

ECOLOGY OF THE GADOIDS IN THE BARENTS SEA
WITH SPECIAL REFERENCE TO LONG-TERM CHANGES IN
GROWTH AND AGE AT MATURITY OF NORTHEAST ARCTIC COD

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"Cod is nothing but cod, a fish species, Gadus morhua L."

From G.V. Nikolsky (1969): Intraspecific structure and variability in relation to fisheries management. FiskDir. Skr. Ser. HavUnders., 15: 259-265.

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SYNTHESIS

BACKGROUND AND OBJECTIVES

The limitations of the single-species approach to fisheries management have become more evident in recent years as the importance of species interactions (especially predator-prey relationships) has been appreciated or better documented (Mercer 1982, Beverton 1984, Sugihara 1984, Daan 1987). A number of multispecies models have been made, varying in complexity from inclusion in the model of a few key species (Helgason and Gislason 1979, Pope 1979, Tjelmeland and Bogstad 1989) to complex ecosystem models (Andersen and Ursin 1977, Laevastu and Favorite 1980). So far, however, multispecies approaches have been of only limited usefulness (Gulland and Garcia 1984) and single-species models largely remain the basis for management. This is basically a result of inadequate knowledge of the importance and relative significance of inter- and intraspecific interactions as population regulatory processes and the technical problems of obtaining reliable in situ estimates of food composition and consumption of fishes. The empirical evidence that interspecific interactions strongly influence the regulation of populations is moreover weak (Beverton 1984), although predation has been shown to play an important regulatory role for a depleted prey stock (Hamre 1988). Intraspecific interactions may be of greater importance and furthermore,

interactions may be largely confined to the early stages (Jones 1989) and recruitment regulated at these stages to the overall production so that there is always adequate food for the adults (Cushing 1981). A better understanding of the ecosystem in general and of single-species dynamics in particular, and especially of the mechanisms that regulate population sizes, is therefore needed. Such information will improve the applicability of the single-species approach and is a prerequisite for multispecies modelling (Cushing 1981, Pomeroy *et al.* 1988).

Despite the existence of an extensive literature on the commercially important fish species (especially cod (Gadus morhua) and haddock (Melanogrammus aeglefinus)) and the physical environment of the Barents Sea, a thorough understanding of the significance of alternative interactions and regulatory mechanisms in the fish community is lacking. Moreover, no attempt has been made to synthesize the available information with the aim of making a comprehensive comparative analysis of ecology and life history of these fishes, and apparently only one community level study has been made (Burgos 1989). There is also a virtual lack of descriptive information on long-term changes in vital population statistics of even the most studied species. As the stocks of many commercially important fishes have been heavily reduced by exploitation during the last decades (Gulland 1983), such information may indicate direction and extent of stock responses to fishing and reduced stock size. Long time series also make it possible to detect relation-

ships of potential predictive value that on a shorter time scale are obscured by perturbations caused by the fluctuation of other variables (e.g. recruitment and hydrographical regime).

The main objectives of the work presented in this thesis were:

- i) to review the published information on the gadoid fishes of the Barents Sea and to make a comparative analysis of their life history and ecology in order to identify major gaps in our knowledge;
- ii) based on a (re)analysis of the comprehensive time series of data on cod collected by the Institute of Marine Research, Bergen, to study growth and long-term changes in growth and timing of the onset of sexual maturity in the Northeast Arctic cod.

The following three papers are included in the thesis:

- I. Bergstad, O.A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. *Fish. Res.*, 5: 119-161.
- II. Jørgensen, T. 1989. Long-term changes in age at sexual maturity of the Northeast Arctic cod (Gadus morhua L.). *J. Cons. int. Explor. Mer.* (In press).
- III. Jørgensen, T. 1989. Growth of the Northeast Arctic cod (Gadus morhua L.) with special reference to long-term changes and the effects of variations in stock abundance and temperature on growth.

SUMMARY OF PAPERS

I. The gadoids of the Barents Sea

Of the 19 gadoids (all members of the family Gadidae) occurring in the Barents Sea, research has focused on the commercially most important species: cod, haddock, saithe (Pollachius virens) and to some extent Polar cod (Boreogadus saida). These are also the more abundant species and they are of obvious ecological importance in the Barents Sea. The extensive information collected on their life-history, distribution and ecology was reviewed.

Clear similarities in the life-history strategies of cod, haddock and saithe were noted. The impression was nevertheless that present-day interactions among the gadoids are weak. An important objective of a comparative analysis was therefore to identify the mechanisms that allow these large fish stocks to co-exist. It was concluded that distributional overlap is generally low due to differences in temperature or habitat preferences, timing of migrations etc. When distributional overlap is high, as between juveniles of cod and haddock, two mechanisms that will reduce intergadoid interactions were suggested:

i) competition is reduced by differences in feeding behaviour and diet or unimportant due to superabundance of common prey taxa; ii) predation is low due to the size structure of potential predators compared to that of their prey.

Since interspecific interaction seemed weak, it was suggested that intraspecific regulatory mechanisms may be of greater importance. However, insufficient information was available to evaluate the extent of cannibalism and intraspecific competition. Our understanding of the role of the gadoids in the Barents Sea food web is also poor, due to the lack of quantitative information on food consumption. Considering their abundance and wide distribution, however, the gadoids probably exert a substantial predation pressure on the stocks of some prey species, as suggested by Ponomarenko and Ponomarenko (1975). This conclusion is supported by recent estimates of food consumption by the cod stock (Mehl 1989).

It was also noted that we lack observations on changes in some vital statistics of the gadoids of the Barents Sea. Even for cod, only suggestions exist of the possible relationship between stock density and growth, maturation and fecundity.

II. Long-term changes in age at maturity of the cod

A study of long-term changes in age at maturity was made based on data from the spawning fishery at Lofoten. Maturity ogives were calculated for each year class from the proportion of first-time spawners at each age. Age at first spawning was determined from the growth pattern of the otoliths. No overall trend in median age at maturity was

seen for the year classes before 1950, while an almost linear overall decline of approximately 2.5 years was found across the year classes 1958 to 1970. A reduction in mean age in the spawning stock by approximately 2.5 years was also observed, but changes in mean length were less pronounced. Males generally matured at a lower age than females, but the difference by sex in median age at maturity has been reduced from approximately 3/4 year for the year classes before 1950 to 1/4 year for those after 1950.

Unfortunately, no estimates of median length at maturity were available, but circumstantial evidence (i.e. the long-term trend in length of first-time spawners of different age groups) indicated that median length at maturity also has decreased. Thus, the fish now mature younger and probably at a somewhat smaller size than before. It is suggested that the changes in age and size at maturity are primarily caused by improved feeding conditions as a result of the marked decline in the size of the cod stock. This is also supported by the concurrent abrupt change in size at age and age at maturity in the early 1980's.

The question of whether size or age is the more important determinant of maturation has frequently been discussed, and a number of apparently contradictory results are found in the literature. The model presented by Stearns and Crandall (1984), however, assumes that for each growth rate there exists a corresponding combination of size and age at maturity that maximizes the fitness of the fish. As growth rate

changes the optimum value describes a path in the plane of age and size at maturity termed the plastic trajectory. Knowing the shape of the trajectory makes it possible to predict how size and age at maturity will change as growth rate is altered.

A higher fishing pressure on late maturing than on early maturing individuals could, however, also explain the decline in age at maturity. The slowest growing individuals of a year class are generally found farther east in the Barents Sea than the faster growing ones (Paper III). If age at maturity is basically a function of growth rate, higher fishing pressure in the eastern than in the western areas of the Barents Sea would reduce the proportion of late maturing fishes in the population and thereby increase the proportion mature by age.

Observed changes in age and size at maturity have also tentatively been interpreted as a result of genetic changes in the populations, caused by selective fishing. Although such changes are possible and the idea appealing (May 1984, Wohlfarth 1986, Nelson and Soulé 1987), no rigorous documentation of genetic changes in age or size at maturity caused by fishing exists (R.J.H. Beverton, pers. comm.).

III. Growth pattern and growth changes of the cod

The analysis of growth and growth changes was based on samples from trawl catches taken by research vessels in the Barents Sea in the period 1953 to 1988. Only samples collected in the first quarter of the year were used and the analysis was restricted to immature fish.

The results showed a linear growth pattern for cod between the ages 2 and 10 years and no significant sexual dimorphism in growth was observed for age 5 and younger. The larger fish of an age group were found farther west than the smaller. The data also indicated that the growth of cod is largely confined to the period May to October. Marked short-term variation in length at age was observed and the results indicated that a large part of these differences was established in the youngest juvenile stages, i.e. before age 2. Observed changes in annual growth rate of age groups 2 to 6 could not be accounted for by variations in temperature or stock abundance of cod. It is suggested that the effect of competition for food is primarily confined to the youngest cod, while there is generally enough or nearly enough food for the adults, in accordance with the view held by Cushing (1981). If so, the linear growth pattern of cod with no reduction in growth at onset of maturity is expected as cod may normally have available sufficient energy to fill the requirements of both somatic growth and gonadal development.

This conclusion was however mainly based on data from the 1970's. That period was characterized by a low stock of cod and an overall high abundance of at least two important prey species, capelin (Mallotus villosus) and shrimp (Pandalus borealis) (see Paper I). The mechanisms may be different at higher stock densities of cod and for different densities of prey. The radical decrease in length at age and in condition from 1985 onwards clearly shows that food may be limiting to growth, but the abundance of available prey in these years was probably exceptionally low.

The northeastern boundary for the distribution of cod is found in the Barents Sea. In years with above average inflow of Atlantic water, the available feeding ground increases. Increased inflow also results in higher productivity (Skjoldal et al. 1987). Sætersdal and Loeng (1987) hypothesized that strong year classes of cod were observed at the onset of (or slightly before) a period of increasing water temperature. If this hypothesis is correct, there can be a tuning of year class strength of cod to the productivity in the area. Such a mechanism is in accordance with Cushing's hypothesis of abundant or superabundant food for the adult populations (Cushing 1981) and may explain why variations in growth rate were not related to fluctuations in stock size. Low stock size in the last two decades compared to the virgin stock would also make it difficult to detect density-dependent responses in this period, although such responses actually exist at higher densities (Jones 1989).

Although no significant relation was found between growth rate and stock abundance, indications of decreasing growth with increasing stock size were observed. Generally, the analyses of density-dependent growth based on mean length at age are flawed because length reflects the whole past of the fish and not necessarily the growth rate when stock abundance was measured (Lett 1978, Sinclair *et al.* 1982). Nevertheless, the overall increase in mean length at age from the 1950's to the 1980's is an indication of a long-term change in one or more of the factors affecting growth. No overall increase in temperatures has been observed for this period. The stock size has however declined markedly, and it is suggested that the trend in length at age may reflect a general increase in abundance of food relative to the stock size of cod. Jakobsen (1989) pointed out the significant decline in the ratio of nominal catch to SOP (sum of products of weights and numbers at age calculated using the fixed set of weights at age used by the ICES Arctic Fisheries Working Group) from 1946 to 1982, also an indication of a long-term change in weight at age across the period.

GENERAL DISCUSSION

The literature review showed that substantial gaps still exist in our knowledge of the gadoids in the Barents Sea and that even for the more well-studied species, we lack a true understanding of how populations are sustained and regulated. In an attempt to supplement current knowledge, growth

and long-term changes in growth and age at maturity of cod were analysed based on the data made available by the Institute of Marine Research, Bergen.

There are, however, two major problems connected with this approach. Firstly, when studying long-term changes in biological parameters there is always a possibility that the observed trends are artifacts caused by the way data were collected. A critical evaluation of the data and methods is therefore essential, but nevertheless rarely included in presentation of such analyses.

The study of growth and growth changes was based on the estimated mean lengths at age. Due to considerable geographical variation in length at age, but no consistent pattern from year to year, the accuracy of the population mean lengths at age are critically dependent on the adequacy of the sampling scheme. However, except in the 1980's, the geographical coverage of the distributional area was generally poor and highly variable between years. Differences in fishing pattern between years may also generate variation in mean lengths at age by removing varying proportions of the fastest growing individuals from the different year classes.

Growth rate was estimated from mean length at age for the same cohort in two consecutive years. Thus, the above sources of bias in length at age will also affect the estimated growth rates, but the coefficients of variation for the growth rates will be much larger than for the estimated

mean lengths at age. Furthermore, if the fastest growing individuals of a year class mature first, growth rates of the older immature age groups are likely to be biased downwards. The ideal approach would have been to base the analysis on individual growth rates. However, no such data are available and backcalculation from broken otoliths is problematic, as the size of rings in cross sections depends on where the break occurs (Williams and Bedford 1974).

Although it is reasonable to assume that the observed inter-annual variation in mean length at age is biased, the analysis indicated that the more pronounced trends are real. On the other hand it is likely that much of the variance in growth rate not accounted for by stock size and temperature is a result of bias in the estimated growth rates. The analyses also depend crucially upon valid determination of age and the study of changes in age at maturity in addition depend on determination of age at first spawning. However, the counts of annuli and (especially) spawning zones are, although to some extent subjective, not considered a major source of error in the analyses.

The second major problem is that the holistic approach and a retrospective analysis of long-term changes in population parameters form no basis for conclusion regarding underlying mechanisms. More specifically, the observed changes in growth and age at maturity may be a result of density-dependent mechanisms, genetic selection, environmental changes or partly or wholly an artifact of sampling, but the

study does not clarify which of these is the more important. Although it has been argued for density-dependence as the most probable regulatory mechanism for cod in the Barents Sea, better quality of field data are needed to confirm this. Moreover, it will be necessary to supplement field data with experiments carried out under controlled conditions to study processes in greater detail.

The study has shown a marked long-term decline in age at maturity for the Northeast Arctic cod and indications of a long-term density-dependent growth response to the decline in stock size of the cod. However, we still lack basic knowledge on the dynamics of single species in particular and on the ecosystem in general. It is suggested that future research on the gadoids should focus on intraspecific regulatory mechanisms as well as on their interaction with other species. As exploitation and highly variable recruitment may change important demographic aspects of the fish community and hence interaction patterns, such knowledge is fundamental for better management of the resources.

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