Structure and dynamics of the cod population and trophic interactions in Masfjorden: A contribution to a large-scale cod enhancement experiment

by

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CONTENTS

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LIST OF PAPERS

The present thesis is based on the following papers:

I. Salvanes, A.G.V. 1991. The selectivity for cod (*Gadus morhua* L.) in two experimental trammel-nets and one gillnet. Fish. Res. 10: 265-285.

II. Salvanes, A.G.V. and Ø. Ulltang. Population parameters, migration and exploitation of the cod (*Gadus morhua* L.) in Masfjorden, western Norway.

III. Salvanes, A.G.V., J.H. Fosså and J.T. Nordeide. The fish fauna in a west Norwegian fjord: Distributional patterns and trophic relations.

Synthesis

Structure and dynamics of the cod population and trophic interactions in Masfjorden: A contribution to a large scale cod enhancement experiment

Introduction

Management of exploited fish populations is generally achieved by regulating exploitation rate and pattern through restrictions on harvest levels or fishing effort, enhancing the population by releasing young reared fish or improving the habitat or aquatic environment.[1] Regulating exploitation is normally used in management of marine fish populations (Beverton and Holt 1957). Enhancement and rehabilitation effects have primarily been applied to anadromous and freshwater fish populations which have been reduced or eliminated due to factors such as hydroelectric development or pollution (Isaksson 1988; Kirk 1987; Mills 1989). However, these latter techniques have also been applied to some marine fish and shellfish species in coastal areas of Japan (Nose 1985).

There have been proposals to increase recruitment to coastal marine fish populations through large-scale releases of young reared fish. Supplementing natural production should increase the number of adult fish and, thus, increase subsequent harvests. This hypothesis should be tested through ecological investigations and large-scale experiments before major commercial programmes are initiated (Peterman 1991; Ulltang 1984). This thesis is a part of the large-scale enhancement experiments on cod (*Gadus morhua* L.) in Masfjorden, western Norway. Ecological investigations conducted in the fjord adress the question whether large-scale releases of juvenile cod result in increased productivity. This experiment, with its multispecies approach, is the most comprehensive investigation designed in connection with an enhancement programme.

Three primary conditions must be met in such an enhancement experiment. First, mass production techniques to rear organisms to suitable sizes for release are required. Second, effective techniques to mark many fish prior to release are essential to obtain biological information, to estimate contribution to the populations, and to assess migration

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[1] Worth mentioning is also the attempts to increase the landings of plaice in inshore areas of Denmark in the years 1901-1957 by transplantating juveniles from regions with poor growth to areas with better growth conditions (Kirk 1987). Transplantation of plaice from inshore areas in Scotland to Doggerbank were also attempted the years 1903-1930 (Kirk 1987). However, the programmes were terminated because cost exceeded the value of increased catches of plaice.

Another alternative technique used when enhancing fish populations is illustrated in DeVries and Stein (1990). Sports fisheries for carnivore freshwater fish in North America have often been enhanced by releasing high numbers of their preys, such as shad.

patterns (Hilborn *et al.* 1990). Finally, knowledge about the ecosystem at the experimental sites both before and after release is needed to evaluate how the introduction of large numbers of young fish will affect the stock size and structure of other populations as well as the introduced species. In the large-scale cod enhancement experiment in Masfjorden, all three conditions needed for a concluding evaluation of the results are fulfilled. Mass production and mass marking techniques exist, and ecological investigations are conducted both prior to and after large-scale releases.

This thesis is primarily concerned with the investigations conducted before large-scale releases. Hence, the thesis will not alone provide a concluding evaluation of the total experiment, but will provide results necessary to evaluate whether the enhancement experiment as a whole may be successful. Specifically, the main objectives of this study are to :

i) Design an experimental sampling strategy to use when sampling fish from Masfjorden. Emphasis is put on the selectivity of two types of trammel-nets and one type of gillnet when catching cod. Whether combined samples from a group of the three types of nets can be used as approximately random samples from the cod population are also studied (Paper I).

ii) Estimate population parameters (stock size, age structure, recruitment, growth, natural mortality and fishing mortality) and study migration patterns and exploitation of cod in the fjord from 1986 through 1989. This period includes the first one and a half year after the initial large-scale release of juvenile cod (Paper II).

iii) Describe the seasonality in distribution and abundances of the fish fauna in Masfjorden before large-scale releases of cod and study the food resource utilization with emphasis on the diet of different size groups of cod (*Gadus morhua* L.), pollack (*Pollachius pollachius*), saithe (*P. virens*) and one size group of *Trisopterus* sp. (mostly poor-cod) to uncover inter- and intraspecific trophic relationships which may be important for the survival of cod released in the fjord (Paper III).

Background

More than a century ago, suitable mass production techniques were available for salmonid species.[2] Large-scale fish marking techniques have been available for these species for over fifty years (McFarlane *et al.* 1990). Large enhancement programmes were initiated on Pacific salmon species within the US, Canada, USSR and Japan (Isaksson 1988; Nose 1985; Shelbourne 1964). In the 1970's over 2 billion salmonid eggs, larvae and juveniles were released annually (Nose 1985; Ryther 1981). Atlantic salmon and various Pacific salmon species have also been transplanted for over 100 years to areas without native stocks within the US, Canada and USSR (Kirk 1987), between North America and many European countries (Mills 1989) and to other parts of the world with no native salmonid stocks such as Australia, New Zealand and Tasmania (McNeil 1979; Mills 1989).

Many of these programmes were considered successful as they resulted in an average return between 2-5% (Thorpe 1980) and made up approximately 30 percent in weight of the annual world salmon catches in e.g., 1978 (Ryther 1981). The programmes have, however, all been conducted without ecological investigations at the release sites. Hence, it is unclear why some enhancement programmes of salmonids seem to have worked while others have failed (cf., Dumont *et al.* 1988; Peterman 1991). Lack of ecological investigation at the release sites is considered a major weakness of the salmon enhancement programmes and is the main reason why new experimental designs, which include ecological field investigations, have been implemented for populations such as the Fraser River sockeye salmon and the Columbia River coho salmon (Peterman 1991).

For marine species, mass production techniques for yolksac larvae have been available for over a century. Because of large fluctuations in the landings of marine fish, release programmes on yolksac larvae of cod, haddock, pollack and flounder were initiated in the US, Great Britain and Norway around the turn of the century (Shelbourne 1964). It was intended that such releases should stabilize the recruitment to the populations and, thus,

[2] Mass production techniques for nonanadromous and freshwater fish such as tilapia, carp, buffalo, walleye, striped bass and sturgeons have also been available. These species have been released both in connection with enhancement programmes, but have also been introduced to new areas worldwide for many years (Stickney 1986).

stabilize the catches in the coastal fisheries. However, there has been major scientific controversy of whether the releases positively influenced the recruitment (Kirk 1987; Solemdal and Sinclair 1989). One major reason for the controversy was that no recapture of released individuals could be recorded because large-scale marking techniques were not developed for yolksac larvae at that time.[3] Potential effects from released yolksac larvae on the fish populations had therefore to be evaluated in other ways. The first field investigation in Norway in 1903-1905, searching for an evidence, was inconclusive (Shelbourne 1964). More recent analyses of time-series of beach seine samples up to about 1970 concluded that it was impossible to distinguish any increase in the recruitment of cod which could be ascribed to releases of yolksac larvae from the natural fluctuations in cod recruitment (Tveite 1971; Tveite 1984). Hence, there was no reason to continue releasing yolksac larvae and the release programmes were terminated.

Generally, the possibility to survive increases with size because of decreasing predation pressure on larger fish (Werner 1986). Higher survival of released individuals is, therefore, expected in enhancement programmes if larger individuals are released. This has been shown for the Read sea bream (*Pagrus major*) released in Japan (Tsukamoto *et al.* 1989), and seems likely for coastal cod in Norway. (Tveite 1984) found a positive correlation between the abundance of 0-group cod in the autumn and the abundance the of 1-group cod the next year, indicating a higher survival of 0-group cod than of cod larvae. Thus, enhancement programmes using 0-group cod instead of yolksac larvae should result in higher survival of released fish and increased recruitment of cod.

Large-scale release experiments should be combined with ecological investigations in order to assess the possibilities for enhanching fish stocks. Since 1983 such experiments have been possible for cod in Norway primarily because a mass production technique has been developed, but also because mass marking techniques are available. In the production technique, releasing millions of yolksac larvae into a saltwater basin with naturally occurring zooplankton in an environment without predators showed high survival rates until the

[3] Recently a genetic marker detectable at all life history stages for cod has been developed (Svåsand 1990).

0-group growth stage (Øiestad *et al.* 1985). This technique has recently been improved. To obtain better survival, the saltwater basin is fertilized to increase the abundance of prey organisms before larvae are released (Blom *et al.* 1991). Moreover, fish marking techniques for cod are available. A large-scale group marking method (fluorescent pigment administered through the food) and external individual tags (Floy tags) are used on cod (Svåsand 1990). It is, thus, possible to collect information both on biology and distributional patterns of released cod as well as of wild cod.

The first enhancement experiment was initiated in Austevoll in 1983, western Norway (Svåsand 1990). Other experiments started in 1985 when the Norwegian Council of Fisheries Research decided to support a nation-wide enhancement research programme with experiments in three different regions of Norway. Masfjorden, western Norway, considered in the present study, was selected as one of these experimental sites.

Experimental sampling

The type of gear chosen for the experimental sampling strategy will depend on whether the target fish species are pelagic or demersal. Midwater trawling is normally utilized when sampling pelagic fish populations. Such trawling was utilized in Masfjorden by Giske *et al.* (1990) when studying the distribution and trophic interactions within the pelacic fish assemblages.

When sampling from fish populations which inhabit the bottom connected habitats, one must consider the topography of the species' distributional area more closely before choosing sampling gears. Demersal fish populations in offshore regions, often distributed over large areas of relative plain and soft bottoms, are normally sampled utilizing standardized bottom trawling combined with acoustic surveys. However, the topography is totally different in west Norwegian fjords. Masfjorden is considered a typical west Norwegian fjord according to Syvitski *et al.* (1987). It is about 22 km long, narrow (0.3-1.5 km wide) and deep with sections of varying bottom types. The maximum depth is about 500 m. It has a relatively deep sill (75 m) and its approximately 70 km long macroalgae covered shoreline is generally rocky and has steep sides that alternate with a few bays with sandy and muddy bottoms (Paper III). Therefore, the alternative acoustic surveys and bottom trawling appeared not to be the best sampling strategy for fish populations in the fjord. The sampling of demersal fish populations in this fjord requires a somewhat different type of sampling design. The gears used were beach seines in the shallows (mostly 0-5 m depth), gillnets and trammel-nets in somewhat deeper water (mostly 5-20 m), and bottom trawling at greater depths (180-480 m). Gillnet and trammel-net sampling was conducted monthly and the bottom trawling only occasionally.

Generally, fishing gears are selective and do not provide random samples of all fish sizes within any population. Selectivity may, therefore, affect any estimate of population parameters requiring random samples from the population. The selectivity of gears used in Masfjorden is considered in this thesis. Emphasis is put on the selectivity of two types of trammel-nets and one type of gillnet when catching cod (Paper I). The selectivity of nets is illustrated by selectivity curves, showing how the possibility of catching a fish species changes according to the length of the fish (Hamley 1975).

Experimental sampling of cod

According to e.g., Regier and Robson (1966), length samples corrected for the selectivity can be used as estimates of true length compositions within fish populations. Moreover, such selectivity adjusted length compositions may be utilized as representative samples and can, thus, be used to obtain unbiased parameter estimates for the population considered (Hamley 1975). Approximately true length distributions were estimated in Paper I for cod in Masfjorden in the length range 18-58 cm using samples from each of the two trammel-nets (those having 45mm and 70 mm stretched mesh in the inner-net).

An alternative approach, when seeking representative samples, is to use the acquired knowledge of selection properties to make simplifications, e.g., varying net types can be combined to get nearly nonselective net groups for specified length ranges (Regier and Robson 1966). In Paper I it is concluded that composite samples from experimental net groups consisting of one net of each of the three types used when catching cod in Masfjorden did not differ significantly from the apparent true length composition obtained by the method referred to in the previous section. The simplified method could, thus, also be used to get representative samples for length range 18-58 cm of cod.

It is also assumed that the selectivity of cod larger than 58 cm is negligible because these large cod, if present at the sampling sites, have a size which can be entangled in the trammel-nets. In other words, it is assumed that the experimental net groups generate nearly the same fishing mortality on all length classes of cod greater than 18 cm. Thus, representative samples from the cod population in Masfjorden can be obtained by two means; either from selectivity adjusted samples of cod from each of the nets, or from combined samples from the experimental net groups. Of the two methods available the latter, simplified, sampling approach was chosen for the stock assessment on cod in Paper II.

Experimental sampling of other fish species

A detailed study of the selectivity of all fish species sampled in Masfjorden is beyond the scope of this research. Therefore, the same approach as used for cod (i.e., combined samples from the experimental net groups) is used in Paper III to estimate abundance indices for different species present in the 5-20 m depth zone of the fjord. This may bias the obtained results because factors such as body shape and behaviour of the fish species may influence how efficiently different species and sizes are captured. It is not possible to properly evaluate this potential bias in the thesis. However, since these combined samples were not used for stock assessment, but only to estimate abundance indices, the bias is probably not severe.

The beach seine used to sample the 0-5 m depth zone of Masfjorden is also selective. Such samples generally underestimate abundance because large stones, macroalgae and other hindrances often cause escapement (e.g., Fosså 1989; Tveite 1971). The alternative drop-net, developed by Fosså (1989) for sampling fish in shallow waters, captured more individuals of the two-spotted goby (*Gobiusculus flavescens*) per square meter than the beach seine.

However, although Fosså (1989) did not study in detail how efficiently the drop-net captured other species, the results indicated that shy species such as cod were underrepresented in the samples. Fosså (1989) also recorded that more species were caught by the beach seine, a feature probably explained by the difference in the sampling area between the beach seine (120 m^2) and the drop-net (16 m^2). Hence, because shy species seemed to be underrepresented in samples from the drop-net compared to samples from the beach seine, and because the beach seine caught more species, the beach seine was chosen when sampling the shallows in the study of distributional patterns of the fish species in Paper III.

Structure and dynamics of the cod population

Knowledge about the dynamics of the local cod population in Masfjorden is vital for the assessment of whether large-scale releases of juvenile cod will increase the yield of cod from the fjord. In Paper II a stock assessment for cod is presented. Combined samples from experimental net groups are used on data prior to and for the first year after the first large-scale release of juvenile cod. These samples cover a 4 years period. Catch per unit of effort estimates are generated from an experimental fishery, and are, combined with absolute abundance estimates from tagging experiments and commercial and recreational catch statistics, used for stock assessment.

Parameters to be estimated in studies concerning the structure and dynamics of exploited fish populations are stock size (in weight), age structure, recruitment, growth, natural mortality and fishing mortality. The simplified relationship between these parameters is illustrated in Figure 1: The stock loses members by *Natural mortality* and by *Catch*. Renewal is undertaken by *Recruitment* of young individuals and by *Growth* of the already recruited members.

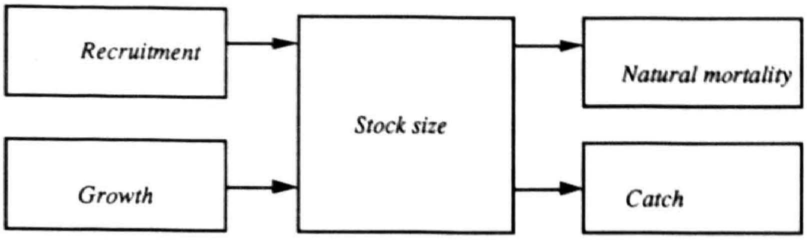

Figure 1. Simplified diagram of the dynamics of an exploited fish stock (from Ricker 1975).

The following parameters are estimated for cod in Masfjorden in Paper II:

Recruitment: Although 0-group cod was not fully recruited to the experimental net group used when catching cod in Masfjorden, tagging experiments on 0-group cod made it possible to estimate the number of 0-group cod present in the autumn of 1985, 1986 and 1988. The recapture period used for estimation purpose included only completely recruited ages. Age groups 1 year and older were considered recruited to the experimental net group. The number of 0-group cod present in November and December, 1985 and 1986 was low; about 14000 in 1985 (including 15.4% released cod) and around 11000 in 1986 (including 10.4% released cod). The number of 0-group cod in August 1988, immediately after large scale releases of juveniles, appeared to be much higher (180000, including the about 46.2% released individuals).

The maximum abundances of 1-group cod (1984 and 1987 year classes) were about ten times higher than the minimum abundances (1985 and 1986 year classes). The abundance of 1-group cod in the 1988 year class was about three times higher than for the 1985 and 1986 year classes.

Stock size: Estimated annual mean numbers of cod of recruited age groups varied between 28800 and 83800 individuals from 1986 - 1989 with minimum mean number in 1987 and maximum in 1988. The estimates correspond to an annual mean biomass of about 20 tonnes.

Growth: The estimated length-weight relationship indicated isometric growth for individual cod in Masfjorden. The growth in length as a function of age depicted that maximum size is attained slowly. The estimated growth parameter K in the von Bertalanffy growth equation is 0.128. This growth rate is similar to the Baltic and the Barents Sea population (K=0.12), but lower than for the North Sea cod (K ranging between 0.269 - 0.333) as referred to in Daan (1974).

Catch: The total annual catches, including commercial, recreational and the small experimental catches, increased from 1986/1987 to 1988/1989, and were at a maximum in both numbers and weight in 1989 (around 17000 individuals or 9.5 tonnes). The increase was probably a result of the strong 1987 year class which dominated the 1988 and 1989 catches.

Mortality: The results in Paper II indicates that the average total mortality Z increased from age group 1/2 to 2/3 ($\overline{Z}_{1/2}$=0.81 and $\overline{Z}_{2/3}$=1.19).[4] As the corresponding fishing mortalities were $\overline{F}_{1/2}$=0.09 and $\overline{F}_{2/3}$=0.20 , a high natural mortality seems likely for these young age groups of cod in Masfjorden. Another possible explanation, high emigration, is discussed later.

The calculated fishing mortalities over the calendar year increased with age and were at a low level on 1-group ($\overline{F}_1$=0.06) and moderate level on 2-group ($\overline{F}_2$=0.18), but high on 3-group ($\overline{F}_3$=0.37). For age groups 4+, F appears to be much higher ($\overline{F}_{4+}$=0.85). The estimated fishing mortalities for cod in Masfjorden were, except for the oldest age groups, lower than those estimated by Virtual Population Analysis (VPA) on commercial catches of tagged cod off Austevoll (0.6 per year for age group 2+ (Svåsand and Kristiansen 1990)).

The validity of the population parameters

Many factors may influence the estimation methodology and, thus, the validity of obtained population parameters. For the stock assessment on cod in Masfjorden such factors are primarily connected to the sampling strategy, tagging experiments and to the migration pattern within the population. It is concluded in Paper II that the estimates are not likely to

[4]Age groups $a/a+1$ denotes the interval from approximately the middle of the year when the fish is a years old to the middle of the year when it is $a+1$ years old.

be biased with regard to factors concerning the sampling strategy. The assumption of a constant catchability coefficient q (q=4.2x10^{-5} per setting of the experimental net group) for recruited ages seems valid. All estimated parameters are critically dependent on this assumption. One factor which can cause a biased estimate of the catchability coefficient is extra mortality on released cod, a feature leading to overestimated recruitment and stock size (Paper II). Field investigations conducted in connection with the 1987 Masfjorden cod releases indicated a slightly increased predation immediately after release (Nordeide and Salvanes 1991). The parameters can be adjusted for this apparent extra predation mortality if the predation rate is quantified.

The migration characteristics may affect some population parameters. For instance, estimates of total mortality Z includes any migration rate (Paper II). High emigration rates will lead to overestimated Z's while high immigration rates may underestimate this parameter. The following three aspects should therefore be evaluated in connection with enhancement experiments : 1) migration of juvenile fish, 2) migration of adult fish, and 3) whether the released fish will pick up the same pattern as their wild congener.

Although some individuals migrated between the fjord and other areas, the overall results in Paper II indicated that juvenile cod were nearly stationary. The estimated total and fishing mortality rates for juvenile fish are, therefore, not expected to be biased by migration. However, it seems likely that the estimated mortality rates can be biased in years with high net immigration during the spawning season, because stock assessments in Paper II cover the local area and not the total distributional area for the adult cod. A net immigration in the spawning season was indicated for cod in 1988. Over 10 % of fish tagged at the spawning grounds left the area after spawning and were recaptured in other areas, whereas 16 % were recaptured in Masfjorden. Thus, part of the cod biomass available for the 1988 fishery consisted probably of migrating mature individuals (3 years and older) not stationary in Masfjorden. This may reflect another characteristic often recorded in coastal populations of cod in Norway. The spawning population often consists of two spawning units, one local remaining in the area the entire year, and the other migrating from contiguous fjords and more distant areas to the spawning grounds and then returning (Godø 1984; Jakobsen 1987; Jørstad 1984; Jørstad and Nævdal 1989).

With regard to whether released cod will pick up the same migration pattern as wild cod, one should note that all earlier studies on migration of coastal cod are descriptive (e.g., (Danielsen 1969; Dannevig 1954; Godø and Sunnanå 1984; Templeman 1974). No study concerning the underlying processess determining migration is available for cod as for salmon, where both genetical and environmental conditions in connection with migration has been studied (Hasler 1971).

For marine species, and particularly for clupeids, there is a relationship between the abundance of the total population and the migration distance (Beverton *et al.* 1984). For the Norwegian spring spawning herring, Dragesund *et al.* (1980) reports that the migration distance decreased with decreasing population. The distribution of young herring was also found to vary with the different year classes.

It is uncertain whether there is any relationship between the size of the local cod population in Masfjorden and the distributional area or migration distance. Results presented in Paper II indicate that cod released in 1985, 1986 and 1988 were nearly stationary. However, several cod (30 individuals) released in 1987 were primarily recaptured from a contiguous fjord during the spawning season. It is not known whether this was a spawning migration or represented some permanent emigration from Masfjorden. Although the evidence is not strong, the fact that 1987 was a year with high recruitment indicated that this degree of emigration of cod could be density dependent.

Population regulation

The population levels of exploited marine fish stocks are regulated through many underlying processes. Biological and environmental conditions as well as exploitation rate and pattern determine the balance between the increase in stock size due to recruitment and growth and losses caused by fishing and predation mortality (see Figure 1). The factors determining recruitment and within population regulation on the adult stage have been emphasized when studying fish populations, while regulative processes determining the survival from the juvenile stage have rarely been considered (Beverton *et al.* 1984).

The underlying processes determining recruitment are considered the major structuring forces for a fish stock. Sissenwine (1984) presents a review of the processes regulating the pre-recruit stages. There is a general lack of correlation between larval abundance and subsequent recruitment. It is common that large fluctuations occur in the recruitment to fish populations because of highly variable mortality rates in the early planktonic stage. Mortality rates may vary between 5 and 20 % per day in these early stages (Blaxter 1988). For cod in Norwegian waters the mortality of these early life history stages must be high. The spawning period ranges from February to May, and the planktonic stage lasts until July/August when cod settle in nearshore habitats (Godø *et al.* 1989).

Hjort (1914; 1926) believed that high survival of larvae was critically dependent on whether larval food and larval distribution matched or mismatched when the larvae switched from endogenous to exogenous food. Moreover, the predation pressure is an additional factor determining the survival from this planktonic stage (Blaxter 1988; Hunter 1981; Hunter 1984) The fluctuating environmental conditions may modify these effects from starvation and predation (Sissenwine 1984). It seems thus that the recruitment level in fish populations is determined by factors other than the numbers of eggs spawned or the size of the spawning population. Hence, the most likely explanation for the failure of the earlier larvae release enhancement programmes around the turn of the century is that most of the millions of released yolksac larvae died before they settled in nearshore areas as 0-group cod. Those who survived until this stage were too few to significantly increase recruitment to the population.

In Masfjorden, the year-to-year fluctuation in recruitment was about 10-fold between rich and poor year classes for the period considered (Paper II). The fluctuation in the recruitment of the Barents Sea cod and haddock is, however, much higher. Evidence of a 60-fold difference between a rich and a poor year class is documented for the period 1902-1983 (Bergstad *et al.* 1987; Sætersdal and Loeng 1987). The variability in the North Sea haddock is even higher (over 100-fold, Ursin 1982). The difference in the variability in recruitment between the local cod stock in Masfjorden and the total stock of the Barents Sea cod may partly be explained by the short period considered for cod in Masfjorden, but one may also speculate whether recruitment is more stable in small local populations than in large oceanic stocks. For instance, Sissenwine (1984) hypothesize that space limitation during the post-larval stage can be a strong compensatory mechanism which potentially stabilize the recruitment in coastal areas.

The biological regulatory processes on the mature part of local exploited populations are primarily density dependent effects, but also genetic responses can occur (Beverton *et al.* 1984). Conditions often associated with a pronounced decrease in population abundance are increased growth rate and decreased age or size at first maturity (Sterns and Crandall 1984). If a decrease in population abundance is fishery induced, an increased food supply per individual will normally lead to increased growth rate and faster maturity.[5] On the contrary, at very high adult densities, depression in growth rates and fecundity often occur (Beverton *et al.* 1984). Unfortunately, it has not been possible to study such regulation of the adult part of the cod population in Masfjorden because the samples mainly consisted of immature 1-3 year old cod. A preliminary analysis of immature cod indicated, however, a depressed growth rate for the first year after the first large-scale release of cod (Jarle T. Nordeide, *unpublished*).

The reduced growth rate for cod which Nordeide (*unpublished*) found for both the 1987 and 1988 year classes after the first large-scale release could result in a higher predation mortality on these small fish because small fish potentially have more predators than large. Such a result was supported by the slight increase in natural mortality from 1987/1988 to 1988/1989 as indicated in Paper II. The results in Paper II also indicate that a slightly higher emigration rate for cod released in 1987 than for the groups released the other years. Whether this apparent increase in emigration for the 1987 release group was a result of the high abundance of young cod in 1988/1989 is uncertain.

[5]Genetic responses may act in the opposite way. A developing fishery selectively removes the faster growing individuals resulting in a lower average size at age in the catches (Beverton *et al.* 1984).

Trophic interactions

Multispecies approaches have a deep tradition in ecological studies, but have seldom been taken into account in fisheries management, probably because the single species approach has been successful for many long-lived species in temperate regions (Sugihara *et al.* 1984).[6] Of the few early exceptions, Larkin (1963; 1966) and May *et al.* (1979) considered optimum exploitation in competition and predator-prey systems and Andersen and Ursin (1977) developed the dynamic simulation model for the North Sea ecosystem which is a multispecies extension of the Beverton and Holt theory of fishing. Recently, multispecies approaches are also found necessary for concluding evaluation of enhancement experiments (Peterman 1991; Ulltang 1984).

Large-scale releases of juveniles of one species into a fish assemblage can influence the productivity of other fish populations, and, similarly, other fish populations may influence the productivity of the population to be enhanced. Hence, it is not necessarily true that an increased production of the target population is the only response of large-scale releases of juveniles. Existing interspecific, as well as intraspecific, trophic relations may be decisive factors in regulating the size of the population intended to be enhanced. Thus, the response of large-scale releases of cod in Masfjorden can be an increased stock size of cod, but the releases can also, theoretically, operate as a large food supply for the predators on cod. Some enhancement programmes in North America even take advantage of known predator-prey interactions and release preys instead of predators. For instance, shad (the prey) have been released in order to increase the populations of crappies and largemouth bass (the predators on shad) (Devries and Stein 1990).

The most important trophic relationships in the fish assemblage of Masfjorden before large-scale releases are illustrated in Figure 2. Of the eleven dominating species shown in Figure 2, only cod, pollack and saithe are of direct commercial value (cf., Salvanes 1986), with cod as the most valuable. The other eight species are expected to influence the

[6] The need for multispecies models became particular apparent lately when tropical fisheries were developed (Sugihara *et al.* 1984). Tropical fisheries occur in regions having a high fish diversity, and target many species (often up to 100 species).

productivity of the commercially interesting species through existing trophic interactions, and are thus of indirect commercial value. For example, the three dominating gobies are eaten by all the four gadids. Cod and pollack also eat dominating members of the Labrid family as well as other gadids and their own congeners.

Although the trophic interactions in Masfjorden seems complicated, the interactions are even more complex than depicted in Figure 2. Because the food resource utilization and the risk of predation generally vary with body size, ontogenetic niche shift leads to successive changes in the interactions among species (Werner and Gilliam 1984). When comparing the diet of different length groups of cod, pollack, saithe and poor-cod in Masfjorden, it was indicated that two-spotted goby and benthic crustaceans were the major preys in early life for cod, pollack, saithe and poor-cod, but the importance of gobies in the diet decreased as individuals grew larger. For cod and pollack this decrease in importance of gobies in the diet with increasing size coincided with increasing importance of the large gadids and labrid preys (Paper III).

Moreover, co-occurring fish populations exploit common resources consisting of prey species which may fluctuate seasonally in abundance, but some preys may also be preferred. The strongest interactions were in fact indicated between the dominating fish populations in the summer or autumn when they had maximum abundances (Paper III). The small gadids´ maximum predation on gobies coincided with the maximum abundance of gobies in the summer, while the predation of gobies was low in seasons with low abundance of such preys (Paper III; see also Fosså 1991). The results in Paper III may also be taken as a supporting evidence for cod being a preferred prey for the large cod and pollack. The large predator groups showed maximum predation on cod in the summer or autumn despite that e.g., labrid preys were numerous.

In conclusion, the multispecies approach used in the study of the fish assemblage of Masfjorden has illustrated important knowledge about existing intra- and interspecific relations between dominating species. It seems likely that the discovered interactions may affect the survival of released cod. One should therefore quantify the strengths of trophic relationships by estimating predation rates before a concluding evaluating of the cod enhancement experiment in Masfjorden.

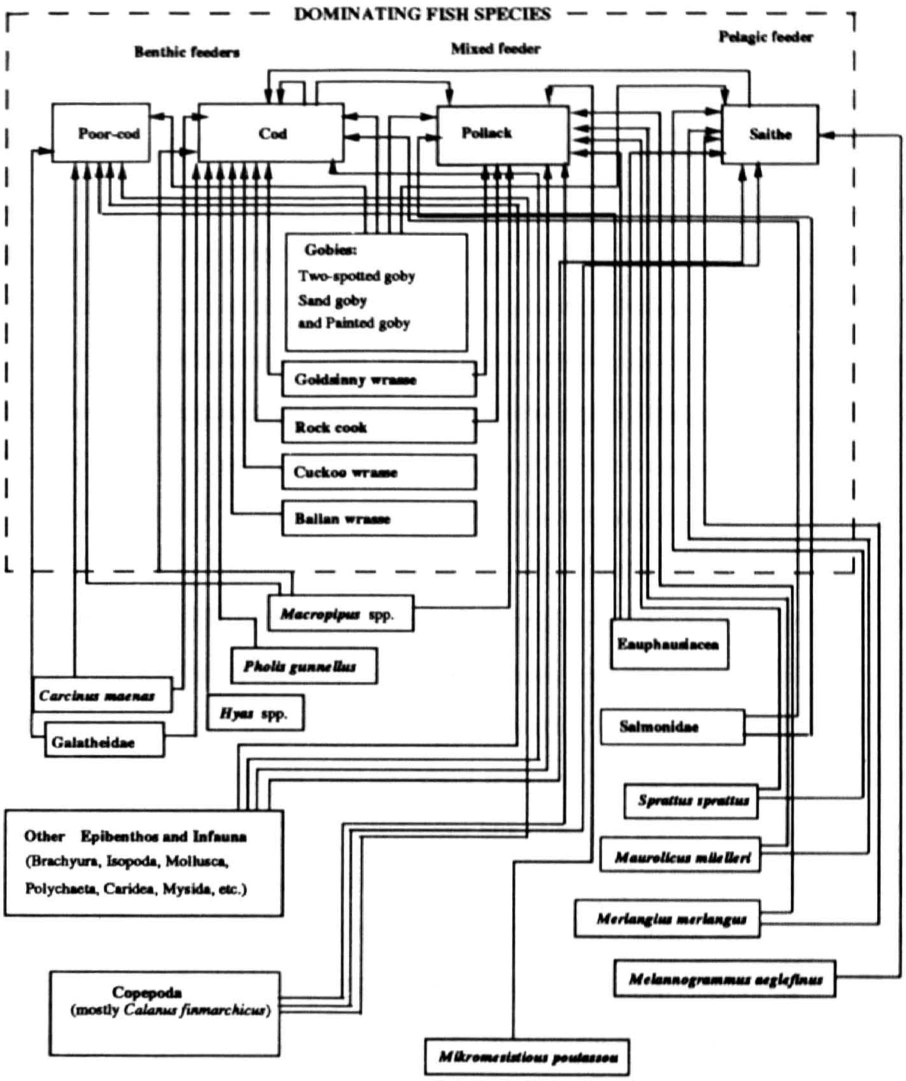

Figure 2. The trophic links between bottom connected fish species in the 5-20 m depth zone of Masfjorden discovered from a study of the diet of cod, pollack, saithe and poor-cod. Size groups and seasons are pooled.

Concluding remarks

The aspects adressed in this thesis in connection with the investigations and experiments assosiated with a large-scale cod enhancement project in Masfjorden are: First, a sampling strategy is designed to provide representative samples from the cod population in the fjord (Paper I). Second, this sampling strategy is used to obtain data for estimating stock size, age structure, recruitment, growth, natural mortality and fishing mortality for the local cod stock for a period which includes the first one and a half year after the initial large-scale release of juveniles (Paper II). These data have also been used when studying migration patterns in the cod population. Finally, using the same sampling strategy as for cod, data for estimating relative abundances of other bottom connected fish species present in the fjord have also been obtained (Paper III). The diet of the captured cod, pollack, saithe and poor-cod has been studied in detail to uncover trophic interactions between dominating fish species before large-scale releases (Paper III). An analysis of yield per recruit at different release strategies is left for future studies.

This research is only a part of the overall evaluation of the cod enhancement project and is, therefore, insufficient in drawing any conclusion of the viability concerning large-scale cod enhancement programmes. However, it does provide necessary information for assessing the large-scale releases of cod. The dynamics in the local cod stock of Masfjorden is illustrated by the estimated stock size and age structure and the estimates of recruitment, growth, natural mortality and fishing mortality. The average annual stock size was around 20 tonnes in the period 1986-1989 whereas the annual mean numbers varied between 28800 and 83800 with minimum in 1987 and maximum in 1988. One major question for the enhancement experiment is whether it is possible to increase this stock size through large-scale releases of juveniles or whether density dependent processes (which often are reported to regulate the stock sizes of marine fish) will lead to no significant enhancement effects. These issues are discussed in the following sections.

The strongest structuring forces in marine fish populations are the underlying processes responsible for the highly fluctuating recruitment. The recruitment of 1-group cod in Masfjorden showed a 10-fold year-to-year fluctuation between a rich and a poor year class. The maximum numbers of cod present in Masfjorden in 1988 is explained by the high recruitment in 1987 and the minimum mean numbers in 1987 is a result of two successive years (1985 and 1986) with low recruitment. The level of recruitment is in fact a combined response of: 1) whether the annual reproductive cycle of fish and the annual production cycle of larval prey match or mismatch; 2) the predation pressure on the egg and larval-stage from post-larval fish; and 3) the effects of environmental variability (Sissenwine 1984). The combined effect of processes results in fluctuating and unpredictable mortality on these early pre-recruit stages, and explain the high year-to-year fluctuations in recruitment shown for cod in Masfjorden. These fluctuations may as well explain the failures of the earlier enhancement programmes releasing yolksac larvae. The number of individuals surviving of the larvae released were probably to few to significantly increase the subsequent recruitment to the cod stocks.

However, it is at present possible to increase the recruitment by releasing juveniles instead of larvae. The juveniles can be reared by first releasing yolksac cod larvae into a controlled environment free for predators, and with suitable and sufficient preys available (Blom *et al.* 1991; Øiestad *et al.* 1985). This production technique increases significantly the survival through the very vulnarable pelagic life stage. The major question is whether the releases of juveniles in fact result in increased stock size of cod, or if density dependent processes will depress the survival rate for both released and wild cod. The positive association between the average annual biomass of one year old cod (two tonnes in 1987 and over 15 tonnes in 1988 (cf., Paper II)) and the biomass of gobies the previous autumn after cod have settled in the littoral zone (two tonnes in 1986 and over 22 tonnes in 1987 (cf., Fosså 1991)) may be taken as a supporting evidence for such processes. However, one may also speculate whether this positive assosiation indirectly reflects the regulative proccesses on the planktonic pre-recruit stage. Such an explanation is supported by the findings in Giske *et al.* (1991): It was indicated that the transport of zooplankton (the food for gobies) to the littoral zone regulates the abundance of gobies (the major prey for young cod) and the subsequent recruitment of cod.

The growth of the already recruited cod in Masfjorden influences the renewal of biomass in the local stock (cf., Figure 1). The estimated rate of growth in length as a function of age is low (K=0.128) indicating that the maximum size of cod is attained slowly. If there is a carrying capacity for young cod in Masfjorden, we may expect that the growth rate decreases after large-scale releases of juveniles because of a lower food supply per individual compared to a situation with no juveniles released. It seems that the growth rate decreased both for the 1987 and 1988 year classes during the first year after the initial large-scale release of cod in the fjord (Jarle T. Nordeide, *pers. comm.*). If also other fish species and sizes overlapping in diet with young cod were numerous during this period, this is an additional factor which may limit the food availability, and, thus, the growth of young cod.

The cod stock loose members by natural mortality and fishing mortality (cf., Figure 1). Because the estimated average total mortality ($\overline{Z}_i$) on immature cod ranged between 0.81 and 1.19 whereas the corresponding fishing mortality ($\overline{F}_i$) was in the range 0.09-0.20 for the period 1986-1989, and because the young cod were nearly stationary, the natural mortality ($\overline{M}_i$) for young cod is high in Masfjorden. This high mortality is largely explained by predation from large predators such as cod and pollack (cf., Papers II and III). Although the evidence is not strong, it seems that a slight increase in natural mortality occurred during the first year after the initial large-scale release (Paper II). This may partly be explained by a higher predation risk for the apparently slower growing fish after the release because small fish is expected to have more predators. If the predator abundance was high during the same period, this could be an additional factor resulting in increased predation on young cod. Hence, it is possible that the natural mortality increases after large-scale releases because of density dependent effects.

Another factor which also may reduce the enhancement effects is a higher predation mortality on released cod than on wild cod. Nordeide and Salvanes (1991) found more tagged cod than untagged individuals in the stomachs of cod predators captured immediately after release. The predation mortality has not been estimated separately for wild and released cod, but it seems that the extra predation was restricted to the period immediately after release. An effect such differences may have for enhancement experiments have been demonstrated for e.g., plaice released in a fjord of Scotland in the early 1960's. The metamorphosed plaice released, disappeared the first few days after release because of intensive predation (Anon. 1966). The enhancement effect became, thus, negligible. Blaxter (1974) ascribed this high predation on the released plaice partly to deviant behaviour and partly to the transition from hatchery conditions to a totally different natural environment with different types of food. The experiment in Scotland illustrates the importance of estimating the predation mortality for wild and released juveniles separately before assessing the viability of enhancement programmes.

In conclusion, this research has illustrated the dynamics in the local cod stock of Masfjorden and has discovered important trophic interactions in the fish assemblages of the fjord. It seems likely that density dependent processes can be important in regulating the size of the local cod stock through both interspecific as well as intraspecific trophic relationships. Such processes may reduce the expected enhancement effects after large-scale releases of juveniles. In addition to the results obtained, the study has indicated that at least the following three aspects should be studied in more detail before a total evaluation of the cod enhancement experiment in Masfjorden. These are: a) the density of fish species and sizes overlapping in diet with young cod and their consumption of major preys such as gobies should be quantified, b) the consumption of young cod by large predators should be estimated, and c) released and wild cod should be treated as different taxa and separate predation mortalities should be provided for the two groups.

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