SOME ASPECTS OF THE INTERRELATION BETWEEN THE 
HERRING IN THE NORWEGIAN SEA AND THE STOCKS OF 
CAPELIN AND COD IN THE BARENTS SEA

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ABSTRACT

The paper reviews the life history and exploitation of the Norwegian spring spawning herring, the Barents Sea capelin and the north-east Arctic cod. On this basis and from relevant knowledge of climatic conditions, the effects of the fisheries on the stocks and on the interrelation between the stocks are analysed and discussed in view of the recent crisis which has developed in the coastal cod fishery. It is concluded that the crisis is linked to an unbalanced state of the predator/prey relationship in the Barents Sea, which has developed after the herring stock was fished out in the late 1960ies. Herring and cod are defined as the key species in this relationship, because they are the largest stocks in the area and their success of recruitment is determined by common environmental factors. The capelin is found to be an opportunist in the system because its recruitment success is inverse to the abundance of the juvenile herring stock. The releasing factors for the events occur to be a shift from a cold to a warm climate in the early 1980ies which favoured recruitment of herring and cod. Extraordinary strong yearclasses of cod were recruited, but the spawning stock of herring was not rebult to a sufficient level to take full advantage of the improved climatic conditions.

In the period 1983-86 the rapid growing cod stock, together with other predators grazed down the plankton feeders in the area, and starved cod, sea-birds and seals have appeared on the Norwegian coast since 1986. It is evident that the capelin fishery has accelerated these processes, but seems to have had a minor effect on the present state of the ecobalance compared to the herring fishery prior to 1983. In order to obtain a more balance state of the eco system at fish level in the future, highest priority should be given to the rebuilding of the herring stock. The conceptual model which the paper describes, will serve as basis for the construction of a mathematical model for management that takes into account species interactions.
INTRODUCTION

The two largest fish stocks in the North-Eastern Atlantic, the Norwegian spring spawning herring and the Barents Sea capelin, have been depleted in recent years. The herring collapsed in the late 1960ies, and has not yet been rebuilt, and the capelin was depleted in the middle of the 1980ies. These are the main stocks of plankton feeders in the area, and represent the key-species in a context of predator/prey relationships. The dominating predator, the North-East Arctic cod, has perished in recent years due to lack of food. Crowds of underfed seals have moreover invaded Norwegian coastal waters and thousands of dead seabirds have drifted ashore on the north Norwegian coast. These dramatic events demonstrate that the upper tropical levels of the ecosystem of the area are out of balance. The traditional coastal cod fisheries are struck by the most serious crisis on record, and in a management context the question arise what are the causes. Are the prime causes of natural origin beyond human control, or are they linked to overexploitation. The present paper aims at giving a comprehensive review of the foregoing exploitation history of the fish stocks concerned. On this basis and from knowledge of the relevant environmental conditions, the possible effects of the fisheries on the stocks are considered. In addition, some aspects of the interrelation between the stocks are analyzed and discussed.

THE ECOSYSTEM

The marine ecosystems in the North-Eastern Atlantic are governed by the inflow of Atlantic water through the Faroe-Shetland Channel (Fig. 1). Two main branches of the Atlantic current, one going south into the North Sea and one going north into the Norwegian Sea and the Barents Sea, creates two different ecosystems. The area associated with the northern branch contains two highly productive areas, one in the Norwegian Sea along the Polar front and one in the marginal ice zone of the Barents Sea. The production processes in the latter area are linked to the movement of the ice edge (Gjøsæter et al. 1983). The plankton production in these areas has been harvested by two large pelagic stocks of plankton feeders, the adult herring in the Norwegian Sea and the adult capelin in the Barents Sea (Fig. 2). The herring spawns on the Norwegian west coast, the capelin on the coast of northern Norway and USSR. These spawning migrations transferred huge quantities of biomass from far distant waters to the shelf off the Norwegian coast. The spawning migration of herring was disrupted when the stock collapsed in 1969 and the feeding migration to the high production area in the Norwegian Sea has not been resumed. No extensive spawning migration of capelin has been detected since 1986. The juvenile herring (age 0-4) are distributed in Norwegian coastal waters and in the southern parts of the Barents Sea where their distribution area overlap the nursery area of 0-group capelin.

Two large semipelagic stocks feed in the same areas, the blue whiting in the Norwegian Sea and the polar cod in the arctic. The growth potential of the semipelagic stocks is probably linked to the current state of the pelagic ones. The semipelagic stocks are, however, of minor importance in this respect because they spawn in other areas.

The herring and capelin have been the main food source for a large variety of fish stocks, mammals and birds. The north-east Arctic cod is probably the largest predator in the system and seems to play a decisive role in the balance of the predator/prey relationships. The cod spawn on the central Norwegian coast and feed in the southern and
central part of the Barents Sea and in the Spitsbergen area (Fig. 2). During its spawning migration in winter and early spring the adult capelin is available as food for cod whereas the juvenile herring and capelin are available throughout the year. This is in broad terms the structure of the system. The relative abundance of the species is balanced by recruitment and growth which are linked to varying environmental conditions. The physical environment is governed by the influx and properties of the Atlantic water which vary in periods. Mean temperature and salinity for the years 1964-85 are shown in Fig. 3.

STOCK ABUNDANCE AND EXPLOITATION

**Herring.** The state of stock and exploitation from 1950 onwards are summarized in Fig. 4. The adult herring was estimated at 7 to 10 million tonnes in the 50ies, but declined to a level of some 3 million tonnes in the early 60ies. This was mainly due to poor recruitment in the period 1951-58. Two strong yearclasses were recruited in 1959-60, but the stock was depleted in the late 60ies due to increased exploitation (Dragesund et al. 1980). In the middle of the 1970ies the spawning stock was estimated to about 100 000 tonnes, and increased slowly to some 500 000 tonnes in 1983. In 1983-85 three relative strong yearclasses were recruited as 0-group in the Barents Sea. They suffered, however, mass mortality by an increasing stock of juvenile cod, especially the yearclasses 1984-85. The 1983-yearclass matured in 1988, and the spawning stock increased to above one million tonnes (Anon. 1987, Anon. 1988, Mehl 1987).

The recruitment is variable and very strong yearclasses in relation to parent stock have occurred in 1950, 1959-60, 1963, 1973 and 1983. The fishery has been regulated by national catch quotas since the early 1970ies. Although the fishing mortality was rather low, the fishery delayed the rebuilding of the stock prior to 1983-85, when the stock was considered as grossly recruitment overexploited (Anon. 1983).

**Capelin.** The capelin has been fished as prespawners off the coast of Finnmark during winter since the early 1950ies. After 1968 juvenile capelin have also been fished in the northern parts of the Barents Sea during summer and autumn. The catch increased in 1959-61, but a sudden collapse of the fishery occurred in 1962 (Fig. 5). From 1965 onwards the catch increased and reached a record catch of 2.9 million tonnes in 1977. Since 1978 the fishery has been regulated by separate catch quotas for the autumn and winter fishery. From the autumn 1986 onwards the capelin fishery has been banned.

No stock abundance estimate of capelin is available prior to the late 1950ies. Olsen (1965) estimated the relative stock abundance in the years 1959-64. He found that the stock increased by 4 times in the period 1959-61, but declined below the 1959 level in 1962-64. The capelin spawns at an age of 3 to 5 years, and this rise and fall in stock size reflects increasing recruitment from the yearclasses 1955-58 and an abrupt failure of recruitment in the subsequent years. From 1965 onwards the recruitment increased considerably and the 1967 yearclass is reported to be very strong (Dragesund et.al. 1971). This resulted in a corresponding increase in the stock, as indicated by the increasing yearly catches.

Acoustic estimates of stock abundance are available since 1972. The estimates were obtained in September and cover the age groups 2 years old and older (Dommasnes and Rottingen 1984). The estimates 1972-87
are shown in Fig. 6. The maturing of the capelin is correlated to the size, the capelin above 14 cm is expected to mature and spawn the subsequent winter (Hamre and Tjelmeland 1982). The estimates of the maturing stock are shown by the broken line in Fig. 6. The latter estimates adjusted by the natural mortality and the catch in October-April is taken as the stock biomass of spawners in the subsequent year (dotted line). The corresponding year class strength (X) is derived from the acoustic estimate of 2 years old and backcalculated to 1 year by VPA. Finally, the exploitation rate on immature capelin (E) are calculated and shown in Fig. 5 (Anon. 1987, Anon. 1988).

The capelin stock continued to increase in the first half of the 1970ies and reached a maximum in 1975 of about 7 million tonnes. In this period three strong yearclasses were recruited (1971-1973). These yearclasses were distributed far north and east in the Barents Sea, where the condition for growth is poor (Gjøsæter 1984). The capelin suffers mass mortality after spawning and the reduced growth and corresponding delay in maturation increased the survival of the immatures. The extraordinary high stock abundance in 1974-76 was thus a result of high recruitment and the accumulation of older age groups in the immature stock. The 1971-73 yearclasses matured and spawned in 1975-1977, and the stock declined to a level of 4 million tonnes in the autumn 1977. This decline in stock size was determined by the spawning mortality mainly and was little influenced by the fishing. In 1980 the individual growth rose to the highest level recorded and the stock biomass went up accordingly. A large portion of the stock matured and spawned in the winters 1981 and 1982, and the stock declined to some 2.5 million tonnes in 1982-84. This decline in stock size was also caused by increased spawning mortality mainly and was little influenced by the fishing.

The fishing mortality on immatures has been low compared to the natural mortality which is estimated to 0.61 in 1974-78, 0.86 in 1979-83 and 1.68 in 1984-85 (Anon 1987). The rate of exploitation of juvenile for the years 1974-85 is shown in Fig. 5. The dramatic increase in M in later years is associated to the increase in the stock of young cod from 1982 onwards (Mehl 1987). In 1984 and 1985 the recruitment also failed and the stock is now very depleted as in the middle of the 1960ies.

The rate of exploitation of immature capelin in the 1980ies is low and cannot explain the abrupt decline in stock size in 1985-86. The fishing mortality on the mature stock has been high and may indicate that the stock has been recruitment overexploited. An assessment of the sustainable yield of the yearclass 1974-79 shows that MSY is obtained at a spawning stock biomass of 400 000 tonnes (Hamre and Tjelmeland 1982). According to this the capelin has been recruitment overexploited in 1974, 1975, 1979, 1980, 1983 onwards. The 1981 and 1982 yearclasses, which constituted the spawning stocks in 1985-86 are, however, recruited from the largest spawning stocks on record. Recruitment-overexploitation as reason for the stock collapse in 1985-86 is therefore unlikely. On a whole it may thus be concluded that the capelin fishery has to some extent contributed to the stock decline in the 1980ies, but was of minor importance for the stock collapse in 1985-86.

Cod. The state of the north-east Arctic cod stock and fishery in 1950 onwards is illustrated in Fig. 7. In the middle of the 50ies a very strong 1950-yearclass was recruited and the stock increased to about 5 million tonnes. In the subsequent years the stock declined to 2
million tonnes in 1964. This reduction was mainly due to increased exploitation. In later years the variation in stock size reflects to a large extent the variation in yearclass strength. In the cold period 1976-81 the recruitment is poor and the stock declined to 1 million tonnes in 1983. From 1982 onwards several abundant yearclasses were recruited, but the stock biomass has not develop as expected. Shortage of suitable food since 1985 has caused a dramatic fall in the individual growth rate, and there is evidence of high mortality by cannibalism. A serious crisis has struck the coastal fisheries and the present state of stock is considered with concern. Although the fishing mortality has been high throughout the period, the slow recovery of the stock in recent years is obviously caused by a limited food supply and not by overexploitation of the cod stock (Anon. 1988, Anon. 1986, Anon. 1982, Mehl 1987).

REPRODUCTION MECHANISMS

The climatic conditions in the area concerned vary and are determined by the strength and properties of the inflowing Atlantic water masses. Periods with high temperature are favouring strong yearclasses of herring and cod, whereas a cold climate is associated with low recruitment (Støtersdal and Loeng 1984). Extraordinary strong yearclasses of cod and herring occurred in 1904, 1918, 1937, 1950 and 1963. In the warm period of the 1970ies, when the herring stock was depleted, several abundant yearclasses of cod were recruited. In relation to spawning stock the 1973-yearclass of herring was also very abundant. In the warm period 1983-85 abundant yearclasses of herring and cod were recruited (Devold 1963, Marty and Fedorov 1963, Anon. 1986).

The capelin seems to have adapted to this environment in a special way. The capelin may react to increasing temperature by increased growth rate in the maturing part of the population (1980-82, 1970-72) which increases the spawning stock biomass. The shift from a cold to a warm climate is associated with an increased inflow of Atlantic water which distributes the recruits more to the north and east in the Barents Sea where the condition for growth is unfavourable. The pronounced linkage of growth rate and maturing of the fish can thus be explained as an adaptation to the environment to ensure optimum use of favourable conditions prior to recruitment of strong herring/cod yearclasses and to survive in unfavourable periods, when young herring and cod are struggling for life in the southern and central parts of the Barents Sea.

Plots of recruitment versus spawning stock are shown in Fig. 9. An important conclusion which may be drawn is that the strength of the outstanding herring yearclasses is proportional to the parent stock biomass, whereas the strong yearclasses of cod are recruited from rather low stock levels. It should be noted that the recruitment figures are back-calculated by VPA (except the herring yearclass 1983) and increased mortality on juvenile herring in warm periods is not accounted for. The outstanding herring yearclasses are therefore considered as underestimates. However, judging from the survival of the yearclasses 1983-85 and from the herring/cod recruitment pattern in general, it seems likely that the yearclasses recruited subsequent to the outstanding ones are the most underestimated cohorts. They may originally have been strong, but have served as food resource for a growing stock of young cod.
The stock/recruitment relationship of capelin appears from Fig. 9. The plots are closely related to a Beverton/Holt recruitment curve, except for the years 1984-85 when recruitment failed. The recruitment failure is probably associated with the presence of herring, and disregarding 1984-85, the plots may be taken as a valid stock/recruitment relationship when herring is absent.

DISCUSSION AND RESULTS

In the search for trends and general rules for stock interrelationships in these observations it is natural to assume as a working hypothesis that herring is the key prey species at fish level of the food chain in the Norwegian Sea-Barents Sea ecosystem and that the cod is the dominant predator. The capelin stock may be regarded as an opportunist which prospects of survival and growth are determined by the state of the herring stock. It is primarily the abundance of immature herring which determined the role of herring as food for cod, but the relationship is linked to the adult herring by the stock/recruitment function shown in Fig. 9.

The role of the cod as the main predator is obvious and no other stocks of plankton feeders in this area is comparable in size to the herring, except for the stock of capelin in the 1970ies. The high abundance of capelin in this period may, however, have been abnormal and created by overfishing the herring stock. The assumption that herring and cod are the main predator/prey species of the system is supported by their common reproduction cycle, which means they are adapted to similar environment and linked together through evolutionary processes. The role of the capelin needs, however, some further consideration.

Prior to the 1970ies the capelin was regarded as an important stock as food for cod, but not as a large potential resource for exploitation. Ponomarenko el.al. (1975) concluded that in the case of a significant increase in the stocks of cod and haddock there would be no room for a capelin fishery at all, and the cod would have to change to other food resources, the young cod included. This statement was derived from a calculation of the cod's demand for food, and the production capacity of the capelin. The capelin stock seems to have collapsed also in previous periods, when the capelin fishery was insignificant. The data presented by Olsen (1965) indicate that the stock collapsed in the middle of the 1960ies, and the trend in strength of the yearclasses 1955-58, which was the basis for the build-up of the stock in the late 50ies, indicates that the capelin stock was small also in the middle of the 1950ies. According to Möller and Olsen (1962), the capelin disappeared from the Finmark coast in the period 1938-42. These periods are characterized by the occurrence of strong herring yearclasses in the preceding years. Taking into account the distribution pattern and feeding behaviour of the young herring, this decline in stock size provide evidence to assume that competition or predation of herring on young capelin plays a decisive role for the survival of O-group capelin (Øiestad,V. and E. Moksness 1979).

The effect of herring on O-group capelin may be analysed in more details in the data from the 1980ies. In 1984-85 the recruitment of 1-group capelin in relation to spawning stock falls to a very low level compared to the forgoing years (Fig. 9). Even with large stocks as in the middle of the 70ies these yearclasses would probably have been poor and with the high estimated natural mortality due to predation by cod, the capelin stock would have declined to an
insignificant level in 1987-88, even without any fishery. The most probable reason for the abrupt drop in the survival of 0-group capelin in 1984-85 is the presence of the 1983-herring yearclass in the Barents Sea. It may be argued that the spawning stock estimates in 1984 and 1985 are uncertain, and that the failing recruitment merely reflects depletion of the spawning stocks. The larvae production of capelin has, however, been measured since 1981 (Alvheim 1984, Anon. 1987) and these measurements are shown in the text table below:

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Although the index is considered as a very rough estimate of spawning capelin it demonstrates clearly the timing of the stock collapse.

The growth rate plays a special role in the population dynamics of capelin. High growth rate and increased spawning mortality contributed significantly to the stock decline from 1979 to 1982. An increased growth rate is recognized in the age composition of the spawners. With normal growth rate most of the capelin mature at age 4, but the contribution of the 3-year olds increases with increasing growth rate. According to Olsen (1965) the 3 years old capelin dominated the spawning stock in 1959. A similar change in the age composition of capelin is reported from the early 1950ies (Prokorov 1965), which indicates that a high growth rate also occurred prior to the stock decline in the 1950ies and 1960ies. According to Gjøsæter and Loeng (1987) the growth of the capelin is correlated with the temperature, a warm climate favouring high growth. The impact of a warm climate on the herring/capelin/cod relationship is thus improved recruitment conditions for herring and cod whereas the prospects of capelin survival are proportionally reduced. The general condition for capelin being an opportunist of the system is therefore present.

This hypothesis implies that the capelin's role as food for cod is inversely correlated with the state of the juvenile herring stock. The cod feeds on the age groups 3+ mainly, and presupposing that the herring effects the survival of 0-group capelin only, one should expect a time lag of some 3 years between the recruitment of an outstanding herring yearclass and a drop in the availability of capelin as food for cod. This drop should be well pronounced because the availability of mature capelin prior to the drop is expected to be high (high growth rate). Annual changes of the occurrence of capelin in the stomach of cod are shown in Fig. 8 and fits remarkably well with the expectations (Ponomarenko et al. 1978).

The effects of the adult herring stock on the predator/prey relationships in the Barents Sea is linked through the stock/recruitment relationships of herring shown in Fig. 9. The differences in the stock/recruitment functions of herring and cod are probably decisive for the ecobalance in the area and may explain the dynamics behind the recent abrupt decline in stocks and fisheries. In periods with favourable recruitment condition for herring and cod, the supply of food for the cod in form of juvenile herring is proportional to the state of the adult herring stock. The stock/recruitment relationship for cod shows, however, that cod recruits strong yearclasses on relative low stock levels. This means that in a state of depleted stock size for both the stocks, as in the 1980ies, the balance in the predator/prey relationship may change dramatically in a shift from cold to warm climate when the condition for favourable recruitment does occur. In 1983-85 the adult herring was not rebuilt
produce enough young herring to meet the food demand of the growing stock of young cod. Under such circumstances the cod may graze down all other available food items in the area, including its own progeny. The capelin fishery in the 1980ies has probably contributed to this development, but has, most likely, had minor effect on the changes in the ecobalance compared to the herring fishery prior to 1983.

The cod recruited several strong yearclasses in the first half of the 1970ies, and the maturing stock of capelin declined to a very low level in 1974 and 1975. A further stock decline was, however, avoided by the huge recruitment from the capelin yearclasses 1971-73. These events rise the question whether the predator/prey relationship without the herring has a higher stability than the normal one with the herring included. According to generally accepted ecological theory the answer to this is no, and refers to the theory of diversity. The cod stock was, moreover, heavily fished in the 1970ies, and reduced to less than half of the stock size in the 50ies and 60ies, which also contributed to avoid depletion of the capelin stock in the late 70ies. One shall, however, not overlook that the most unstable state of the predator/prey relationship in the Barents Sea may occur when the herring stock is sufficiently abundant to reduce the survival of the capelin larvae significantly, but too small to meet the predators' demand for food as seems to have been the situation in the middle of the 1980ies. Judging from a report on the state of the fisheries in Northern Norway by Hjort (1903) a similar situation may have occurred in the beginning of this century. According to Hjort the cod arrived late at the spawning grounds in 1903 and the fish was meagre and had underdeveloped gonads. Large flocks of seals had invaded the coast and mass mortality of sea birds was reported. Hjort's description of the situation in 1903 could as well has been a description of the stocks and fisheries in 1987. It is in this respect interesting to note that prior to 1903 the herring stock had been depleted for 30 years and was in a state of rebuilding. The 1904 yearclass became an outstanding one which dominated in the herring catches in the next 15 years (Hjort 1926). Common causal factors for the events in 1903 and 1987 are therefore possible.

Overexploitation was no doubt the main reason for the collapse of the herring stock in the 1960ies, and the present study provides evidence to conclude that the lack of a rebuilt herring stock is the main cause for the failure of the expected recovery of the cod stock in recent years. In a fishery management context, aiming at a more balanced state of the predator/prey relationship in the Barents Sea, the highest priority should therefore be given to the rebuilding of the herring stock.

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Fig. 1. The circulation of the Norwegian Sea (Helland-Hansen and Nansen 1909).

Fig. 2. Distribution and migration pattern of herring, capelin and cod.
Fig. 3. Mean temperature (continuous line) and salinity (broken line) in autumn 1964-1985 (Midttun and Loeng 1986).

Fig. 4. Estimated spawning stock (S), fishing mortality (F) and recruitment (X) of herring 1950-1983 as 1 year old.
Fig. 5. Catch (C) and rate of exploitation (E) of capelin 1959-1986.

Fig. 6. Acoustic stock measurement of 2 years old and older capelin ($B_{2+}$) and maturing stock ($B_m$) in the autumns 1972-1986. Calculated spawning stock ($B_s$) in the subsequent winters 1973-1987. The corresponding recruitment as 1 year old ($R_1$) is marked by X.
Fig. 7. Estimated stock of 3 years old and older cod ($B_{3+}$),
the spawning stock (S) and corresponding recruitment
as 3 years old (X).

Fig. 8. Frequency of occurrence (in %) of capelin in the
stomachs of cod in the years 1947-1976 (Ponomarenko and Yaragina 1978)
Fig. 9. Stock/recruitment relationships for herring, capelin and cod. Spawning stock in million tonnes, recruitment in billion individuals.