mortality and also that currents could transport larvae into unfavourable areas. May (1974), who reviewed the extensive literature from field and laboratory investigations on factors influencing survival and growth of larvae, found that:

1) The relation between starvation induced mortality at yolk sac and year-class strength remains unclear. It seems likely that year-class strength is influenced in many cases by food availability for first feeding larvae, as Hjort hypothesized, but the case is based largely on circumstantial evidence.
2) Different species react differently to food deprivation, and the feeding conditions facing a given species will vary both spatially and temporally. Whether a critical period in Hjort's sense of the term exists in a given instance will depend on a number of environmental and species specific factors.

During the 1970s, scientists became increasingly concerned with some conflicts in results between laboratory experiments and field investigations regarding the survival and growth of fish larvae, particularly the lower density limit of suitable prey items needed for larval development and survival. Laboratory experiments indicated a much higher level of this limit than seemed reasonable judging by field data. In order to bridge the gap between laboratory and sea work, scientists opted for enclosure studies, i.e., studies of the development of *known initial numbers* of larvae of *known age* in large controlled volumes of water (plastic bags or basins) under conditions which approximated those in the field (Solemdal, 1981). Enclosure studies had, by then, been used for more than a decade in order to obtain detailed information about ecosystem processes at lower trophic levels, including primary production and zooplankton grazing and growth, as well as in benthos ecology (Parsons, 1978).

The enclosure studies together with results from field work with improved sampling methodology revealed spatial and temporal distribution patterns not observable some decades earlier. Laboratory investigations on food and nutrition requirements of fish larvae have also greatly improved our understanding of when and why offspring die. A considerable contribution to this understanding is the knowledge of how turbulence affects the contact rates between larvae and their prey (Rothschild and Osborn, 1988; Sundby and Fossum, 1990; MacKenzie, 2002). The discovery of daily growth zones in the otoliths, which made it possible to make better use of larvae survival curves, was another major step in the development. Houde (1989), who investigated growth, mortality, and energetics of marine fish larvae worldwide, found that both growth and mortality increased with increasing temperature. Increased growth is the result of increased consumption and may, thus, lead to an increase in competition for food and generate cannibalism among larvae unless the availability of suitable prey also increases (Folkvord, 1991).

Recruitment in cod is probably one of the most investigated subjects throughout the history of ICES. Already 30 years ago, there was evidence that cod in the North Sea showed a decrease in recruitment with increasing temperature (Dickson *et al.*, 1974), while there were indications that increasing temperature favoured recruitment in the more northerly cod stocks. During the 1950s–1970s, the main cause of the apparent temperature–recruitment relationship in many stocks was hypothesized to be a match-mismatch in time between larvae and their prey. For Northeast Arctic cod (Arcto-Norwegian cod), studies in the 1970s–1980s led to the establishment the situations seen in Figures 1 and 2. Figure 1, which shows the plot of recruitment at age 3 (estimated from catch-at-age data) against the temperature at the spawning grounds, indicates clearly that recruitment is positively related to temperature. Figure 2 shows the occurrence of copepodites of *Calanus finmarchicus*, the main prey item for cod larvae, and suggests a possible contributor for the relationship in Figure 1. At low temperatures, *Calanus* spawning is so late that the majority of cod larvae, hatched in April, do not find food. Helle (2000) discussed the importance of *Calanus* as food for cod fry also at later stages (3–5 months of age). Investigations during the 1990s have clarified the difference in the relationship between temperature and recruitment for "southern" and "northern" cod stocks, as indicated in Figure 3. In his recent comprehensive review of the subject, Sundby (2000) proposed that this difference is caused by changes in the advection of *Calanus* from the core production regions in the central part of the North Atlantic Subpolar Gyre to the areas where the various cod stocks have their habitat, i.e., that the apparent temperature–recruitment relationship in Figure 3 is a proxy for a food abundance–recruitment relationship due to large-scale variations in food transport.

Also in the Baltic cod stock, recruitment depends largely on the mortality during the pelagic phase of early life stages (Aro, 2000). However, in contrast to the other cod stocks in the North Atlantic, it is found that year-to-year changes in the physical environment itself may directly affect egg survival through variations in the size of the so-called "reproductive volume". This volume is defined by boundaries of salinity and oxygen

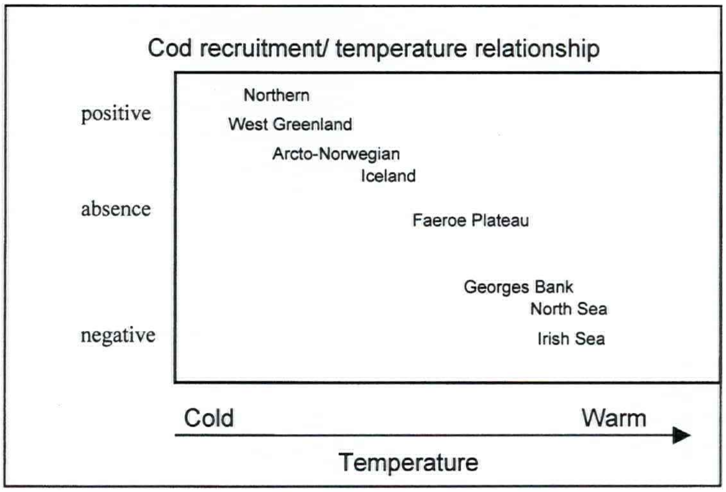

Figure 3. The nature of the relationship between temperature changes and recruitment in North Atlantic cod stocks (Planque and Fox, 1998; Ottersen, 1996).

which meet the requirements for successful egg development. The volume changes in size with the aperiodic renewals of Baltic deep waters, and is shown to be a rather good indicative measure of cod-spawning possibilities and thus recruitment (see Aro, 2000 for references). Hence, a "cause-and-effect" explanation for the correlation between high salinity and increased year-class strength observed more than 50 years ago (Alander, 1952) seems established.

Stock assessment and environment – growth, consumption (natural mortality), catchability, recruitment

In his discussion on stock assessment and biological knowledge, Ulltang (1996) concluded that the quality of assessments would improve considerably by making use of a large amount of knowledge and data, biological and environmental, which in a stock assessment/management context remained unused. Some findings which elucidate his point are briefly mentioned below.

Growth of a predator means consumption and, as a consequence, natural mortality of the prey. The substantial effects of temperature on fish growth have long been known and have been demonstrated in more recent years both by feeding experiments and by studies of field data (Jobling, 1994; Brander, 1994, 1995; ICES, 2000a). In a stock assessment context, where estimates of consumption by the predator fish are used as estimates of partial natural mortality of prey species, it is thus required that the ambient temperature of the predator is known (ICES, 1998). Ambient temperature for a given age or size group may vary greatly between and within years depending on the spatial and temporal distribution of both field temperature and fish, and may, for some stocks, be related to their abundance (Ottersen *et al.*, 1998). Since food consumption increases by about 15% per degree Celsius and growth by about 10% per degree Celsius, it seems vital that estimates of ambient temperature for use in consumption calculations are worked out on the basis of the actual spatial distributions of both temperature and fish. Michalsen *et al.* (1998) showed that the differences between the actual ambient temperature and the temperature used for calculating food consumption by Northeast Arctic cod amounted to 1–3°C, indicating that consumption estimates might have been biased by 10–40%, a matter that could seriously affect the estimates of stock numbers of cod prey (capelin, young cod and haddock, redfish, etc.).

Changes in the distribution of stocks due to environmental effects may seriously influence our perception of stock abundance. Figure 4a illustrates how catch per unit of effort of Northeast Arctic cod was maintained during a period of pronounced stock decline. The major explanation for this paradox is that, in 1979–1981, intense cooling caused a redistribution of Barents Sea cod to the south and west (Figure 4b, from Nakken and Raknes, 1987), resulting in the maintenance of fish densities and catch per unit of effort in the Norwegian fisheries.

The Report of the ICES/GLOBEC Workshop on the Application of Environmental Data in Stock Assessment (ICES, 1998) states: "In order to facilitate the use of environmental data in stock assessment, environmental life history indices, preferably for each age (stage) and year should be established for each particular stock according to the scheme used for stock variables (parameters). The available time-series of environmen-

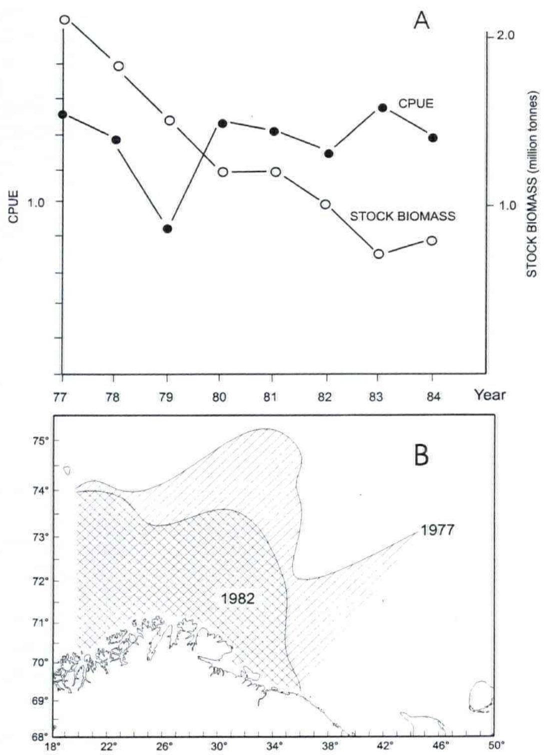

Figure 4. Northeast Arctic cod. A) Estimated stock biomass and catch per unit effort (cpue) for Norwegian trawlers, 1977–1984. Source: ICES (2000b). B) The distribution in February 1977 (normal temperature) and February 1982 (low temperature).

tal indices together with the substantial amount of information on spatial distributions gained from surveys in recent decades could be utilized for the purpose. The work necessitates close cooperation between experts in various fields of marine science with in depth knowledge of the ecology (fish and environment) of the area, and should be conducted as an integral part of the preparatory work for each assessment working group meeting." Apart from the obvious reason for the establishment of environmental (or ambient) temperatures given above – their importance for growth and consumption – historic estimates of environmental or ambient indices would provide time-series for comparison with the information from the historic records of stock numbers at age.

In the course of the past 5–10 years, the effects of the environment on fish stock production and mortality has been incorporated qualitatively and quantitatively in several stock assessments (ICES, 1998). Where this has been achieved, it is based upon a good understanding of the ecology of the system, allowing comprehension of the mechanisms underlying the statistical correlation, as exemplified by the development, in recent years, in the assessment of Baltic cod (Sparholt, 1996; Aro, 2000). The future development of the inclusion of environmental data in stock assessment is dependent on the active participation of experts on the environment in stock assessment-related work, or as formulated by Sverdrup (1952): "In all this work hydrography will not assume a unique position, but must take its place as an integral and indispensable part of the combined effort."

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