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Realizing the basis for overfishing and quantifying fish population dynamics

Øyvind Ulltang

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ICES was established in part because of serious concerns that North Sea fish stocks were being overfished, although great difficulties were experienced with defining overfishing. Hjort provided a new synthesis of the causes of fluctuations in landings by introducing age compositions of stocks and explaining the fluctuations by year-class variations. This explanation opened up revolutionary new possibilities for stock predictions. There is a close connection between solving the problem of defining overfishing and the development of fish population dynamics theory and models. In the 1930s, an operational definition of the term overfishing was made possible by Hjort's theory of optimum yield using population growth models, and this was applied by Graham to North Sea fisheries. Later developments of stock-recruitment theory and yield-per-recruit models made it possible to define the terms growth overfishing and recruitment overfishing. In the early days of fish population dynamics modelling, a particular problem was the mathematical treatment of mortality. Baranov had solved this problem in 1918 by defining instantaneous mortality rates, but his contribution was not recognized until the late 1930s by Graham and others, and Ricker appears to be the first to have fully understood Baranov's paper. The analytical approach by Baranov and Ricker was further developed in the pioneering work of Beverton and Holt in 1957. The influence of the work of Beverton and Holt was enormous. Their models became standard tools in stock assessments and laid the basis for the development of virtual population analysis (VPA) and modern catch prediction methods. Andersen and Ursin formulated a multispecies extension of Beverton and Holt's theory which became a key reference for later work with multispecies models. Also, quantification of the effect of a fluctuating physical environment on fish stocks has recently received more attention. Quantifying multispecies and environmental effects and developing stock assessment models capable of utilizing all sources of data that may contain information on the stock are the main challenges of today.

Keywords: history, ICES, overfishing, population dynamics, stock assessment.

Øyvind Ulltang: University of Bergen, Department of Fisheries and Marine Biology, Bergen High Technology Center, N-5020 Bergen, Norway; tel: +47 55 58 44 57; fax: +47 55 58 44 50; e-mail: oyvind.ulltang@ifm.uib.no.

Introduction

Many explanations have been offered for fluctuations in fish catches. The dominant theory during the second half of the 19th century was that fluctuations in catches were the result of varying availability and migrations, not of changes in production.

The existence of separate, self-sustaining, local populations within the geographic area of a species, as demonstrated for herring by Heincke towards the end of the 19th century (see Sinclair and Solemdal, 1988), contributed to the refutation of this theory and made overfishing a realistic possibility.

Although there was a gradual move away from explaining the variation in catches by variable migration patterns alone, the need for more insight into the life cycle and whereabouts of migrating fish was obvious. Very little was known, for example, about nursery and feeding areas for the large populations of herring and cod. At the beginning of the 20th century, two main problem areas were thus identified: the danger of overfishing and the whereabouts of migrating fish.

At the 1902 inaugural meeting of ICES, Hjort proposed that the biological programme be organized in two committees, one (Committee A) to study the migrations of herring and cod and the influence of these migrations on the fisheries, and the other (Committee B) to study the question of overfishing. The proposal was adopted with the addition of a third committee (Committee C) for the Baltic Sea fisheries. The work of the Committees became extremely important for improving the understanding of the effects of fishing and quantifying fish population dynamics. Studying the effects of fishing and realizing the basis for overfishing required a deeper understanding of fish population dynamics and the causes of variations in fish catches. Quantifying fish population dynamics was a prerequisite for operationally defining the term overfishing.

What is overfishing?

Committee B had great difficulty in defining the term "overfishing". The debate inspired the important paper by Petersen in 1903 entitled "What is overfishing?" in which he distinguished between different effects of fishing, including i) reducing the mature stock so that too few eggs were produced, and ii) reducing the average size or age of the fish. The first possibility he thought very unlikely. The second effect was a natural consequence of fishing; the problem was how to determine if this effect had gone too far as it depended on growth and mortality rates and the price of fish.

There is a close connection between solving the problem of defining overfishing and the development of fish population dynamics theory and models. The development of fish population dynamics models will be discussed in more detail later, but some brief comments in relation to the overfishing concept will be offered here. An operational definition of overfishing, in the sense of reducing the population below the level giving maximum production, was made possible by the work of Hjort *et al.* (1933) and Graham (1935), using population growth models. Later developments of stock-recruitment theory and yield-per-recruit models made it possible to distinguish between growth overfishing and recruitment overfishing (Cushing, 1972). It should, however, be noted that the distinction made by Petersen (1903) described above was similar.

Although modelling developments made possible the formal definition of different forms of overfishing, it is still often a major problem in fisheries research to determine whether overfishing occurs, especially with respect to recruitment overfishing.

Why do fish populations vary?

Stock age compositions

By the beginning of the 20th century, examples of using structures in scales or otoliths for age determination of fish were known. The Bergen group under Hjort's leadership showed that scales could be used for age determination of herring, and the method was soon used for other species as well, especially cod and haddock. Hjort had also worked on accident insurance for fishermen, and human population studies raised in his mind the prospect of being able to assign whole fish stocks to age-class systems. Hjort's vision was to mobilize the sampling power of ICES scientists to collect ageing material over a broad area for several years, but he only succeeded in 1909 in obtaining ICES support for a small programme for the North Sea (Smith, 1994).

The British Delegate to ICES, D'Arcy Thompson, disagreed with Hjort on the interpretation of the rings on the scales. The dispute between Hjort and D'Arcy Thompson continued for a long time (for details, see Smith, 1994, and Sætersdal, 2002). After a confrontation at the 1913 ICES meeting, Hjort declared that no programme for herring research could be drawn up until this question was settled, and it took 10 more years before the scale method was adopted. Smith (1994) contended that the dispute was ultimately valuable in demonstrating that the tools of the mathematical statistician were useful to the biologist, while Lea claimed that the dispute set back fisheries research for many years (Went, 1972). Sætersdal (2002) also argued that the remarkable lack of response to Hjort's repeated messages over the years 1907–1914 concerning the importance of stock age compositions had wide and long-lasting effects.

Despite the lack of ICES support, the work by the Bergen group continued with material from herring and cod, resulting in "Fluctuations in the great fisheries of northern Europe" (Hjort, 1914). Here Hjort provided a new synthesis of the causes of fluctuations in landings by introducing age compositions of stocks with a limited geographical distribution and explaining the fluctuations by year-class variations in these stocks. Hjort and his collaborators made a fundamental contribution to fishery science through their utilization of representative age compositions of stocks as a tool to study stock fluctuations, stock identity, and vital stock parameters, and for making stock predictions.

It should be noted that the sampling of cod and herring catches, initiated by the Bergen group, has made it possible to carry out virtual population analysis (VPA) of Arcto-Norwegian cod back to 1913 (Hylen, 2002) and of Norwegian spring-spawning herring back to 1907 (Toresen and Østvedt, 2000).

Monitoring year-class fluctuations

In the 1920s, Hjort's idea of monitoring stock development by age samples of the population was taken up by other scientists. Harold Thompson (working with D'Arcy Thompson) in Aberdeen, and William Hodgson in Lowestoft, both using scale readings, developed sampling programmes for monitoring year-class strength of haddock in the North Sea and East Anglian herring, respectively. They both succeeded in establishing measures of year-class strength at an early stage and using this for catch predictions for the next year (Smith, 1994).

In 1929 and 1930, ICES called two special meetings on year-class fluctuations (ICES, 1930a, 1930b). In an introductory address to the 1929 meeting, Hjort noted that "it is remarkable that we have actually been able to compile *representative statistics* by selecting comparatively small samples of the organisms of the sea, and then to prove that the distribution of ages in these samples was *representative of the whole stock*. But, of course, it is precisely in the selection of representative samples, even more than in the discovery and development of the methods of determining ages, that we see the true art of applying 'vital statistics' to marine organisms" (ICES, 1930a, p. 6). Hjort further said that a biological service should be organized for the regular observation of age distributions and numerical strength of year classes and that in the organization of this, "the International Council will have a task which in itself will repay all the work and expense that its existence during the past thirty years has occasioned".

Monitoring year-class fluctuations soon became an essential part of fish-stock monitoring programmes in the ICES Area. Later, ICES also assumed a central role in coordinating some of the young fish surveys (e.g., the International Young Fish Survey in the North Sea initiated in the 1960s) and as a forum for discussing young fish survey methodology.

Explaining year-class fluctuations

For explaining year-class fluctuations, Hjort (1914) pointed out a particular direction with his "critical period" concept, which emphasized early life history stages and especially the stage when the larvae have consumed their yolk and commenced searching for food. The hierarchical levels of explanations and the non-existence of a final explanation was clearly seen by Hjort, noting that

> It will be evident from the foregoing, that a study of the conditions which determine the numerical value of the year classes can only attain its object when based upon a very extensive plan. As a matter of fact, the object *can never be fully attained*; new questions will constantly arise, as *the knowledge obtained creates the demand for new* . . . (Hjort, 1914).

It was also realized that a relationship between recruitment and parent stock was critical to population stability, and Ricker (1954, 1958) and Beverton and Holt (1957) proposed forms of a relationship between spawning stock and recruitment underlying the observed variability. In 1970, ICES, ICNAF, and FAO jointly convened a symposium on fish stocks and recruitment (Parrish, 1973). Parrish noted in a foreword to the proceedings that the papers and discussions indicated that recruitment was determined by a complex of density-dependent and density-independent factors. The former could act as the main source of control governing the form of the relationship between recruitment and spawning stock size (egg production), and the latter gave rise to the well-known, short-term, irregular fluctuations in recruitment. It was further indicated that these factors operated mainly during the early stages. The symposium also raised serious doubts about the validity of the previously widely held hypothesis that the level of recruitment was mainly independent of spawning stock size over the range of stock sizes "encountered in practical fishery situations". Slobodkin (1973), in his summary of the symposium, noted that it was the consensus of the meeting that density dependence occurs in all fish stocks at some point, and that this was a major transition from earlier dogma. He further drew attention to Fisher's (1930) concept of reproductive value and reproductive value curve, suggesting a connection between survivorship patterns and the distribution of reproductive values with age of stocks.

Techniques currently exist for studying the microstructure of the otoliths from fish and fish larvae. The age in days can be estimated, and the larval and juvenile growth history of sampled individuals can be reconstructed from the otoliths. The resulting possibilities for studying mechanisms operating at early life stages, in particular the interrelations of growth, mortality, and size, have been discussed by an ICES–IOC Study Group and the ICES Working Group on Recruitment Processes (ICES, 1992a, 1992b, 1994, 1996, 1999). By dividing a year class into different cohorts (e.g., different groups of larvae which have been spawned at slightly different times and locations) which can be followed during the early life stages, this may result in a similar scientific revolution as Hjort's breakthrough by dividing the total stock into age groups and following these. It has been shown for several stocks that survivors do indeed originate from distinct subsets of the temporal distribution of eggs (ICES, 1999). Unfortunately, there has been little interaction between this working group and the stock assessment working groups.

The Working Group has also considered ongoing studies of fecundity (ICES, 1999). For example, recent work on Arcto-Norwegian cod has shown that relationships between fish length, condition, and fecundity result in a ratio of egg production to spawning biomass which varies both with the size composition of the spawning stock and fish condition (Marshall *et al.*, 1998). The impact of the physical environment is usually regarded as a density/stock size-independent factor.

However, Kjesbu *et al.* (1996) illustrated how there could be a combined effect of maternal factors and environmental variability for Arcto-Norwegian cod. Combining stock and environmental factors was addressed at the Theme Session on "Cod and Haddock Recruitment Processes: Integrating Stock and Environmental Effects" at the 1999 ICES Annual Science Conference.

Quantifying fish population dynamics

Fish population dynamics models

Russell (1931) formulated an arithmetic yield function that described yield as a function of recruitment, growth, natural mortality, and fishing mortality, but the practical usefulness of the function was limited by the partial interdependence of the parameters. In those early days of fish population dynamics modelling, a particular problem was the mathematical treatment of the two mortality components working together. Baranov (1918) had solved this problem by defining instantaneous mortality rates, but his contribution (published in Russian) was not recognized until the late 1930s by Graham and others, and Ricker (1944) appears to be the first to have fully understood Baranov's paper (Smith, 1994).

Using present-day notation, Baranov said that the effect of fishing (F) and natural mortality (M) rates on the number of fish (N) could be described by the differential equation:

$$dN/dt = -(F + M)N \quad (1)$$

leading to

$$N(t) = N(0)e^{-(F + M)t} \quad (2)$$

where N(t) denotes population number at time t and N(0) population number at time zero. Taking logarithms, this results in a straight line with slope $-(F + M)$ when ln N(t) is plotted against t. Equation (2) resulted in what is usually called Baranov's catch equation (Ricker, 1975)

$$C = F \times N(0)[1 - e^{-(F + M)}]/(F + M) \quad (3)$$

where C is the catch in number during a year and N(0) the numbers present at the beginning of the year.

Baranov performed his analysis in terms of length of fish rather than age, but as noted by Smith (1994), the mathematics are the same to within a constant of proportionality since Baranov assumed that length was increasing linearly with age in the exploited life span.

At this point, it may be interesting to ask how history would have changed if Baranov's work had been recognized when it was published in Russian and if, at the same time, the ageing techniques and Hjort's idea of representative stock age compositions had been accepted. Equations (2) and (3), together with the growth equation of von Bertalanffy (1938), are the basic equations in the analytical model developed later by Beverton and Holt (1957), and a major part of the fundamentals of their age-structured model thus existed 40 years before the model was realized and published.

Instantaneous rates were also applied by Volterra (1928) in an important theoretical paper published by ICES. Volterra described the fluctuations of one predator and one prey population by a set of differential equations. He claimed that his approach provided an easy way of calculating the maximum output of fisheries, but it was not adopted by fisheries biologists.

Hjort and his colleagues, dealing with whales, noted that the interactions of at least two populations needed to be understood for applying Volterra's model, and they had no data on the abundance of whales' prey. Instead, Hjort *et al.* (1933) considered the combined effect of mortality and recruitment (which they called regeneration) in a population growth model and suggested a sigmoid growth curve. At small population size, the rate of increase (population growth) is small. It increases to a maximum for intermediate population sizes and decreases again and becomes zero when the population attains its maximum size. The point of inflection on the curve corresponds to maximum regeneration and is equivalent, in theory, to the population size where the highest equilibrium catch (which they called optimum catch) can be obtained.

Graham (1935) applied Hjort's theory of optimum yield to the North Sea trawl fisheries. For this purpose, he used a particular form of the sigmoid growth curve, namely the logistic curve. His analysis indicated that yield could be increased by reducing fishing effort. Hjort and Graham had finally made overfishing an operational term. Graham (1939) formalized it by saying that "the productiveness of a stock of fish depends on the effort used to exploit it; the productiveness first increasing and then decreasing as the effort increases". Overfishing occurs when yield begins decreasing, and the sigmoid curve could be used for estimating that point, although there were problems in applying the curve to actual fisheries.

Based on the work by Graham (1935), surplus production or biomass dynamic models were further developed by Schaefer (1954) using the logistic curve which results in a symmetrical surplus production curve, and by Pella and Tomlinson (1969), allowing for an asymmetrical curve.

However, developments in ICES became dominated by the analytical approach of Baranov, Russell, and Ricker, which was further developed in the pioneering work of Beverton and Holt (1957). Beverton and Holt divided the population into age groups and described yield as a function of recruitment, growth, natural mortality, and fishing mortality. In contrast to the biomass dynamic models, the analytical model of Beverton and Holt made it possible to calculate short- and long-term effects of changes in trawl mesh size, and this may be one of the reasons why the biomass dynamic models were not pursued in ICES as they were on the west coast of the United States. It was Graham who, in 1946, asked Beverton and Holt to try to put together the whole of fish population dynamics (Beverton and Anderson, 2002). Graham's request for this work was without doubt driven by the questions asked in ICES about dealing with the overfishing question, and the resulting book (Beverton and Holt, 1957) had a tremendous influence on ICES since it was the first successful attempt to assemble the different biological theories into one comprehensive fish population dynamics model.

In their introductory chapter, Beverton and Holt (1957) noted that one essential aspect of their work was the recognition of a fish population as a self-containing *open system*, exchanging materials with the environment and usually tending to a steady state. The system – behaving as a unit through the interaction of the primary processes of birth, growth, mortality, and movement – "is itself but one element in a higher system comprising all the other inter-dependent biotic groups, including man and other predators, competing animals, species at other levels in the food chain and so on". They further noted that the interdependence of the primary factors in Russell's yield function has both direct and indirect components. The direct, formal interdependence is removed in the simple population models in Part I of their book by expressing the primary factors in appropriate mathematical form, i.e., by using Baranov's instantaneous mortality coefficients. However, in that part, the simplifying assumption was made that parameters are constant and independent of population density. In Part II, they introduced indirect interdependence (e.g., elements such as relationships between growth and food consumption and their dependence on population density) into the simple models.

With respect to basic population dynamics modelling, not very much happened between Beverton and Holt (1957) and Andersen and Ursin (1977). Andersen and Ursin carried further the concept of a fish population as a self-containing *open system*, exchanging materials with the environment, in their multispecies extension of the Beverton and Holt theory of fishing. Although their very detailed and extensive model was not suitable for direct application in fish stock assessments, the conceptual framework introducing the basic concepts of feeding level and prey suitability for quantifying multispecies effects on fish growth and mortality has been utilized in later work such as multispecies VPA (Sparre, 1991) and area-disaggregated multispecies simulation and prediction models (Stefánsson and Pálsson, 1997; Tjelmeland and Bogstad, 1998). ICES did not play any role in the development of the Andersen and Ursin model, but the ICES Ad hoc Multispecies Working Group, which was established around 1980, took an active part in the development of multispecies VPA and also in establishing the stomach sampling programme for the North Sea.

Stock assessments

Early assessments

An extensive early assessment of the effect of fishing was reported in Garstang (1900) (see Smith, 1994, for a review). Garstang both reanalysed data from a Scottish trawling experiment in two bays in Scotland in 1886–1895 and analysed data on the catch of bottom fish from the expanding trawl and line fishery on the east coast of England in 1889–1898. Despite many difficulties and deficiencies with the available data, he was able to calculate catch per standardized unit of effort (cpue) and the number of standard effort units that would have been required to catch the fish actually caught each year. He found that cpue had decreased by about 50%, and concluded that the bottom fisheries were not only exhaustible, but in "rapid and continuous process of exhaustion".

During the first years of ICES, the plaice fishery was the main concern of the Overfishing Committee. The Committee initiated the collection of catch statistics and market sampling, and organized research vessel trawl surveys and large-scale marking of plaice. For estimating the effects of a larger size limit, Petersen (1894) had already suggested a method for determining the age of fish based on length compositions. In 1908, Heincke was appointed to summarize the national contributions on plaice and prepare a report. Beverton (1992) gave an enthusiastic description of "Heincke's remarkable report" (Heincke, 1913). Using available systematic length-at-age data for plaice, Heincke showed that if the length distributions were transformed to logarithms, the right-hand side was often close to linear. Although he had difficulties believing it, he had realized that the shape of a length distribution could provide a means of estimating the mortality rate. He also used the data and a rough conversion from length to age to estimate the percentage reduction in numbers from year to year. In fact, this was a type of first catch-curve analysis (assuming linear growth) conducted even before Baranov had published his exponential survival function.

The two world wars demonstrated the effect of reduced fishing, especially on the heavily exploited demersal fish resources in the North Sea. As noted by Sætersdal (2002), Graham's (1935) assessment of these resources was the first presentation in an ICES document of an estimate of the effect of changes in effort on yield. The effect of World War I on the fisheries was essential in Graham's arguments when applying the sigmoid population growth curve. The effect of World War II was reviewed at a special scientific meeting held in conjunction with the 1947 ICES annual meeting. Graham (1948) summarized, as rapporteur, the evidence for each of the stocks reviewed and concluded that, for all stocks except one (Arcto-Norwegian cod), the principal effects were the same, namely:

a) an increase in density due to greater survival; and
b) changes in growth rate, but not of sufficient magnitude to prevent the increase in density.

Analytical stock assessments

The influence of the work of Beverton and Holt (1957) was enormous. Their simple models in Part I of their book became standard tools in stock assessments and laid the basis for modern catch-prediction methods. Their yield-per-recruit (Y/R) model was a simple tool for studying growth overfishing and was applied extensively by the stock assessment working groups established during the 1960s. That the analytical tools created by Beverton and Holt came into practical use in ICES working groups so soon was partly a result of the two courses in population dynamics taught at Lowestoft in the 1950s. These courses had been encouraged by ICES (Beverton and Anderson, 2002).

Beverton and Holt's simple model also made possible the development of "virtual population analysis" (VPA), although it took nearly 10 years before that was realized. The term virtual population was introduced by Fry (1949) and was defined as the sum of the catches of a year class that has passed through the fishery. Gulland (1965) developed a method of estimating population size in numbers and fishing mortality by a stepwise correction of the virtual population. Identical results can be obtained without involving the virtual population. VPA is essentially nothing more than finding F and N from Equations (2) and (3) (see earlier section) year by year backwards in time knowing the catch-at-age for the historical time series, and Murphy (1965) discussed the solution of the equations.

VPA became a standard tool used by the ICES assessment working groups in the 1970s. As often happens with new tools, it was both used and misused. For applying the technique, one needs independent estimates of stock size or fishing mortality by age for one year; such values are usually given for the last year of the analysis. Pope (1972) analysed the effect of errors in the starting values and sampling errors in catch data. Ulltang (1977) analysed the effect of errors in assumed values of natural mortality (M) and also considered the effect of stock migrations on the estimates. Although the limitations of the technique were known in theory, there were strong tendencies to place too much weight on VPA results even when the required independent estimates were mere guesses. Pope and Shepherd (1982) developed separable VPA for reducing the number of unknowns by making an extra model assumption [relative fishing mortalities by age (exploitation pattern) constant from year to year]. While VPAs were manually tuned to independent information from, e.g., scientific surveys during the early years of applying the technique, computer programs like extended survivors analysis (XSA) (Shepherd, 1999) were developed during the 1980s and 1990s for calibrating VPAs to multiple time series of independent relative stock size estimates. In recent years, another type of assessment model has been developed where a self-containing population model is fitted to data, in contrast to the VPA type, where a population is reconstructed using the catch numbers at age. Examples are integrated catch-at-age analysis (ICA) (Patterson and Melvin, 1996) and Flexibest (ICES, 2000). These models have some advantages over XSA, for example, flexibility to use all sources of data which may contain information on the stock, not only the catches. For a more thorough review of recent developments in stock assessment models, see Skagen and Hauge (2002).

Special problems with assessment and management of pelagic stocks

In the late 1960s and the early-to-mid-1970s, several pelagic fish stocks collapsed or were reduced to very low levels. Typical examples from the ICES Area were the Norwegian and Icelandic spring-spawning components of Atlanto-Scandian herring, Icelandic summer-spawning herring, Celtic Sea herring, North Sea herring, and North Sea mackerel. It became clear that the assessment and management of the schooling pelagic stocks required special attention, and it was consequently decided to hold a symposium in 1978 to consider the events leading to collapse and to identify those aspects of behaviour and population dynamics of pelagic stocks that might account for their greater vulnerability to exploitation (Saville, 1980a). One of the main conclusions of the symposium (Saville, 1980b) was that there is strong evidence that as stock size decreases in pelagic fish, the catchability coefficient increases (Pope, 1980; Saville and Bailey, 1980; Ulltang, 1980). As a consequence, catch and effort data from the fishery cannot be utilized in estimating current abundance of these stocks. Therefore, much more effort should be devoted to obtaining alternative, fishery-independent measures of stock size from, e.g., acoustic surveys, egg or larval surveys, and tagging experiments. Later assessments of pelagic stocks have, to a large extent, been based on such measures, and in particular the use of acoustic surveys has escalated.

Quantifying ecological interactions

The problem of species interactions was introduced early by, e.g., Garstang (1900) in the discussions of the effects of fishing. Garstang explained the increasing catch rates of long rough dab in the Firth of Forth, Scotland, by decreasing competition from a declining plaice stock. However, quantifying ecological interactions in ICES stock assessments has been a rather slow process even after the development of multispecies models.

In the North Sea and the Baltic, estimates of age-specific predation mortalities are at present obtained from multispecies VPA (MSVPA). In assessments of the prey species in the North Sea, predation mortalities from MSVPA are averaged over all years, thus limiting the usefulness of the estimates, whereas in the Baltic (containing only one predator species), they are varied over years based on changes in predator biomass. In both areas, models for predicting predation mortalities are lacking.

While MSVPA only estimates the mortality component of species interactions, the area-disaggregated multispecies simulation and prediction models MULTSPEC (Tjelmeland and Bogstad, 1998) and BORMICON (Stefánsson and Pálsson, 1997) also estimate growth as a function of food availability (and sea temperature). In addition to utilizing Andersen and Ursin's (1977) concepts of feeding level and prey suitability, fish migration is modelled to take account of variations in fish distribution and species overlap. Although the Barents Sea model MULTSPEC has not yet been used directly in the annual assessments of cod, results have been utilized in attempts to predict likely changes in cod growth from expected changes in prey (capelin) biomass. Estimates from MULTSPEC of predation mortality generated by cod on Barents Sea capelin have been used directly in capelin stock predictions.

In conclusion, although there are examples of quantifying ecological interactions in annual ICES assessments, such interactions are generally not taken into account in stock predictions.

Quantifying effects of environmental conditions

The idea that environmental conditions may affect the fisheries is an old one and was discussed in ICES right from the beginning.

Smith (1994), noting that correlations of the strength of year classes with environmental changes have been pursued in many places since the 1920s, drew attention to the following problem: initial data might suggest a high correlation between year-class strength and some environmental factor; subsequent data might support that correlation for a few years, but eventually the correlation would fail. While the initial high correlation might be published, the subsequent breakdowns seldom were. In a short paper presented to a special scientific meeting on "Climatic Changes in the Arctic in Relation to Plants and Animals" held in conjunction with the 1948 ICES annual meeting, Lee (1949) discussed a similar problem with respect to predicting climatic fluctuations. He drew attention to fundamental problems with correlation analyses when selecting several factors out of many, merely because they have an apparent close relationship, and said that only by searching for the physical explanation can we solve the problem of climatic fluctuations.

The above problems are special cases of a more general question in fisheries science discussed briefly in Ulltang (1998), namely that fisheries science has traditionally been dominated by an inductive philosophy, searching for confirming instances. However, science develops through a process of conjectures and refutations. The key to progress is to look as hard as possible for observations that disagree with the tentatively accepted theory.

Although there is increasing knowledge of the environmental effects on fish stocks [gained in, for example, the ICES/GLOBEC programme on Cod and Climate Change (CCC)], these are, in general, not taken into account and quantified in regular ICES stock assessments. Lack of use of such knowledge has been identified as a main factor limiting the reliability and time horizon of fish-stock predictions. In some cases, there are good correlations between environmental parameters and fluctuations in fish stocks, but the actual mechanisms causing the stock fluctuations are largely unknown. In other cases, the mechanisms are known to some extent, so that correlation can be supported and explained by "cause and effect" considerations, but it is difficult to predict the future state of the environment. There is a need for the establishment of relationships between environmental data and fish-stock characteristics or parameters, as well as the incorporation of such relationships into assessments, to be based on a good understanding of the ecology of the particular system or region and some understanding of the mechanisms underlying the statistical correlations. Environmentally based models of key direct inputs (e.g., growth, survival, and distribution) to stock assessment models, and models to predict the environmental variables, are most urgently needed.

Concluding remarks

Right from the beginning, progress in fishpopulation dynamics theory was driven by the need to understand the natural basis for the great fisheries and to deal with the overfishing question in a scientific way. When ICES later became an advisory body for the fisheries commissions and Member Countries, progress was, to a large extent, driven by the need for reliable stock assessments. However, as in all of science, the personal scientific interests of outstanding individuals have strongly influenced developments.

There is an overwhelming difference in complexity between the first assessments at the beginning of the 20th century and present applications of, e.g., VPA-tuning models, statistical catch-at-age methods, and multispecies assessment models. Survey methods have also greatly improved, following research on fish behaviour, fish capture technology, and fisheries acoustics. However, the extent to which basic elements in present theories of the mechanisms governing fish population dynamics and surplus production were known or anticipated during the first half of the century is remarkable. Due mainly to Hjort, the importance of monitoring year-class fluctuations became clear, and research aimed at explaining the fluctuations was initiated. During this period, ICES certainly played an important role as a discussion forum for the development of fish population dynamics theory. However, the mathematical modelling was, to a large extent, the result of the work of a few individuals, some playing a central role in ICES (e.g., Russell, Graham, Hjort), while others had little or no contact with the organization (e.g., Baranov, Schaefer, Ricker). ICES' most important achievement during the early years with respect to understanding the reaction of fish populations to exploitation was the organization of cooperative international investigations (Sætersdal, 2002).

The second half of the 20th century started with Beverton and Holt's tremendous effort to assemble the different biological theories into a comprehensive fish-population dynamics model. When ICES stock assessment working groups were established in the 1960s, Beverton and Holt's simple model became the main tool. During the early years of the stock assessment working groups (1960s and 1970s), methodological development for adapting this tool to the actual problems and questions took place within the assessment working groups. One example is the annex to the report of the Arctic Fisheries Working Group in 1965 where John Gulland developed a method that was a forerunner of the standard VPA developed later. During the 1980s and 1990s, less methodological development took place in the assessment working groups themselves. A main reason for this was the emphasis on standardized tools in the assessment and management advice process. As noted by Skagen and Hauge (2002), this led to conservatism and an emphasis on consistency, which may have hampered the further development of methods. Methodological questions were, however, addressed in the Working Group on Methods of Fish Stock Assessment and, in the most recent years, the Comprehensive Fishery Evaluation Working Group.

Ulltang (1996) noted that the development in ICES stock assessments since the establishment of the assessment working groups in the 1960s has largely consisted of computerizing the calculations and introducing statistical/mathematical refinements of Beverton and Holt's basic model, including development of VPA models. Less attention has been given to the problem of predicting changes in basic parameters (recruitment, growth, survival), recognizing Beverton and Holt's notion of a fish population as a "self-containing open system, exchanging materials with the environment".

With respect to overfishing, it has been realized that an operational definition depends on the management objectives, e.g., whether the objective is to maximize sustainable yield in weight (the traditional default objective for biologists) or to maximize economic yield or profit. Stability may be an additional objective. Stock-recruitment studies and other research aimed at explaining year-class fluctuations have demonstrated the problematic nature of concepts like sustainability and stability, but have also given new indicators of overfishing in relation to these concepts. Environmental variability and multispecies interactions affect both recruitment and other stock parameters and are, therefore, key factors in relation to productivity, sustainability, and stability. Quantifying multispecies and environmental effects and developing stock assessment models capable of utilizing all sources of data that may contain information on the stock is the main challenge of today.

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