

Ecosystem model for evaluating potential cod production in a west Norwegian fjord

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ABSTRACT: The carrying capacity for cod in a Norwegian fjord was analysed by means of a simulation model. Four age groups of cod were represented as well as the main prey groups labrids, gobies and benthic organisms. These groups made up a near-shore compartment of the model, while nutrients, phytoplankton, herbivorous, carnivorous and gelatinous zooplankton comprised a pelagic compartment. The 2 compartments were coupled through water exchange. The primary production was driven by solar radiation, temperature, freshwater runoff, and deep water convection. Water exchange across the sill regulated the magnitude of advection of secondary producers serving as prey for higher trophic levels. Generally, simulation models including predation are sensitive to the feeding representations, and we propose a new method for obtaining estimates of the 'half-saturation' parameter. Simulations of 1 yr indicate that cod production is sensitive to the amount of zooplankton advected into the fjord and to the availability of benthic preys. Under good environmental conditions maximal cod production is estimated to be 0.5 to 1.3×10^6 ind. yr^{-1} , which is 7 to 8 times higher than the average levels of natural cod recruitment. Recruitment beyond 0.5 to 1.3×10^6 ind. yr^{-1} will reduce the overall cod production because of food shortage and cannibalism. Validity of the model is indicated, as good agreement between predicted and observed diet composition of the cod is demonstrated. The 2 main implications from the present simulations regarding extensive cod mariculture are: (1) optimal cod production is obtained if the sum of released and wild recruits is within the range of the carrying capacity of juveniles; and (2) that releases of the same number of juveniles in several years gives dissimilar cod production due to interannual variations in the magnitude of advection, and its influence on zooplankton availability in Masfjorden.

INTRODUCTION

During the last 2 decades there have been proposals to increase recruitment to coastal marine fish populations through large-scale releases of young reared fish in order to stabilise subsequent catches in the coastal fisheries. About 10 yr ago, Atlantic cod *Gadus morhua* L. was chosen as the first marine species to be enhanced in Norway. Recently, similar experiments have also been initiated for European lobster *Homarus gammarus*, Atlantic salmon *Salmo salar* and shad *Alosa alosa* (Anon. 1992). Cod enhancement was also attempted 100 yr ago when millions of newly hatched cod larvae were released on the Norwegian Skagerrak coast (see e.g. Shelbourne 1964). Because of high larval mortality these releases failed to increase the cod population significantly (Tveite 1971). Tveite (1971) found, however, a positive correlation between the abundance of older life stages and the 0-group.

Releases of 0-group cod can therefore be more successful than the releases of newly hatched larvae. Whether there exists a potential for increasing cod populations by means of releasing juveniles will generally depend on intra- and interspecific density-dependent interactions in the community (Peterman 1991). Ecological investigations and large-scale experiments should therefore be conducted before major commercial programmes are initiated (Ulltang 1984, Peterman 1991).

A mass-production technique for rearing 0-group was available in 1983 (Øiestad et al. 1985), and Masfjorden in western Norway was chosen for a large-scale cod enhancement experiment. This fjord was selected because: (1) it is small and clearly separated from the bordering areas by 1 narrow outlet; (2) it contains a cod population which supplies a small local fishery; and (3) the ecology was known from earlier investigations (Gjøsæter 1973, 1981).

Natural cod recruitment (as 0-group) in Masfjorden was estimated to be in the range 15 000 to 200 000 ind. yr⁻¹ (Salvenes & Ulltang 1992). The total cod biomass approximated 28 t, and the average yearly catch was about 5 t for the period before the large-scale releases (cf. Salvenes & Ulltang 1992). About 90 000 individuals of mean length 11.6 cm were released for the first time in 1988 (Smedstad 1991). Similar releases were conducted in 1989 and 1990. Field studies have been conducted since 1985 and are planned to continue at least through 1994 in order to investigate the effect of cod releases.

Several alternatives for estimating fish production exist (e.g. Hanson & Leggett 1982, Sissenwine et al. 1984, Nixon 1988, Bax & Eliassen 1990, Christensen & Pauly 1992), but none of these methods were feasible for the purpose of our study. It was intended that the modelling approach used for the Masfjorden ecosystem should provide knowledge on the underlying processes regulating the cod productivity in the fjord. This required predator-prey relationships and dynamics of water masses to be expressed in the model. We have extended the model in Giske et al. (1991), covering trophic levels from phytoplankton to 0-group cod and the major prey group (gobies), to include the entire cod population. For the shallow near-shore compartment of Masfjorden the present version includes age groups 0, 1, 2 and 3+ of cod, with gobies, labrids and benthic organisms as prey. The near-shore habitat is coupled with the pelagic habitat through water exchange also affecting exchange of zooplankton between the 2 habitats (renewal rate of sublittoral water). Details concerning processes in the pelagic habitat are given in Giske et al. (1991). Indications of carrying capacity limitations and processes regulating cod production are given in the present simulation study.

NATURAL HISTORY OF COD AND ECOLOGY IN MASFJORDEN

Masfjorden (Fig. 1) is ca 22 km long, narrow (0.3 to 1.5 km wide), deep (maximum depth 494 m), and is separated from the outer Fensfjorden and the coast through an outlet having a 75 m deep sill. A population of coastal cod inhabits the fjord and supports a small local fishery. Juveniles are nearly stationary, but older and mature individuals seems to be more migratory (Nordeide & Salvenes 1991, Salvenes & Ulltang 1992). The growth rate of cod in Masfjorden is similar to the growth rate of the Baltic and Barents Sea cod populations, but lower than for North Sea cod (Salvenes & Ulltang 1992). Average age at maturity is 3 yr (Salvenes unpubl.). Spawning occurs at grounds located at

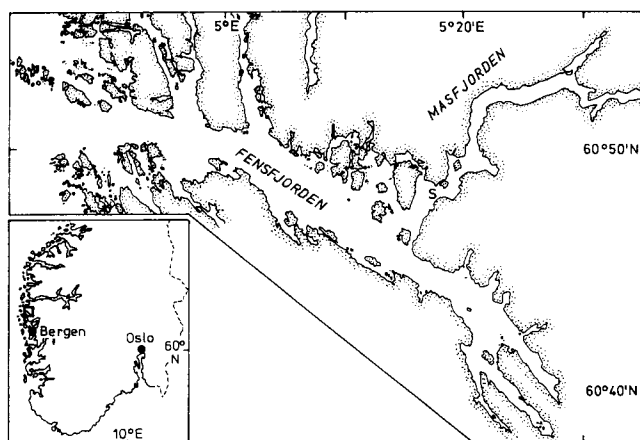


Fig. 1. Masfjorden, Norway. Location of sill is indicated by S

ca 50 m depth. The spawning period, February–April, was determined from pelagic net-samples of eggs taken above spawning grounds from January through May in 1986 and 1987 (Salvenes unpubl.). Generally, juvenile coastal cod settle in the shallow near shore areas during summer and early fall and inhabit mainly areas of ca 0 to 20 m depth in western Norway (Godø et al. 1989, Svåsand & Kristiansen 1990). In Masfjorden several age groups, especially ages 0 to 3, inhabit this depth range (Salvenes & Ulltang 1992).

In addition to cod, 3 gadids (pollack *Pollachius pollachius*, saithe *P. virens* and poor-cod *Trisopterus minutus*), 4 labrids (*Centrolabrus exoletus*, *Ctenolabrus rupestris*, *Labrus bimaculatus* and *L. bergylta*) and 3 species of goby (*Gobiusculus flavescens*, *Pomatoschistus minutus* and *P. pictus*) were found to dominate in the shallow near-shore habitat of Masfjorden (Salvenes et al. 1991). The larger cod and pollack are the main top-predators. Gobies are the principal prey for juvenile cod, pollack and saithe, and serve also as prey for poor-cod. Benthic organisms (e.g. polychaetes and crustaceans) are the second most important prey group for juvenile gadids (Salvenes 1986a, Salvenes et al. 1991). Large cod and pollack rely more on the benthic community, although labrids, gadids and their own congeners also serve as prey. Labrids feed primarily on benthic organisms, but some zooplankton have been recorded in labrid stomachs (Jon Alvsvåg, Department of Fisheries and Marine Biology, University of Bergen, pers. comm.).

The principal cod prey, gobies, feed on zooplankton (Fosså 1991, Martinussen 1991). Zooplankton are also the most important food item for pelagic populations of krill, prawns and mesopelagic fish (Kaartvedt et al. 1988, Aksnes et al. 1989, Giske et al. 1990). Zooplankton are to a large extent advected into Masfjorden (Aksnes et al. 1989), and this advection is forced by the dynamic conditions in the water masses

consisting of 3 main layers (Aksnes et al. 1989). The intermediate layer (3 to 75 m depth) is the most important with respect to zooplankton advection. Here, changes in the Norwegian coastal current rapidly propagate through Fensfjorden to Masfjorden. These dynamic conditions severely affect the availability of zooplankton above the sill (Aksnes et al. 1989, Giske et al. 1991), and thus the food availability for the planktivores. The magnitude of zooplankton advection into the pelagic habitat of Masfjorden thus seems to indirectly regulate fish production of the fjord. Moreover, since both intraspecific (Nordeide & Fosså 1992) and interspecific (Salvanes et al. 1991) diet overlap occurs in the shallow near-shore fish community, both competition for food and cannibalism can be important regulators of fish production.

Another interesting feature of the pelagic habitat is the regular visit of spurdog *Squalus acanthias*, primarily in May–July, and occasional visits of herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus* and also the squid *Todaroes sagittatus*. A few individuals of the seal *Phoca vitulina* and the cetacean *Phocaena phocaena* have also been recorded in some years by local fishermen. It seems that spurdog is the most important of the pelagic visitors. Some years this species has supplied the local fishery with significant catches, as in 1986 when the total spurdog catch was about equal to the cod catch (Salvanes 1986b).

METHOD

Model structure. The trophic levels from phytoplankton to 0-group cod is described by Aksnes & Giske (1989) and Giske et al. (1991). Production is driven by solar radiation, temperature, freshwater runoff, deep-water convection and water exchange across the sill, given initial and boundary concentra-

tions of nutrients, phytoplankton, herbivorous zooplankton, 2 groups of pelagic carnivores, sublittoral gobies and 0-group cod in the fjord. In the present model version we have incorporated 5 new major aspects: (1) cod are age-structured to reflect the entire population [cod of age 1 yr (1-group), 2 yr (2-group) and cod older than 2 yr (3+-group)]; (2) labrids (all species and age-groups pooled) and benthos (all species pooled) are represented; (3) competitive interactions between different age-groups of cod are modelled, (4) cannibalism (2- and 3+-group cod eat 0-group and 1-group) are accounted for; and (5) the feeding representation has been improved.

Competition and cannibalism are modelled by specifying the prey types each predator group may consume (Table 1, Fig. 2). However, goby production represents the production of all zooplankton feeders inhabiting the sublittoral, and labrid production represents production by all animals relying strictly on benthic prey. Since cod competitors are not represented in the model, the simulated cod production also represents unspecified fish competing with cod. In the model, competition for gobies occurs between all age-groups of cod, and competition for benthos occurs between the separate age-groups of cod and the labrids. Moreover, competition for labrids occurs between 1-group and older cod, and competition for young cod between the 2-group and 3+-group cod. Gobies compete with pelagic carnivores and benthos for zooplankton.

The fjord is divided into 3 main compartments: the central pelagic, the sublittoral and the benthic habitat. According to Fosså (1991) and Salvanes et al. (1991), the sublittoral is habitat for gobies and 0-group cod, while the benthic is habitat for 1-group, 2-group and 3+-group of cod, labrids and benthos. All details concerning the central pelagic habitat are described in Giske et al. (1991). Definitions concerning the sublittoral and the benthic habitats are presented below.

Table 1. Predator-prey relationships expressed in the simulation model for the production of cod in Masfjorden

Predator	Prey groups						
	Phytoplankton	Zooplankton	Benthos	Gobies	Labrids	Cod 0-group	Cod 1-group
Cod							
3+-group			x	x	x	x	x
2-group			x	x	x	x	x
1-group			x	x	x		
0-group			x	x			
Labrids			x				
Gobies		x					
Pelagic carnivores		x					
Medusae		x					
Zooplankton	x						
Benthos		x					

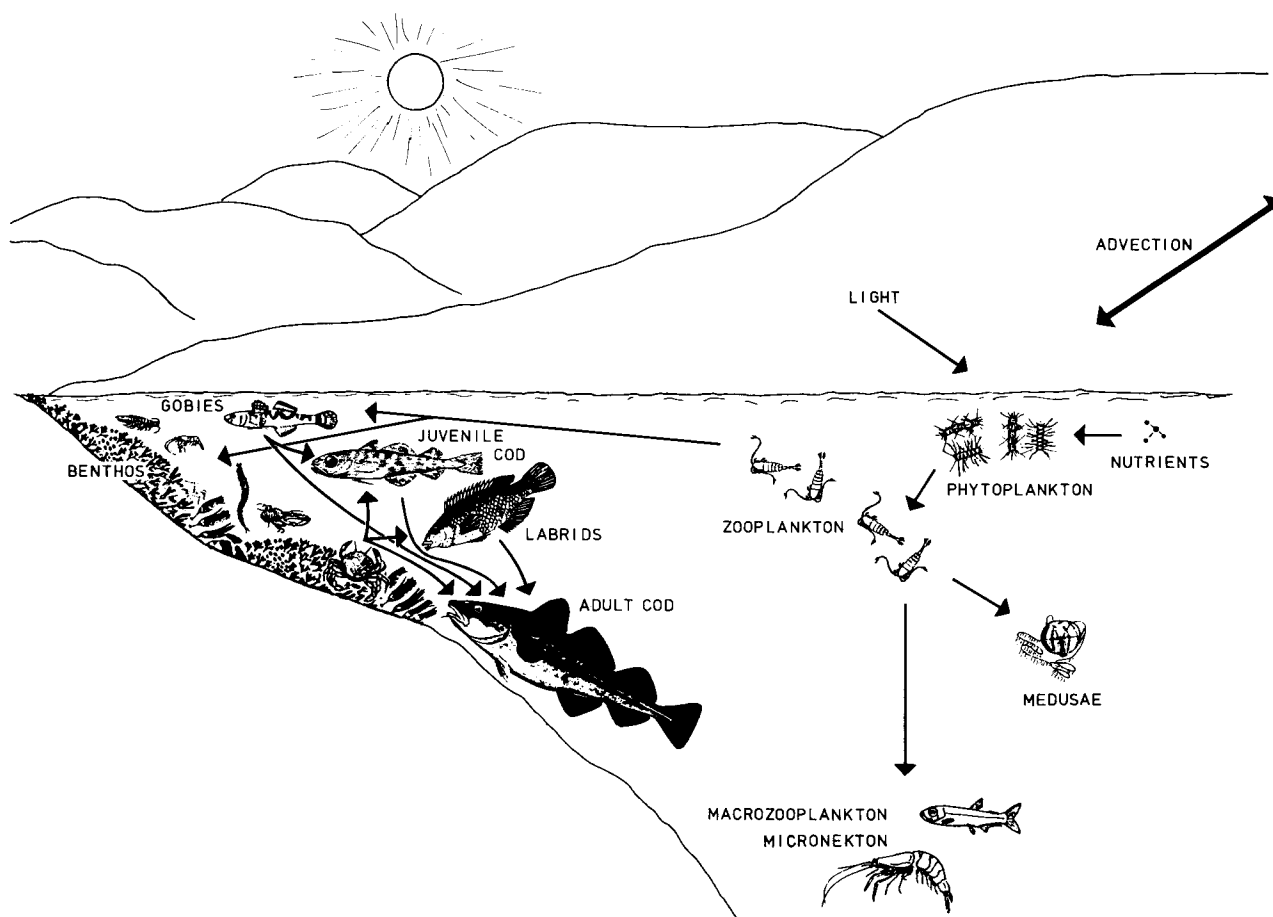


Fig. 2. A simplified food-web of the shallow nearshore and pelagic habitats of Masfjorden

The volume and area of the sublittoral and benthic habitats are estimated assuming a 30° angle from mean tide level down to 3.2 m depth for the sublittoral zone and to 20 m depth for the benthic habitat. The shoreline is 70 km, giving a sublittoral volume of $8.83 \times 10^5 \text{ m}^3$ and a benthic habitat area of $2.24 \times 10^6 \text{ m}^2$.

Feeding representation. Predation is a key process for transferring energy between trophic levels in a food-web. A common way to express the relationship between feeding rate and prey density is to use the hyperbolic, often termed the Michaelis-Menten or Monod equation (e.g. Billings et al. 1978):

$$f = f_{\max} \left(\frac{B}{K + B} \right) \quad (1)$$

where f = feeding rate ($\text{mg C mg}^{-1} \text{C body wt d}^{-1}$); $f_{\max}$ = density-independent maximum feeding rate; B (mg C m^{-3}) = prey concentration; and K (mg C m^{-3}) = half-saturation constant. This feeding representation was also used in the simulation model of Giske et al. (1991). Relatively reliable estimates of maximum feeding rate ($f_{\max}$) can be obtained from laboratory

experiments. The half-saturation parameter, however, is highly sensitive to the experimental conditions as this parameter reflects the encounter rate, visual range, prey size, prey visibility (including shelter opportunities of the prey) and optical properties of the water column (Aksnes & Giske 1992). Faced with these problems, Giske et al. (1991) chose values for the half-saturation constants that were of the same order as the characteristic prey abundance in the predator's habitat. Needs for improved feeding representations were, however, pointed out. In the present paper we estimate the half-saturations from field estimates (in Masfjorden) of prey density, growth of the predator and laboratory-derived estimates of the maximum growth rate. Hence, our half-saturation parameters are integrated over the time and environment under consideration. In order to do this we have to assume that growth rate (g) is linearly related to feeding rate, $g = af$ and $g_{\max} = af_{\max}$. A linear relationship of this sort has been estimated for cod between 100 and 500 g wet wt in experimental studies (E. Lied, Institute of Nutrition, Directorate of Fisheries, Bergen,

Norway, pers. comm.). Although cod smaller than 100 g and larger than 500 g were not included in the experimental study, we assume that the growth rate and feeding rate is nearly linear also for smaller and larger cod. Insertion of the growth-feeding relationship into Eq. 1 and rearranging gives the following estimator for the half saturation constants:

$$K = B \left(\frac{g_{\max}}{g} - 1 \right) \quad (2)$$

where B (mg C m^{-3}) = the natural prey density in Masfjorden derived from Fosså (1991) for gobies, and from Salvanes & Ulltang (1992) for cod; $g_{\max}$ ($\text{mg C mg}^{-1} \text{C body wt d}^{-1}$) is derived from experimental studies (E. Lied unpubl.); and g is estimated from observed growth increments in Masfjorden: $g = \ln(W_{j+1}/W_j)/365$ where W_j = average weight of age-group j in year t ; and W_{j+1} = average weight of age group $j + 1$ in year $t + 1$, as given in Salvanes & Ulltang (1992).

Maximum daily feeding rate is then back-calculated from maximum growth rate:

$$f_{\max} = g_{\max} \left(\frac{1 + E + R}{A} \right) \quad (3)$$

where A = proportion of the consumed food assimilated; E = fraction excreted; and R = fraction respired as measured by E. Lied (unpubl.).

Food-web representation. Another new feature of the extended model is that each age-group of cod is allowed to feed on more than one prey group. In such a situation, a predator's feeding rate on each of the n prey types will be lower than if the predator relies on only one prey type (Legović 1989). Therefore, Eq. 1 is modified and the feeding rates f_{ij} for each age-group j of cod feeding on the prey biomass B_i of prey i are expressed by

$$f_{ij} = B_i \left(\frac{f_{j,\max}}{K_j + \sum_{i=1}^n B_i} \right) \quad (4)$$

where the quantity of prey available to the predator population is the sum of all prey types, and where:

$$K_j = \frac{1}{n} \sum_{i=1}^n K_{ij} \quad (5)$$

Production and mortality rates. The production rate of predator group j consuming $i = 1, 2, \dots, n$ prey at Day k is given by:

$$\frac{dB_{jk}}{dt} = B_{jk} \sum_{i=1}^n (AD_k f_{ij} - \varepsilon - \rho) \quad (6)$$

where A = the fraction of food intake assimilated; D_k = fraction of Day k with sufficient light for visual feeding; ε = weight-specific excretion rate (d^{-1}); and ρ = weight-specific respiration rate (d^{-1}).

The mortality rate M_i ($\text{mg C mg}^{-1} \text{C d}^{-1}$) on prey i from all predators ($j = 1, 2, \dots, m$) is given by:

$$M_i = \frac{1}{B_i} \sum_{j=1}^m (f_{ij} B_j) \quad (7)$$

Input variables. The initial values of the state variable and the process parameter values concerning phytoplankton, herbivore zooplankton, carnivores, medusa and gobies are the same as those in Giske et al. (1991). Initial values for cod, benthos and labrids are given in Table 2. The parameter values of the feeding representations are given in Table 3. Below we explain how the values in Tables 2 & 3 originated.

Table 2. New state variables compared to the earlier version of Giske et al. (1991)

State variable	Initial value (mg C)
Cod	
0-group cod	325 m^{-3}
1-group cod	347 m^{-2}
2-group cod	480 m^{-2}
3+-group cod	440 m^{-2}
Labrids	787 m^{-2}
Benthos	5500 m^{-2}

Table 3. Parameter values used in the model. $f_{j,\max}$ = maximum feeding rate for predator group j ; K_{ij} = half-saturation constant for predator group j feeding on prey i when it is set equal to the characteristic initial prey densities; and $\hat{K}_{ij}$ = half-saturation constant estimated by Eqs. 3 & 4

Predator Prey	$f_{j,\max}$	K_{ij}	$\hat{K}_{ij}$	Units
0-group cod	^a			d^{-1}
Gobies		952	2142	mg C m^{-3}
Benthos		704	–	mg C m^{-3}
1-group cod	0.00856 ^b			d^{-1}
Gobies		375	844	mg C m^{-2}
Benthos		5500	–	mg C m^{-2}
Labrids		787	–	mg C m^{-2}
2-group cod	0.00579 ^b			d^{-1}
Gobies		375	1043	mg C m^{-2}
Benthos		5500	–	mg C m^{-2}
Labrids		787	–	mg C m^{-2}
0-group cod		128	341	mg C m^{-2}
1-group cod		347	910	mg C m^{-2}
3+-group cod	0.00388 ^b			d^{-1}
Gobies		375	1120	mg C m^{-2}
Benthos		5500	–	mg C m^{-2}
Labrids		787	–	mg C m^{-2}
0-group cod		128	380	mg C m^{-2}
1-group cod		347	1006	mg C m^{-2}

^a Temperature-dependent maximum feeding rate; see Giske et al. (1991)

^b Estimated from experimental studies (E. Lied pers. comm.)

0-group cod: It was assumed that all 0-group cod settle in the shallow near shore habitat on 1 August. The initial biomass of recruits was chosen as the average recruitment during the years 1984 to 1988, and was derived from Salvanes & Ulltang (1992) by adjusting estimates on 0-group and 1-group for total mortality backwards to 1 August. The maximum growth rate for 0-group cod was derived from Hawkins et al. (1985). Assimilation efficiency ($A = 0.9$), weight-specific respiration rate ($\rho = 0.00107 \text{ d}^{-1}$) and weight-specific excretion rate ($\varepsilon = 0.00072 \text{ d}^{-1}$) were obtained from experiments (Lied 1983, E. Lied pers. comm.).

1-group, 2-group and 3+-cod: Initial biomasses were the averages of field estimates during the years 1986 to 1989 (Salvanes & Ulltang 1992). The maximum growth rates obtained from experimental studies were converted to maximum feeding rates using Eq. 3. Because the assimilation efficiency was estimated for cod feeding strictly on fish prey, and since 1-group and older fish also consume benthos, we reduced the assimilation efficiency to account for less digestibility of benthos compared to fish prey ($A = 0.8$ for age-groups 1+). The weight-specific respiration and excretion rates were the same as for 0-group cod, as the rates are reported nearly constant (E. Lied pers. comm.).

Labrids: Since no direct biomass estimate was available, the initial labrid biomass was derived by combining the results in Salvanes et al. (1991) and Salvanes & Ulltang (1992), as samples of labrids were obtained from the same net group settings as the cod samples. The initial labrid biomass was then obtained by assuming that the ratio between the catches of labrids and cod reflected the real ratio between these 2 groups.

We are not aware of any experimental studies on the maximum feeding rate of labrids. According to the general literature on energy budgets for fish (e.g. Brafield 1985), ca 44 % of consumed food is respired, and 7 % is excreted. Assuming that the excretion (ε) and respiration (ρ) rates estimated for cod are similar for labrids, the maximum daily feeding rate for the labrids $f_{\max} = (\varepsilon + \rho)/0.51 = 0.00351$.

Benthos: No quantitative estimate was available for the biomass of benthos in Masfjorden or from similar areas along the Norwegian coast. We therefore derived the initial value from McLusky & McIntyre (1988). They report typical benthos densities in the infralittoral of North Sea regions to be 4 to 18 g dry wt m^{-2} , and turnover rates (P/B ratios) between 0.1 and 5.0 yr^{-1} . We assume an initial benthos biomass of 11.5 g dry wt m^{-2} and a turnover rate of 2.6 yr^{-1} . Sensitivity analyses, however, are included to see if this is realistic. The production of benthos is not expressed in the same way as for the other groups. The standing stock is, in each time step, multiplied with the corresponding

turnover rate, and this production is assumed to originate from zooplankton production, which is reduced accordingly by assuming a constant factor between benthos growth and feeding.

Half-saturation constants: Two sets are given. The first set (I) is estimated according to Eqs. 2 & 3, and this set was used in the 'basic run' simulation (Table 3). The second set (II) is set equal to the initial values of the state variables of the prey (Giske et al. 1991).

RESULTS

Basic run

Simulated net annual production was 38.4 to wet wt of cod, 3.2 to labrids, 14.7 to gobies and 46.0 to benthos (Table 4). The fish production corresponds to $2.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the depth range 0 to 20 m. For comparison, Sissenwine et al. (1984) estimated the yearly production of fish on the Georges Bank area to be $4.2 \text{ g C m}^{-2} \text{ yr}^{-1}$, while Yang (1982) and Daan et al. (1990) estimated the fish production (not including 0-group) in the North Sea to be 1.7 to $1.8 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Comparison of the basic run with the run based on half-saturations set equal to characteristic prey densities showed the largest difference in production of 0-group cod (Table 4). Here, the production was 52 % higher than in the basic run. For the older age-groups, the differences were -4.0 to +17 %.

Sensitivity testing

We evaluated the potential effects of interannual variation in initial values of the state variables and major forcing functions, and possible bias in the parameter values. Except for the half-saturation constants, sensitivity analyses were conducted by changing 1 factor at a time, while keeping all other factors as in the

Table 4. Simulated annual accumulated net production (tonnes wet wt) of fish and benthos (I) using half-saturation constants estimated by Eqs. 3 & 4 and (II) using a K_{ij} set equal to the initial prey densities

State variable	I	II
Gobies	14.7	17.3
Benthos	46.0	44.2
Labrids	3.2	3.1
Cod		
0-group	21.9	33.3
1-group	7.8	8.1
2-group	6.6	7.2
3+-group	2.1	2.4

basic run. We paid particular attention to the initial values of the new state variables (Table 2) and to changes in advection. Giske et al. (1991) found that advection was a main factor influencing the production of 0-group cod.

The production of gobies and 0-group cod increases with increasing advection. If the advective rate is twice that in the basic run, the production of gobies increases 110 % and the production of 0-group cod increases by 54 %, whereas production of 1-group, 2-group and 3+-group cod increases by only 5 to 7 % (Fig. 3a). Changes in the advective regime were also reflected in the simulated diet composition. With increasing advection, the importance of gobies as prey for all age-groups of cod increases.

The production of cod and labrids decreases with decreasing benthos biomass (Fig. 3b). If the initial benthos biomass is half that used in the basic run the production is reduced by 26 % for 0-group cod, 43 %

for 1-group, 33 % for 2-group, 55 % for 3+-group cod and 42 % for labrids. However, the production of cod and labrids is only moderately sensitive to moderate changes in half-saturations (Fig. 3c). A 50 % increase in *all* half-saturations gave a 25 to 40 % decrease in total cod production. The sensitivity of cod production to changes in biomass and maximum feeding rate of labrids (i.e. labrids feeding on benthos) was also tested, but cod production is insensitive to such changes. Increased maximum feeding rate of labrids by e.g. 400 % results in only 15 % decrease in total cod production.

Potential cod production

We investigated how changes in recruitment level (between 0 to 20 times the basic run) influenced cod production for 2 advection rates (0.5 and 2.0 times the

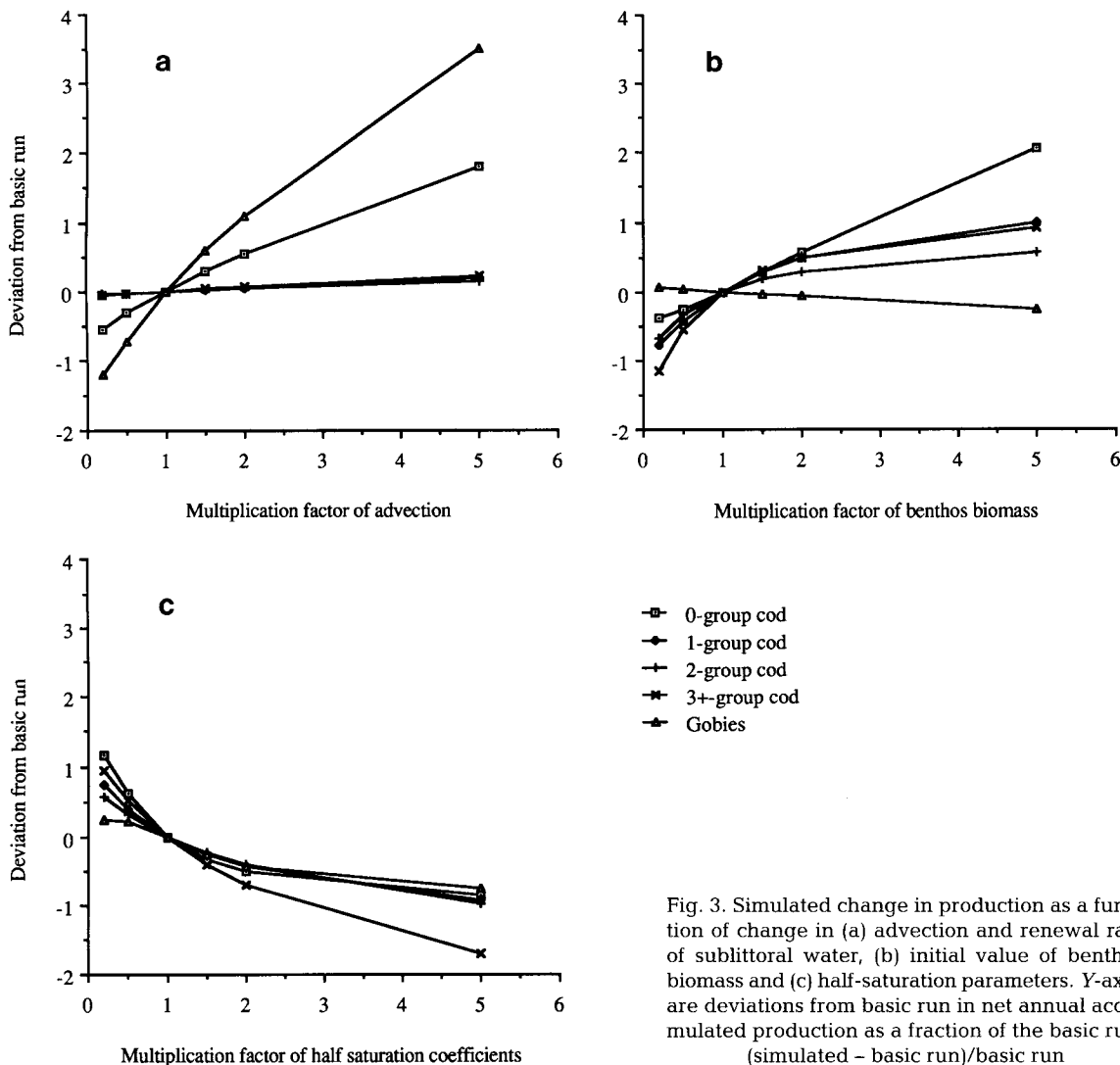


Fig. 3. Simulated change in production as a function of change in (a) advection and renewal rate of sublittoral water, (b) initial value of benthos biomass and (c) half-saturation parameters. Y-axes are deviations from basic run in net annual accumulated production as a fraction of the basic run: (simulated - basic run)/basic run

basic run) and for 1 level of initial biomass of benthos (0.5 times the basic run) (Fig. 4). The recruitment levels chosen were assumed to reflect the sum of wild gadids (the pooled recruitment from cod, pollack, saithe and poor-cod) and hypothetical release numbers of cod in Masfjorden.

In the basic run about 184 000 individuals (average weight = 15.6 g) were assumed to recruit as 0-group on 1 August. This represented the average yearly recruitment before the large-scale enhancement experiment (Salvanes & Ulltang 1992). Simulation indicates that the carrying capacity may be 3 to 7 times higher (Fig. 4) and that the maximal annual cod production is around 58 to wet wt. However, if initial benthos biomass is reduced by 50 % compared to the basic run, the production curve will shift downwards and indicate a maximal cod production of 35 t. Similarly, a doubling in advection rate will shift the production curve upwards and indicate a maximal cod production of 73 t. Higher shifts upwards or downwards are obtained if more than 1 of the factors change in the same direction. If all the 3 factors are half that in the basic run, production will decrease by approximately 70 %.

DISCUSSION

Alternative models (Sissenwine 1984, Nixon 1988, Bax & Eliassen 1990, Christensen & Pauly 1992) could be used for assessing potential fish production in Masfjorden. Fish production could be assessed from e.g. the Ecopath II model (Christensen & Pauly 1992) – used

on both freshwater and marine ecosystems throughout the world – and the model of Sissenwine et al. (1984) applied for the Georges Bank ecosystem, or the numerical ecosystem model applied in the multispecies analysis of Balsfjorden, northern Norway (Bax & Eliassen 1990). However, all of these models does not account for the functional relationship between predators and prey and the influence of advection. It is therefore expected that if these models are applied for the Masfjorden ecosystem, they will fail to explain how fish production is influenced by the magnitude of advection of secondary production. Hence, our ecosystem model represents a step beyond these models since it integrates biological processes with oceanographic conditions in order to explain the underlying processes regulating fish production. It should be noted, however, that our simulated production of cod and its competitors (38.4 to 51 t, Table 4; equivalent to 14.8 to 19.6 kg ha⁻¹ fjord area yr⁻¹) fits well into Nixon's (1988) correlation between fisheries yield and local primary production (Fig. 6 in Nixon 1988). His regression line predicts a fisheries yield of 12 kg ha⁻¹ yr⁻¹ when primary production is 90 g C m⁻² yr⁻¹, not far below total production in Masfjorden. Our approach indicates, however, that the potential yield in Masfjorden is highly dependent on large-scale advection of zooplankton rather than by local phytoplankton production (Fig. 3a). This is probably also the case for Balsfjorden (Bax & Eliassen 1990, Hopkins et al. 1990) and most, if not all, of Nixon's (1988) coastal ecosystems. We believe that advective transport of plankton and the possibility of offshore fish feeding migrations explain much of the higher fisheries yield in coastal marine ecosystems relative to lakes (cf. Fig. 5 in Nixon 1988).

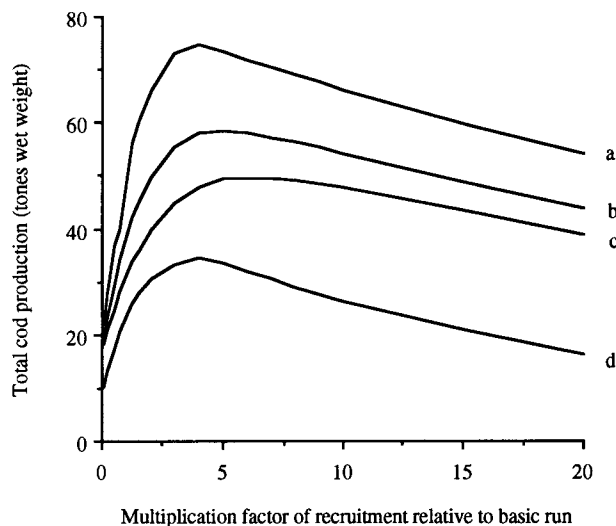


Fig. 4. Simulated production curves for the entire cod population as a function of changes in recruitment. (a) Advection rate is twice as high as in basic run. (b) Advection rate and benthos biomass as in basic run. (c) Advection rate half of that in basic run. (d) Initial benthos biomass half of that in basic run

Validity of the model

Giske et al. (1991) observed that the simulated standing stock of phytoplankton corresponded well with measurements taken in the fjord. This supporting evidence suggests that the model gives reasonable estimates for primary production and processes at lower level of the food web (the composed effect of solar radiation, temperature development, freshwater runoff, deep-water convection). Those aspects considered particularly important for the predictive ability at higher trophic levels are discussed in the following sections.

Food-web representation and simulated fish production

The predator-prey interactions were selected according to analysis of stomach contents for each age-group (Fosså & Nordeide pers. comm.) and length

group of cod (Salvenes 1986a, Salvenes et al. 1991). As gobies, benthos, labrids, cod and other gadids were the principal prey for cod, these prey groups were represented as state variables in our model. Important to cod production was competition for food resources in the shallow near-shore habitat. Presently, the simulated cod production accommodate intraspecific competition. If the model is extended to incorporate other major competitors in the fjord, i.e. pollack, saithe and poor-cod, some of the presently simulated cod production would be transferred to these groups and reduce the cod production accordingly. Hence, the difference between simulated cod production and field-based estimates of cod in the fjord should indicate the biomass level of the competitors. A field-based estimate of cod production can be provided by the following approach. According to Pitcher & Hart (1982) the turnover rate in exploited fish populations is generally assumed to equal the total instantaneous mortality rate Z . For cod in Masfjorden, an average Z was estimated to be ca 1.0 yr^{-1} for the period 1986 to 1988, and the total biomass was estimated as 28 to wet wt (Salvenes & Ulltang 1992). If $P/B = 1.0$ is used, yearly cod production becomes 28 t, giving a difference between estimated and simulated cod production of 10.4 t. These 10.4 t should reflect the production of competitors at the same trophic level as cod inhabiting the shallow near-shore in Masfjorden.

If the turnover rate for the competitors to cod is also ca 1.0 yr^{-1} , the average production estimate becomes 33 to for this group (the estimate is derived using Salvenes et al. 1991 and Salvenes & Ulltang 1992). Compared with the simulated 10.4 t mentioned above, this indicates that a potential unexploited food resource – available for released juveniles in connection

with cod enhancement – probably is very limited in an average year. However, based on the calculation in Table 5, a biological potential for extensive mariculture may exist in years when positive deviations from the average occurs. If, for example, both the density of benthic organisms and the advection of zooplankton is twice as high as in an average year, the simulated cod production becomes 69 t (i.e. 8 t more than the sum of empirical estimates of cod and competitors in an average year). If, additionally, the recruitment is twice as high, the simulated cod production increases even more. Hence, the simulations indicate that releases of juveniles may increase cod production in years when food is abundant.

The pelagic visitors in Masfjorden (spurdog, mackerel, herring, sprat and squids) are not represented in the model as it was impossible to quantify their abundance. However, these groups were accounted for indirectly. Since the pelagic visitors were assumed to either directly or indirectly eat zooplankton, we have defined an extra mortality rate on the zooplankton group ($M = 0.006 \text{ d}^{-1}$; see 'Tuning of parameters' in Giske et al. 1991).

The maximum growth rate and feeding representation

Experimental studies provided input values for the maximum growth, excretion and respiration rates and for the assimilation efficiencies (E. Lied unpubl.). Because the growth potential in captivity is generally believed to be higher than in natural environments (Jones & Johnston 1977, Jones 1978, Jobling 1982, Braaten 1984), one may question whether the growth rates from laboratory experiments are representative for the fjord. In our model the growth rate was reduced due to the availability of prey according to Eq. 4, and the laboratory growth rates would only apply at very high prey densities ($B \gg K$). Furthermore, the half-saturation was estimated indirectly from realised growth rates (Eqs. 2 & 3), and the feeding representation should therefore be fairly realistic. We regard this as an improvement from 'the use of characteristic prey densities' as suggested by Giske et al. (1991), at least for the 0-group cod. Our estimate of K for the 0-group was 72 % higher than that used by Giske et al. (1991). This difference causes a 52 % higher production of 0-group in the earlier model version (c.f. Table 4). For the older age-groups the difference was much smaller: K deviated only by 7 to 23 % from initial prey values and simulated cod production by -4 to +17 % (Table 4). This confirms the sensitivity testing which indicated that moderate deviations in K affect the cod production moderately (Fig. 3c).

Table 5. Relative importance of alterations in recruitment, advection rate and benthos biomass for the production of cod. Model output refers to yearly cod production relative to basic run (Basic)

Change to model input	Changed variables			Change to model output
	Benthos	Advection	Recruitment	
0.5 × Basic	x			0.68
0.5 × Basic		x		0.81
0.5 × Basic			x	0.76
0.5 × Basic	x	x		0.42
0.5 × Basic	x		x	0.45
0.5 × Basic		x	x	0.64
0.5 × Basic	x	x	x	0.33
2.0 × Basic	x			1.50
2.0 × Basic		x		1.33
2.0 × Basic			x	1.29
2.0 × Basic	x	x		1.80
2.0 × Basic	x		x	2.05
2.0 × Basic		x	x	1.72
2.0 × Basic	x	x	x	2.63

Sensitivity to initial values

The initial values of cod were based on field estimates reported in Salvanes & Ulltang (1992). The initial value for labrid biomass also originated from samples from the fjord (Salvanes et al. 1991). The half-saturation values were estimated from observed growth rates (Eq. 2). The initial value of benthos biomass is questionable as no investigations from the fjord, nor from any other coastal area of Norway, could be used to assess the estimate. The initial value is therefore based on average densities reported by McLusky & McIntyre (1988) for the shallow North Sea regions. Simulated cod production was, however, rather sensitive to changes in the initial value of benthos biomass. A reduction of the initial value by 50 % reduced the production of 0-group cod by 26 %, 1-group by 43 %, 2-group by 33 % and 3+-group by 55 % (Fig. 3b). Thus, if the true benthos biomass in Masfjorden differs severely from the initial value

chosen for the basic run, we would expect a very different cod production. We believe that the initial benthos biomass in the basic run is overestimated rather than an underestimated as this is indicated by comparisons of predicted and observed diet composition (see the section below).

Comparison between predicted and observed diet

As indicated in Fig. 5 and Table 6, the simulated fraction of benthos in the diet of cod was similar to that observed in the stomachs when benthos biomass was lower than the value in the basic run (5.5 g C m^{-2}). Increases in benthos biomass relative to the basic run, (factors 1.5 and 2.0), gave marked deviations from the observed diet (Table 6). The best fit between observed and simulated diet was shown for 2-group cod in the basic run (only 0.8 % difference). However, for 0-group and 3+-group fit was best when benthos bio-

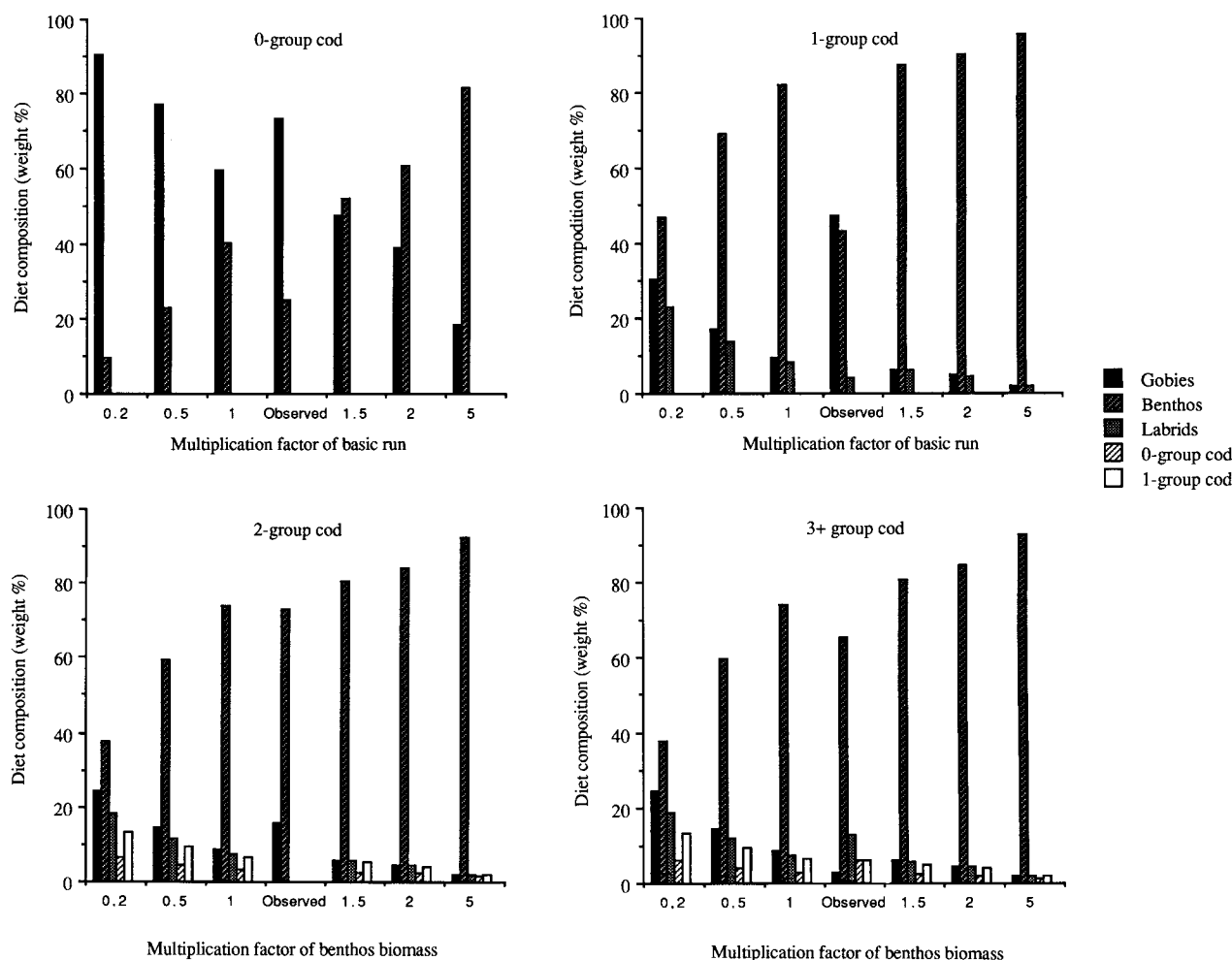


Fig. 5. Changes in simulated diet composition of age-groups 0, 1, 2, and 3+ of cod as a function of changes in initial value of benthos biomass compared with observed diets

Table 6. Percent deviation between observed benthos consumption (Fosså & Nordeide unpubl.) compared with simulated consumption. Different initial benthos biomass refers to fractions of the initial benthos biomass used in the basic run (i.e. $1.0 \times \text{Basic}$)

Initial benthos biomass	0-group cod	1-group cod	2-group cod	3+-group cod	Average
$0.2 \times \text{Basic}$	15.5	3.7	35.5	27.6	20.6
$0.5 \times \text{Basic}$	2.2	26.2	13.7	5.7	12.0
$1.0 \times \text{Basic}$	15.2	39.0	0.8	8.7	15.9
$1.5 \times \text{Basic}$	27.3	44.4	7.4	15.4	23.6
$2.0 \times \text{Basic}$	35.7	47.2	11.2	19.2	28.3
$5.0 \times \text{Basic}$	56.4	52.8	19.5	27.4	39.0

mass was 50 % of basic run (2.3 and 5.7 % difference, respectively), while the differences are slightly higher comparing with basic run (15.2 and 8.7 % difference). Hence, we conclude that the initial value of benthos biomass was somewhat overestimated, but nevertheless it seems acceptable.

Cod production and advective supply of zooplankton

In the present version the productivity of the entire cod population relies both on initial benthos biomass and on the advection and renewal rates of sublittoral water (Fig. 4). The advection rate (i.e. the transport of zooplankton) is more important than benthos biomass as benthos production also relies on zooplankton availability. Simulated changes in advection provided shifts in the production curves in Fig. 4. A doubling of advection rate shifted the production curve in Fig. 4 upwards and increased maximal cod production from 58 to 73 t wet wt. Since advection in Masfjorden is to a large extent meteorological driven (Aksnes et al. 1989), the productivity of the cod population in Masfjorden may also be heavily influenced by inter-annual variability in meteorological conditions. Net transport of zooplankton into the fjord seems to occur when southwesterly winds dominate, whereas net advective loss occurs at northwesterly winds.

Carrying capacity and the potential for extensive mariculture

Previous ecosystem evaluations of carrying capacities in enhancement programmes have primarily concentrated on species at the lower trophic levels. Bacher (1991), Grentz et al. (1991) and Héral (1991) evaluated the relationship between productivity of mussels and oysters and the availability of phytoplankton in coastal Mediterranean areas. Except for Parsons & Kessler (1987), Giske et al. (1991) and this paper, we are not aware of simulation studies on carrying capacity of species at higher trophic levels. Parsons & Kessler

(1987) modelled production of young salmonids off British Columbia (Canada) and found that survival was strongly influenced by the standing stock of their main prey, zooplankton. Giske et al. (1991) found that the advective transport of zooplankton into the fjord, and to the littoral zone, seemed to regulate the abundance of gobies, and thereby juvenile cod. This feature has also been confirmed in field studies in Masfjorden (Fosså 1991). In the present paper we also find that the production of older cod relies on zooplankton advection, although indirectly. Similarly, field studies on Pacific sockeye salmon, reviewed by Peterman (1991), indicate that variability in age-specific body size of adult salmon corresponds with interannual variability in zooplankton abundance. Our study indicates that large-scale releases of cod juveniles should preferably be conducted in years with high zooplankton availability at the release site.

Unfortunately our model does not, generally, predict positive effects of cod enhancement. It is indicated that cod enhancement is most recommended in years better than average. The initial hope of the fishermen was that enhancement might buffer year-to-year variations in recruitment to the fisheries. To some extent this is validated in the model, since Fig. 4 shows that the natural recruitment is below the average carrying capacity. However, the biological potential for large increases of the cod population seems only to exist in years with larger advective input to the fjord, i.e. when the natural cod stock itself is in good condition. A vital scientific goal is then to evaluate the production potential for a specific year early enough to decide whether releases of juveniles will be profitable.

Moreover, as pointed out earlier, the carrying capacity of fish in Masfjorden – and in any other coastal marine ecosystem – cannot be determined from local production and biomasses. This is perhaps the most important lesson from our model studies. The potential for cod enhancement depends to a much larger extent on local meteorology and topography, than for example sea ranching of salmon. While cod are nearly stationary and depend on advective input of indirect food to the release site, salmon migrate from the

release site to highly productive feeding areas in the open oceans (e.g. Thorpe 1980), and thus choose habitats independent of release site, and transport biomass back to the release site. Thus, when evaluating the suitability of a location for mass releases, the species' habitat use and life history should be taken into account.

The trophic interactions (feeding and mortality) are very simplistically stated and do not account for behavioural responses to cod enhancement. A recruitment beyond carrying capacity might force the cod to increase its spatial distribution, as reported for Atlantoscandian herring (Dragesund et al. 1980). A consequence could be that young cod in Masfjorden would utilise the pelagic habitat, as seen in fjords of northern Norway (Pearcy et al. 1979, Falk-Petersen & Hopkins 1981, Klemetsen 1982, Santos & Falk-Petersen 1989). An important factor in this respect may be density dependency in mortality risk of 0-group cod in the sublittoral. Two opposing effects may operate after mass releases: (1) with an increased number of prey available for each predator, the Holling type II functional response curve predicts predator saturation and then decreased individual mortality risk for the prey, while (2) a limitation in suitable sublittoral habitats that allow feeding at low mortality risk, may impose a utilisation of more dangerous habitats with sharply increased predation risk for the less competitive segment of the 0-group cod year class. Werner & Gilliam (1984) and Gilliam & Fraser (1987) have shown that fish can and do trade off mortality risk and feeding opportunities among habitats. Increased numbers of juvenile fishes in the sublittoral might therefore lead to (1) increased competition and reduced growth, (2) relocation and increased mortality, or (3) both effects. Nordeide & Salvanes (1991) found an initial high mortality rate of released juvenile cod, while stomach contents of predators during the months afterwards did not show any sign of elevated mortality rate. They found newly released cod to feed on a dissimilar diet than the natural year class during the first 3 d after release. This difference seemed, however, to disappear after some time. Over a longer period after release, Nordeide & Fosså (1992) found no significant difference in diets of wild and released cod, nor between the subsequent year-classes (0- and 1-group) in a situation of food shortage (Nordeide pers. comm.). Over all years of study in Masfjorden, there has been no indication that cod of any age group has utilised the open water masses, so the relocation hypothesis may only be valid for a wider use of the sublittoral and benthic habitats. The dynamics of growth and mortality within the sublittoral and benthic habitats fit well with the model of predator-mediated prey distributions (Mittelbach & Chesson 1987), indicating that mass releases may

lead to lower growth rather than decreased survivorship. However, the dynamics of these interactions with increasing numbers of all year-classes remain unknown.

In conclusion, 2 main implications can be extracted from our results with regard to extensive mariculture on cod: (1) optimal cod production can be obtained if the sum of released and wild recruits is within the range of the carrying capacity of juveniles and (2) releases of the same number of juveniles in several years will result in dissimilar cod production due to interannual variations in zooplankton availability.

Acknowledgements. This work was supported by the Norwegian Council for Fisheries Research (grant no. I 701.244), by PUSH ('Program for developing and stimulation extensive mariculture'), by the Institute of Marine Research, Ministry of Fisheries and by the University of Bergen. We are particularly grateful to J. H. Fosså and J. T. Nordeide as their knowledge about the Masfjorden ecosystem and their diet composition data was essential for the final structure of our model. We also thank Brian MacKenzie and 2 anonymous referees for constructive criticism on the manuscript, E. Lied for access to unpublished results from experimental studies on cod growth and Elin Holm for drawing the figures.

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This article was submitted to the editor

Manuscript first received: May 25, 1992

Revised version accepted: October 29, 1992