Simulated carrying capacities of fish in Norwegian fjords

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ABSTRACT

The influence of oceanographic and meteorological conditions and topography on the carrying capacity of organisms in coastal areas of western Norway is investigated by field studies and dynamic modelling. Published data on *Calanus finmarchicus*, the dominant species in the zooplankton biomass of west Norwegian coastal waters, demonstrate a strong gradient, with high densities at the outer coastal areas and lower densities at the innermost localities. This gradient spans several orders of magnitude. A similar tendency is found in the data from pelagic trawling and from beach seine catches, and simulation modelling indicates that fish production depends on zooplankton availability. According to the model, the carrying capacity level of fish production is high in the outer areas and decreases with distance from the outer coast according to the decrease in advected biomass of zooplankton. The simulations indicate that while growth prospects for individuals at lower trophic levels vary with the distance from the coast, potential for growth seems largely unaffected by the distance from the coast for the sublittoral piscivores (e.g. cod). This indicates that, for immigration of a new sublittoral piscivore to a habitat, it does not matter whether the habitat is situated close to the outer coast or far from it. A consequence for stock enhancement may be that a small-scale release of sublittoral piscivores will be equally productive in most coastal areas, while the outcome of a large-scale release will be strongly dependent on distances from the coast. The outcome may be high, but variable, in the outer areas and low, but probably more constant in the innermost areas, provided that releases of juvenile, sublittoral, piscivorous fish do not result in a fish stock density in excess of the carrying capacity level.
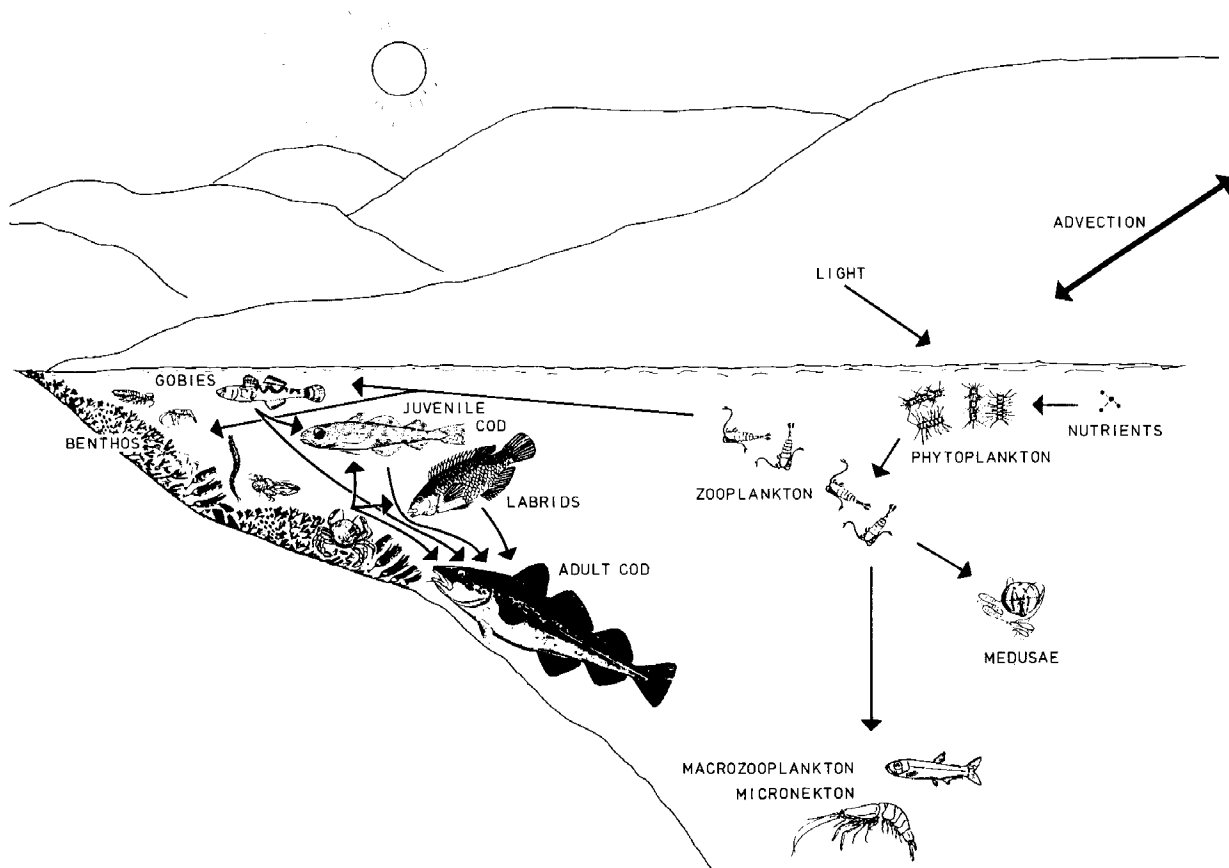
INTRODUCTION

Much attention has been paid to natural recruitment variability in fish stocks (Hjort, 1914) and to human influence (Beverton and Holt, 1957) as important regulators of the sizes of fish stocks. During recent years there has been an increasing tendency for analysing the variability in sizes of fish stocks as a consequence of fundamental properties of the ecosystem under consideration (Southward *et al.*, 1976; Hollowed *et al.*, 1987; Peterman, 1987; Peterman and Bradford, 1987; Sharp, 1988; Aebisher *et al.*, 1990). As such, in a study on the low level of fish production in the Irish Sea, Brander and Dickson (1984) suggested that causal relationships should be sought at the plankton level. Ecosystem simulation models are useful when investigating possible environmental impacts on fish stocks (Parsons and Kessler, 1987; DeAngelis and Cushman, 1990; Giske *et al.*, 1991; Salvanes *et al.*, 1992). For a west Norwegian fjord (Masfjorden), the ecosystem structure (Fig. 1) was investigated by detailed and interdisciplinary field investigations conducted in connection with a large-scale extensive cod mariculture experiment (Aksnes *et al.*, 1989; Fosså *et al.*, 1994; Nordeide *et al.*, 1994; Salvanes *et al.*, 1994; Smedstad *et al.*, 1994). Based on these field studies an ecosystem model was developed (Giske *et al.*, 1991; Salvanes *et al.*, 1992). Central topographical, meteorological, physical and biological characteristics were integrated to analyse the impact of environmental forcing on cod production in a fjord. Simulations indicated that the availability of zooplankton was a key factor for the carrying capacity of cod and its competitors. For Masfjorden, zooplankton availability was found to be regulated by advection rather than local production (Aksnes *et al.*, 1989; Giske *et al.*, 1991). The zooplankton abundance in more enclosed fjord systems, however, is likely to be dominated by local production (Aksnes and Magnesen, 1983; Aksnes and Lie, 1990). In the Masfjorden ecosystem model, zooplankton is the principal prey for gobies, and zooplankton availability therefore regulates gobid production. Gobies in turn are one of the major prey of juvenile gadids, and gobid production therefore influences production of juvenile cod and other gadid com-

Figure 1.   The model–simplified food web for shallow nearshore and pelagic habitats of typical west Norwegian fjords and coastal areas. Note that gobies represent the dominant sublittoral planktivorous fish, cod represents the typical sublittoral piscivorous fish and labrids represent a typical benthivorous fish. (After Salvanes *et al.*, 1992.)

petitors (although predation from older cod and other gadids also takes part in the regulation of juvenile cod survival). Zooplankton availability thus indirectly influences juvenile cod production and production at the higher trophic levels. This interpretation is supported by field studies indicating covariation among cod recruitment, gobid production and zooplankton availability (Fosså, 1991). Among other factors, the variable wind regime along the coast of western Norway is believed to be an important regulator of zooplankton advection into and out of the fjords. Meteorological variability is therefore likely to propagate through water movements, to plankton and further into the food web (Aksnes *et al.*, 1989). The simulation results of Klinck *et al.* (1981a) demonstrate the dynamic control of fjord circulation by offshore wind-driven coastal current. It was also demonstrated that alongshore winds, through Ekman flux, cause a net volume change in a fjord (Klinck *et al.*, 1981b). Thus regional wind seems to be a

common important forcing factor of the coastal ecosystems of western Norway.

In the present paper we extend the scope of the Masfjorden system (Giske *et al.*, 1991; Salvanes *et al.*, 1992), and compare the carrying capacity level for the higher trophic levels in different coastal areas *relative* to the carrying capacity in Masfjorden along a gradient ranging from fjords located close to the Norwegian Coastal Current to fjords located far from it. Analyses are made on the basis of pelagic and sublittoral sampling along a coastal exposure gradient, published data on the quantitatively most important copepod, *Calanus finmarchicus*, in Norwegian coastal zooplankton (Wiborg, 1944; Lie, 1967) and on the basis of the ecosystem model given by Giske *et al.* (1991) and Salvanes *et al.* (1992). The simulated annual production per length of shoreline relative to that for Masfjorden is used as an index for the carrying capacity level of the various fjords.

Figure 2. Map of western Norway. Dots refer to fjords sampled on 23–24 October 1991 and 22 March–2 April 1992. Samples were obtained from pelagic midwater trawl hauls, beach seine hauls and from vertical Juday net hauls.
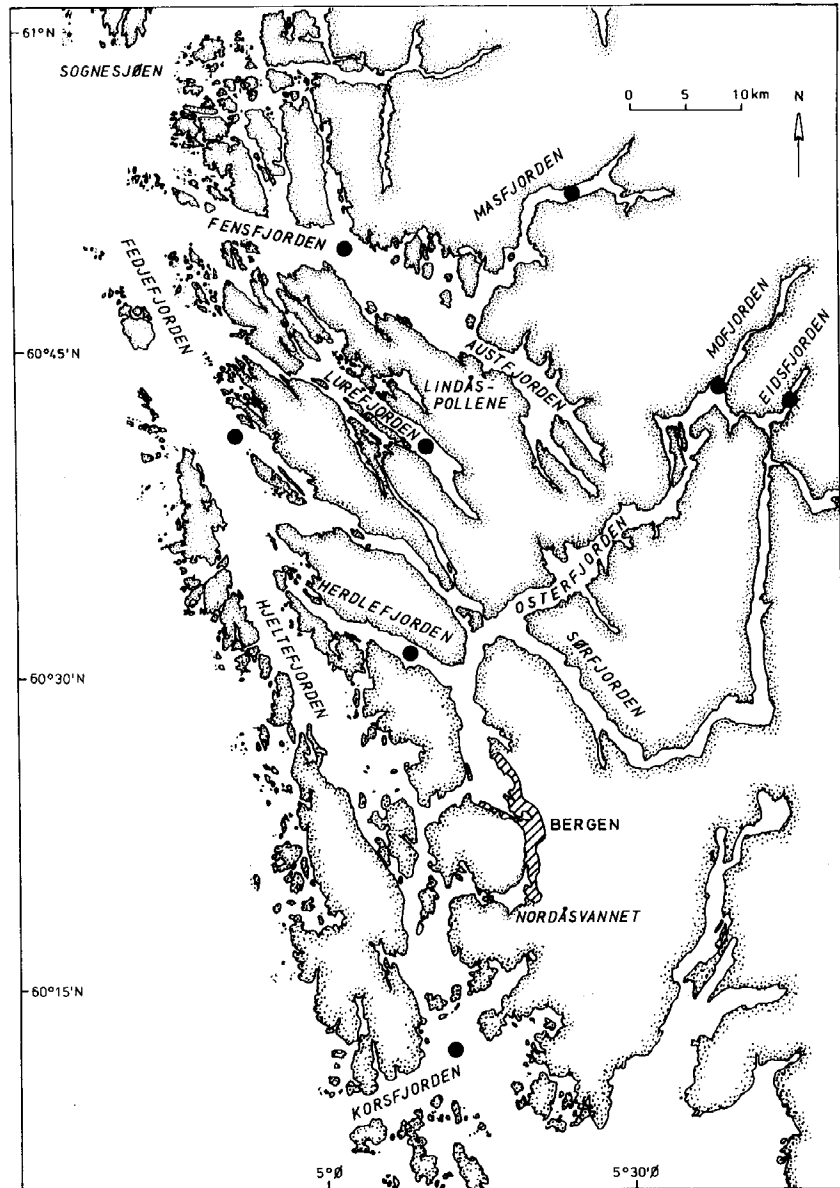
Methods

Sampling

The biological measurements of the investigated fjords (Fig. 2) originate from sampling using RV *Håkon Mosby* on 23–24 October 1991 and 22 March–2 April 1992. A total of 71 trawl samples from a 20 × 20 m² pelagic midwater trawl towed at 3 knots for 10 min (sampling volume = 370 000 m³) provided information on the biomass and species composition in the pelagic habitat. The cod end of the trawl consisted of a small-meshed inner bag and a larger-meshed outer bag. It is assumed that the inner bag of the trawl representatively sampled organisms >1 cm length. For each haul the species were

counted and weighed and biomass (mgC m⁻³) calculated. For very large samples, the total catch was weighed, and subsamples were counted and weighed.

Seventy-four beach seine hauls were obtained using a standardized sampling strategy. The seine was 40 m long, 4 m high, and had 5 mm mesh size with 3 mm mesh size in the 8 m long part. The length of the shoreline sampled by the beach seine and the depth of the outer edge of the sampled area were used to calculate the volume of the haul. The captured species were counted and weighed and the average biomass (g wet wt m⁻³) calculated. These biomasses were converted to mgC m⁻³ using the general assumption of an average 20% dry weight content of the wet weight and an average 50% C content of the dry weight.

Eighty-seven zooplankton stations were sampled using a Juday two-parallel-net (180 μm mesh size and 0.125 m^2 opening) vertically on three depth ranges (0–50 m, 51–100 m, 101 m–bottom) providing one subsample in each of the two nets. From each haul one subsample was filtered on a GFC filter and frozen for later biomass determination, while the other subsample was preserved in buffered 4% formaldehyde for later analysis of species composition. The frozen samples were dried at 60°C to constant weight and burned at 500°C for determination of ash-free dry weight (AFDW). From this the average biomass density was calculated (mgC m^{-3}) as averages of the entire water column according to the general relationship between dry weight, carbon contents and ash content per unit weight given for copepods on continental Atlantic shelves in Parsons *et al.* (1977, p. 54 table 12).

Simulations

Carrying capacity level is simulated for five fjords located at different distances from the outer coast of western Norway relative to the carrying capacity level in the sixth area (Masfjorden) by using an ecosystem model. The simulated annual production per length of shoreline relative to that for Masfjorden is used as an index for the carrying capacity level of the various fjords. Equations for forcing functions, processes and state variables are provided in the Appendix. A model run for Masfjorden is chosen as a standard run because (1) Masfjorden is a typical west Norwegian fjord, (2) its ecosystem structure is known from field investigations, and (3) an ecosystem model has been developed for the fjord (Giske *et al.*, 1991; Salvanes *et al.*, 1992). The model has been calibrated and partly validated in earlier papers (Giske *et al.*, 1991; Salvanes *et al.*, 1992). A large-scale cod enhancement experiment has been undertaken in Masfjorden, and the conclusion from field studies is that it is not feasible to increase cod production by releases of juveniles for that particular fjord (Nordeide *et al.*, 1994). The potential for cod enhancement which may exist in coastal areas other than Masfjorden is still being investigated.

The model structure, forcing functions and processes are described below. The input values to the model are physical, topographic and biological parameters for each fjord.

Model structure   The model includes four age groups of a sublittoral piscivore and its main prey groups: sublittoral benthivores, sublittoral planktivores and benthic organisms making up a near-shore compartment, and nutrients, phytoplankton, zooplankton, pelagic

planktivores (mesopelagic fish and euphausiids) and medusa constituting a pelagic compartment. The first step in development of the model was to express the pelagic ecosystem covering trophic levels from phytoplankton to 0-group cod (Giske *et al.*, 1991). The second step was to include more of the shallow near-shore compartment and the entire cod population by age groups and other major prey groups (labrids and benthic prey) (Salvanes *et al.*, 1992). Competition and cannibalism are modelled by specifying the prey types each predator consumes. The near-shore and pelagic compartments are coupled through water exchange where nutrients, phytoplankton and zooplankton are assumed to be passive elements transported by water. The primary production is driven by solar radiation and temperature, and by nutrient supply from freshwater run-off and deep-water convection. The boundary values together with the water exchange above the sill of the fjord regulates the magnitude of advection of nutrients, phytoplankton and zooplankton.

The time step of the model is 0.01 day, and simulations run from 1 January to 31 December. The simulated production and prey consumption accumulate over one year for each of the trophic levels. Except for tuning of the renewal rate of sublittoral zooplankton to obtain correspondence between simulated and observed sublittoral planktivore production (mainly gobies), we have not used other data to calibrate the model. We have compared the simulated production of cod and other fish with independent production measurements (derived from Salvanes and Ulltang, 1992, and Salvanes and Nordeide, 1993) and obtained good agreement (Salvanes *et al.*, 1992). Simulated yearly consumptions of major prey groups are also compared with observed diet composition of cod, and good agreement is found (Salvanes *et al.*, 1992). This suggests that the biological processes expressed in the simulation model are adequate.

Forcing functions and boundary conditions   The forcing functions advection, convection and freshwater run-off are described below. Detail on the other forcing functions (solar radiation, photoperiod and temperature) are provided by Giske *et al.* (1991). The topographic and physical measurements of each fjord, shorelines, surface areas, volumes, and the cross sectional areas above the sills (Table 1), are digitalized from shore and depth contours on maps with a scale of 1:50 000. These measurements are used to calculate volumes of the pelagic and sublittoral habitats and the area of the benthic habitats, which are input parameters to the model. These parameters affect the renewal rate according to advection, deep-water convection rate and fresh-

Table 1. Length of the shoreline (l), surface area ($a_{surface}$), cross sectional area at the sill (a_{sill}) and volume of advective layer (v_{adv}) of some west Norwegian fjords. Distances from the outer coast (x) are measured from the sill and along the mid section of the main channel outwards to the outer coast.

Fjord	l (km)	$a_{surface}$ (10^6 m^2)	a_{sill} (10^3 m^2)	v_{adv} (10^9 m^3)	x (km)
Lindåspollene	–	–	–	–	25.1
Lurefjorden	199.4	39.6	3.0	1.19	15.7
Osterfjorden	358.5	142.0	476.5	4.26	60.2
Masfjorden	70.0	26.2	44.5	5.4	39.3
Fensfjorden	–	–	699.8	–	8.1
Herdlefjorden	58.3	24.2	512.0	0.73	52.5
Hjeltefjorden, north	140.3	88.1	2734.9	2.64	0.0
Korsfjorden	150.2	80.0	665.5	2.40	2.2
Nordåsvannet	–	–	–	–	32.2
Hardangerfjorden, station 2	–	–	–	–	164.0
Hardangerfjorden, station 5	–	–	–	–	144.0
Hardangerfjorden, station 6	–	–	–	–	120.0
Hardangerfjorden, station 7	–	–	–	–	72.0
Hardangerfjorden, station 9	–	–	–	–	0.0

water renewal rate, which in turn affect the nutrient supply from deep-water, nutrient supply from fresh water, the advection of zooplankton and nutrients into the fjord and further renewal of zooplankton in the sublittoral habitat. The composite of these factors forms the basis for simulated production at higher trophic levels. Another important parameter characterizing a fjord is the distance from the sill to the outer coast (Table 1). This distance is measured along the mid section of the main channels and outwards. It affects the zooplankton densities at the sill (described in the next section).

The model requires values for monthly averages of advection, deep-water convection and freshwater run-off. The advection (cm s^{-1}) is measured by ADCP on the Masfjorden sill and monthly average is used as an output parameter to the model (Giske *et al.*, 1991). We have assumed the same pattern for all fjords. The renewal part of zooplankton in the sublittoral habitat is linked to the renewal rate of water there (Appendix: state equation A13).

The convection rate is calculated according to equation A2 (Appendix) and depends on the sill depth. This is linked to deep-water convection of nutrients which is calculated on the basis of observed nutrient depletion (m s^{-1}) in the water column over an annual cycle (Giske *et al.*, 1991).

Monthly average freshwater run-offs are provided by the hydroelectric power plant of Masfjorden (Giske *et al.*, 1991). For Osterfjorden, estimates of freshwater run-offs are available for January to June (monthly

averages are 595.1, 761.0, 523.4, 185.0, 382.9, and 875.6 m^3 s^{-1}, respectively; Hareide, 1991). For the period July to December, no estimate of freshwater supply is available. We have therefore computed the ratio of freshwater supply to Osterfjorden relative to Masfjorden for the first half of the year (Osterfjorden : Masfjorden freshwater run-off ratio becomes 11) and multiplied this ratio by monthly values for Masfjorden (given in Giske *et al.*, 1991, p. 167: F_1 in table 6B) for the second half of the year. This simplification is realistic when comparing productivity at higher trophic levels as earlier simulations (Giske *et al.*, 1991) showed that production for these groups is insensitive to even large changes in freshwater run-off. The other fjords do not have any large rivers generating freshwater supply and the run-off is therefore assumed to be zero as it would be negligible compared with that in Masfjorden.

Data from Wiborg (1944), Lie (1967), Matthews *et al.* (1978) and Aksnes and Magnesen (1983) were used to generate boundary conditions for zooplankton of the other fjords relative to Masfjorden. Time between samples was from 4 days to 1 month and sampling procedures were similar. Except for Matthews *et al.* (1978), who used samples from oblique hauls with a Longhurst–Hardy serial plankton sampler, all samples were taken by vertical Juday hauls and all data are converted to dry weight m^{-2} to become comparable. [*] *Calanus finmarchicus* was chosen because it dominates

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[*]Bias could occur if there were differences in the sampling efficiencies of the Juday and Longhurst–Hardy samplers.

Figure 3.   The density of *Calanus finmarchicus* (mg dry wt m^{-2}) as a function of the distance from the coast compiled from Wiborg (1944), Lie (1967), Aksnes and Magnesen (1983) and Matthews *et al.* (1978).
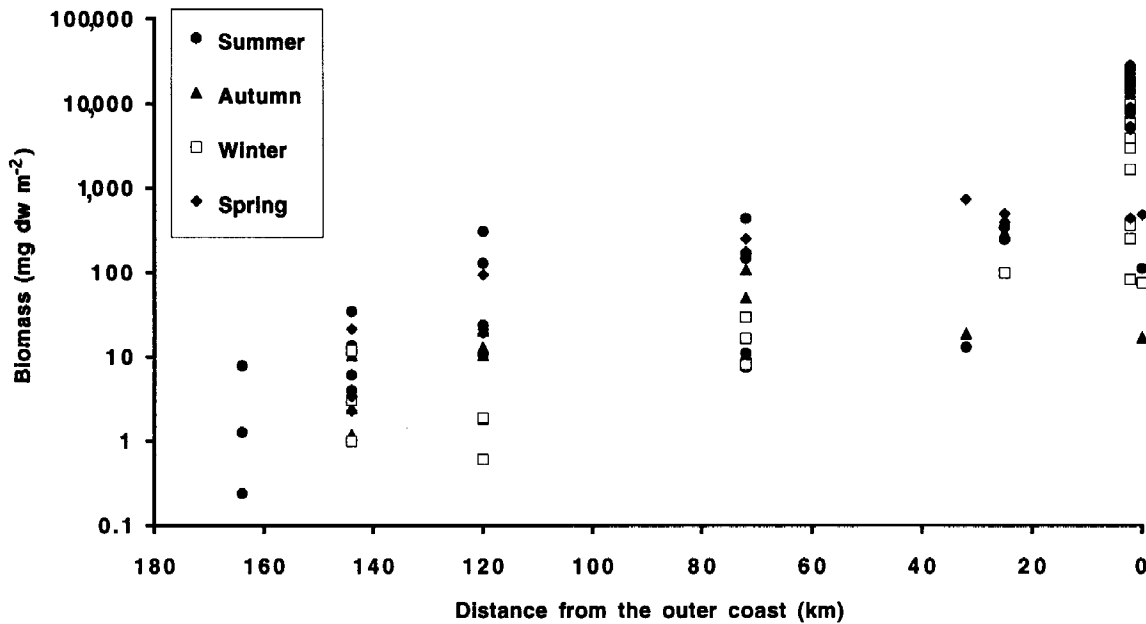
the zooplankton biomass of Norwegian coastal waters (Wiborg, 1944; Lie, 1967). For densities given in terms of numbers of each stage, we calculated first the wet weight using conversion factors for C. *finmarchicus* by stages to wet weight in table 3.2 in Ellingsen (1973). We then calculated the dry weight using the conversion factors given in table 10 in Aksnes (1981). From the data we computed 3-month average densities (mg dry wt m^{-2}) for four seasons [winter (January–March), spring (April–June), summer (July–September) and autumn (October–December)]. A multiple regression equation (Draper and Smith, 1981) was fitted to the observations (Fig. 3). As there generally is a seasonal cycle in zooplankton density, we have used dummy variables (D_1, D_2 and D_3) to distinguish them. This was done to reduce the number of regression equations from four to one. For the spring (April, May and June) all $Ds = 1$ for the summer (July, August and September) all $Ds = 0$, for the autumn (October, November and December) $D_1 = 1$, but $D_2 = 0$ and $D_3 = 0$, and for the winter (January, February, March) $D_1 = 1$ and $D_2 = 1$, but $D_3 = 0$. The regression equation was:

$$\hat{y} = \ln(B) = 9.88 - 1.45 \ln(x) - 0.29D_1$$
$$- 1.49D_2 + 2.02D_3; \quad R^2 = 0.732 \quad (1)$$

where B is zooplankton density, x is the distance to the outer coast and R^2 the regression coefficient (adjusted

Table 2.   Ratios between zooplankton density for investigated fjord distances relative to the density at the Masfjorden distance from the coast. It is calculated from the regression equation of published densities of *Calanus finmarchicus* from Wiborg (1944), Lie (1967), Aksnes and Magniesen (1983) and Matthews *et al.* (1978). Ranges in parentheses refer to the ranges obtained when standard errors of regression parameters are accounted for:

Fjords	Ratio
Hjeltefjorden, north	6.68 (5.32–6.68)
Korsfjorden	6.36 (5.09–6.36)
Lurefjorden	3.16 (2.75–3.16)
Herdlefjorden	0.52 (0.52–0.56)
Osterfjorden	0.35 (0.35–0.40)

for degrees of freedom; i.e. for the number of variables of the equation).

The ratio (Table 2) between zooplankton density for the investigated fjord distances from the coast and the zooplankton density at the Masfjorden distance, as calculated from the regression equation, is multiplied by the monthly average of zooplankton density observed at the sill of Masfjorden (B_5 in table 6A in Giske *et al.*, 1991), to provide boundary conditions of zooplankton at the sill as input to the model. This is done to standardize comparisons of investigated fjords to present situations.

Processes The average of spring and summer measurements of zooplankton, medusa, pelagic planktivores and small sublittoral planktivorous fish given in Table 3 are used as initial values for the densities of the state variables in the beginning of the simulations. We assume that the efficiency of the gears used for sampling was similar in the investigated areas. This may not be strictly true for beach seine sampling, as no areas are identical. The density of phytoplankton was chosen as in Giske *et al.* (1991) for all fjords. This could be done because both unpublished results with the present model and simulations with an earlier simulation model (Aksnes and Lie, 1990) clearly show that phytoplankton production and higher-level production are insensitive (on a time scale of weeks) to the actual value of the initial phytoplankton biomass.

One may question whether the zooplankton measurements of Table 3 are representative for true zooplankton density as sampling was conducted for only a few days once in spring and once in autumn. Because the data were obtained from the same gear and during a few days they originate from similar regional climatic conditions, and we consider these data to represent the same situation. The available data are therefore acceptable for the purpose of this paper, which is to compare various fjords with respect to carrying capacity and productivity.

No quantitative studies of benthos along the Norwegian coast are published. We have therefore derived the initial value for benthos as the average from McLusky and McIntyre (1988). They report typical benthos biomasses from the shallow section of North Sea regions to be 4–18 g dry wt m^{-2}, and turnover rates (production/biomass ratios) between 0.1 and 5.0 year^{-1}. From this we assumed an initial benthos biomass of 11.5 g dry wt m^{-2}, and a turnover rate of 2.6 year^{-1}. Sensitivity testing for Masfjorden (simulated benthos consumption compared with observed diet composition from field studies) indicated that the selected benthos density could be slightly overestimated, and certainly not underestimated when representing the 0–30 m depth range of the fjord (Salvanes *et al.*, 1992). Although the extension of benthic habitats differs between the investigated areas due to different shoreline lengths (Table 1), we have no reason to believe that the average benthos density (g dry wt m^{-2}) for the 0–30 m depth differs much among the types of areas we have investigated. Therefore, the extension of the benthic habitat is different for the different coastal areas in the simulations, whereas the same initial value for benthos density was used.

The initial values for the density of sublittoral piscivores and sublittoral benthivores are chosen relative to

that for Masfjorden given in Salvanes *et al.* (1992), where the ratio between each area and Masfjorden is obtained from corresponding densities obtained from beach seine samples. Hence, the efficiency of the beach seine is assumed to be similar in the six investigated areas as mentioned previously.

The group mentioned as pelagic fish in Table 3 is not expressed as a state variable in the model, but their impact on the pelagic inhabitants is expressed in the model as an additional, but unspecified mortality on zooplankton which they directly or indirectly consume (Giske *et al.*, 1991; Salvanes *et al.*, 1992).

RESULTS

Observations

Biomass estimates for the zooplankton, mesopelagic planktivorous fish, pelagic and sublittoral planktivorous fish are obtained from the cruises in autumn 1991 and spring 1992 (Table 3). In terms of numbers, the zooplankton group consists mainly of *Calanus finmarchicus*, *Oithona* spp. and the group *Paracalanus/Pseudocalanus*. In five of the fjords, *C. finmarchicus* dominates in biomass (own unpubl. data). The exception is Osterfjorden, the fjord located most distant from the coast, where the *Paracalanus/Pseudocalanus* group dominates in biomass. The mesopelagic fishes are *Maurolicus muelleri* and *Benthosema glaciale*. The pelagic fishes are primarily *Merlangius merlangus*, *Micromesistius poutassou*, *Pollachius pollachius*, *Sprattus sprattus* and *Squalus acanthias*. The sublittoral planktivorous fish species are dominated by the gobies *Gobiusculus flavescens*, *Pomatoschistus minutus* and *P. pictus*.

The sublittoral planktivorous fish biomass increased by about 200 times from spring to autumn (Table 3). The estimated biomass is much lower in Osterfjorden, which is located far from the outer coast (60.2 km), than in Herdlefjorden (52.5 km from the coast) and fjords closer to the coast (Masfjorden, Fensfjorden, Hjeltefjorden and Korsfjorden). The lowest biomass of sublittoral planktivorous fish was found in Lurefjorden. This fjord also differed from the other fjords by (a) the absence of mesopelagic fish (or pelagic planktivorous fish), (b) the high biomass density of the deep-water medusa *Periphylla periphylla* (also reported by Fosså, 1992), (c) the high density of zooplankton, and (d) the very low ratio between the cross sectional area at the sill and fjord volume (Table 1 and 3).

Simulations

Production potential in different fjords The simulated annual production per length of shoreline relative to

Table 3. Biomass (mgC m^{-3}) of zooplankton, mesopelagic fish, pelagic fish, medusae and sublittoral planktivores in west Norwegian fjords at different distances from the coast (x) during autumn (23–24 October 1991) and spring (22 March–2 April 1992). Biomass of littoral planktivores refers to near shore, the others are densities in the pelagic fjord volume. "–" means no sample.

Fjords	x (km)	Zooplankton		Mesopelagic fish		Pelagic fish		Medusae		Sublittoral planktivores	
		Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring
Hjeltefjorden, north	0.0	–	8.96	–	4.91	–	0.27	–	0.00	–	8.77
Korsfjorden	2.2	–	2.74	–	4.57	–	0.53	–	0.00	–	4.99
Fensfjorden	8.1	8.98	–	2.90	–	0.19	–	0.00	–	718.00	–
Lurefjorden	15.7	31.60	7.92[a]	0.00	0.00	1.03	0.00	10.40[b]	26.40[b]	100.00	0.43
Masfjorden	39.3	3.92	2.66[c]	1.32	2.63	0.26	0.29	0.00	0.00	750.00	3.26
Herdlefjorden	52.5	4.92	2.90[c]	3.01	5.04	1.21	0.68	0.00	0.00	784.00	–
Osterfjorden	60.2	8.50	7.32	1.87	0.36	0.70	0.00	0.00	0.00	234.50	1.60

[a]Tordis Nesse (pers. comm.).
[b]*Periphylla periphylla.*
[c]Otte Bjelland (pers. comm.).

that for Masfjorden (Table 4) is used as an index for the production potential. The yearly fish production is simulated for five fjords located at various distances from the outer coast (Fig. 4). These simulations indicate that the carrying capacity for fish production is about seven times higher for fjords close to the outer coast than for fjords located far from the outer coast. The simulated production for the sublittoral planktivore, sublittoral piscivore, sublittoral benthivore and pelagic planktivore groups decreases according to an exponential pattern with increasing distance from the outer coast, while the benthos appeared nearly unaffected (Fig. 4).

As indicated by the exponential decrease in the ratio between advected (A) and locally produced (P) zooplankton (Fig. 5), the high fish production in the outer areas depends on advected zooplankton biomass. Zooplankton advected into the fjord and further into the sublittoral habitat feed on the higher trophic levels. Local phytoplankton production is more or less con-

stant along the gradient (Fig. 6), except for the high phytoplankton production for the fjord located at the greatest distance from the coast (Osterfjorden). We also separated the effect of freshwater nutrients and zooplankton grazing on the phytoplankton production for this fjord by comparing model runs when initial values for all trophic levels above zooplankton were zero and then compared the simulated production when freshwater supply was (a) normal and (b) zero. The phytoplankton production (gC m^{-2} year^{-1}) differed slightly (4% lower for the latter case). Hence, the low advection of zooplankton to the innermost fjord results in little zooplankton grazing pressure and increased phytoplankton production.

The predicted diet composition of the sublittoral piscivores reflects the gradients in the carrying capacities of their prey (Table 5); the proportion of planktivorous prey decreases while the proportion of benthic prey increases with distance from the coast.

For individuals with the ability to migrate, it may be not the carrying capacity, but rather the individual growth and survival prospects, that determine where they stay (Fretwell and Lucas, 1970; McFarland and Sibly, 1975; Aksnes and Giske, 1990). To give an indication of the growth and survival prospect for the different areas, we have represented the ratio between the net yearly production and biomass value of the different groups scaled according to the length of the shoreline [g g^{-1} year^{-1} (m shoreline)$^{-1}$] (Fig. 7). We see that for the planktivores the prospects are better in the outer areas, whereas for the benthivores and sublittoral piscivores, the growth and survival prospects

Table 4. Results from the Masfjorden standard run. Simulated annual accumulated net production for the whole fjord for major trophic groups.

Trophic groups	Simulated production
Sublittoral planktivores	14.7 tonnes wet wt.
Sublittoral piscivores	38.4 tonnes wet wt.
Sublittoral benthivores	3.2 tonnes wet wt.
Benthos	46.0 tonnes wet wt
Pelagic planktivores	14.1 tonnes C

Figure 4. Simulated yearly production for five west Norwegian fjords [Hjeltefjorden (Hj), Korsfjorden (Ko), Masfjorden (Ma), Herdlefjorden (He) and Osterfjorden (Os)] located at different distances from the outer coast. (a) Sublittoral planktivores, sublittoral piscivores, sublittoral benthivores and benthos. (b) Pelagic planktivores (macroplankton and micronekton). Production is defined as simulated production per length of shoreline (kg wet wt m^{-1} $year^{-1}$) relative to a standard run for Masfjorden (Table 4).
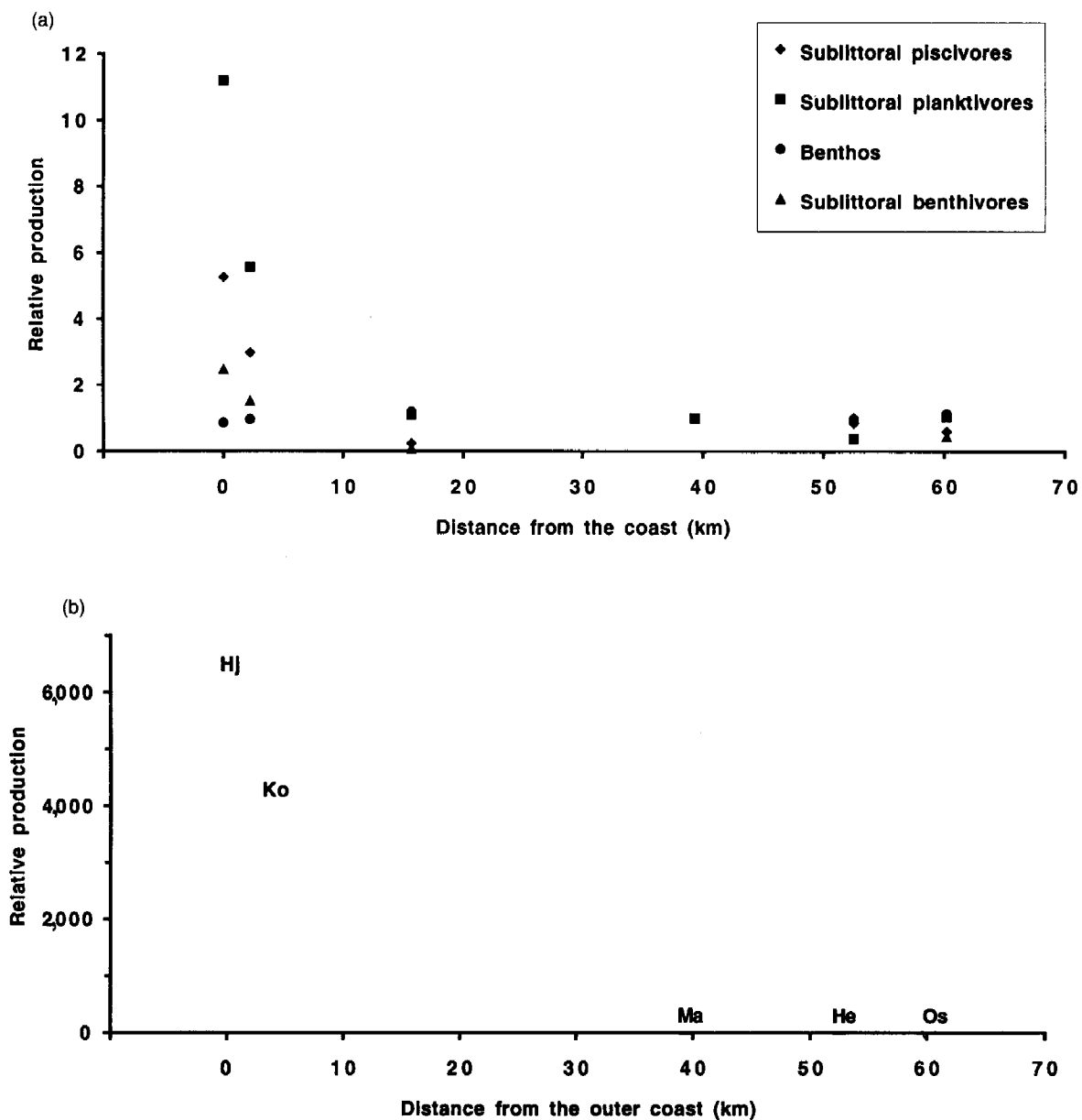
are quite similar in four of the six fjords and show no inward pattern.

DISCUSSION

In both the present and in earlier modelling approaches (Aksnes and Lie, 1990; Giske *et al.*, 1991; Salvanes *et* *al.*, 1992), several factors assumed to be important for the production of coastal ecosystems are integrated: topographical, meteorological, physical and biological. This multidisciplinary approach is a prerequisite to achieve knowledge of causal links between fish production and the environment (DeAngelis and Cushman, 1990). Our simulation approach represents,

Figure 5. Simulated yearly zooplankton advection relative to local production (A/P) for six west Norwegian fjords [Hjeltefjorden (Hj), Korsfjorden (Ko), Lurefjorden (Lu), Masfjorden (Ma), Herdlefjorden (He) and Osterfjorden (Os)] located at different distances from the outer coast.
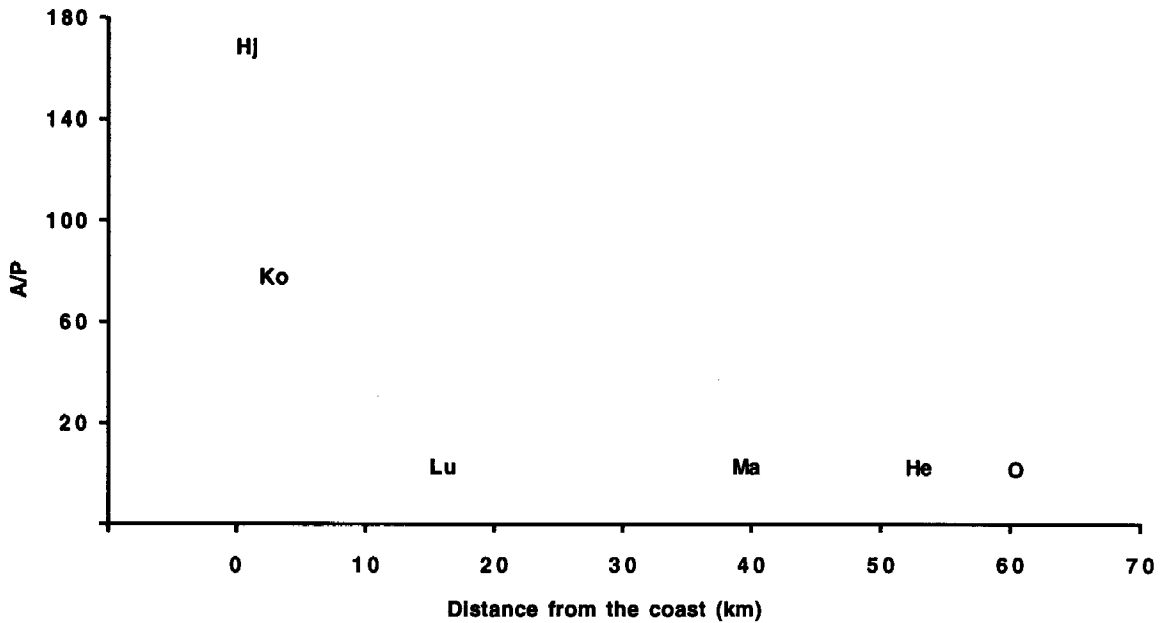
Figure 6. Simulated phytoplankton production (gC m^{-2} year^{-1}) for six west Norwegian fjords [Hjeltefjorden (Hj), Korsfjorden (Ko), Lurefjorden (Lu), Masfjorden (Ma), Herdlefjorden (He) and Osterfjorden (Os)] located at various distances from the outer coast.
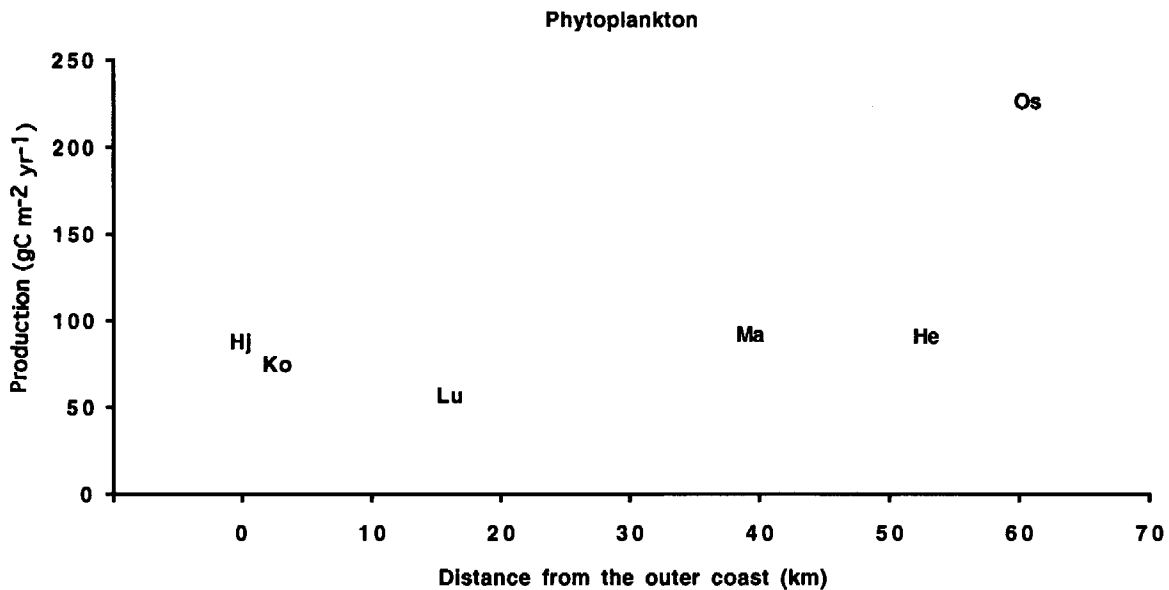

however, an oversimplification of the complex coastal ecosystem, and it can by no means eliminate the need for measurements. On the other hand, we believe that the data themselves (Tables 1 and 3; Fig. 3) are better utilized within a modelling framework instead of strictly as a descriptive presentation. This is also true for other fish-related ecosystem modelling approaches such as those of Sissenwine *et al.* (1984), Nixon (1988), Bax

Table 5. Simulated diet composition of littoral piscivores in west Norwegian fjords located at different distances from the coast (x).

Fjords	x (km)	Prey (% of total prey wt consumed)			
		Littoral planktivores	Benthos	Littoral benthivores	Littoral piscivores
Hjeltefjorden, north	0.0	69.6	22.4	2.6	5.4
Korsfjorden	2.2	61.5	32.7	1.9	3.9
Lurefjorden	15.7	45.2	54.1	0.3	0.4
Masfjorden	39.3	28.4	64.5	3.1	4.0
Herdlefjorden	52.5	19.1	72.5	3.9	4.5
Osterfjorden	60.2	39.6	58.0	1.1	1.3

Figure 7. Simulated specific production (yearly production relative to initial value) for five west Norwegian fjords located at different distances from the outer coast, relative to a standard run for a sixth fjord, Masfjorden for sublittoral planktivores, sublittoral piscivores, sublittoral benthivores and benthos.
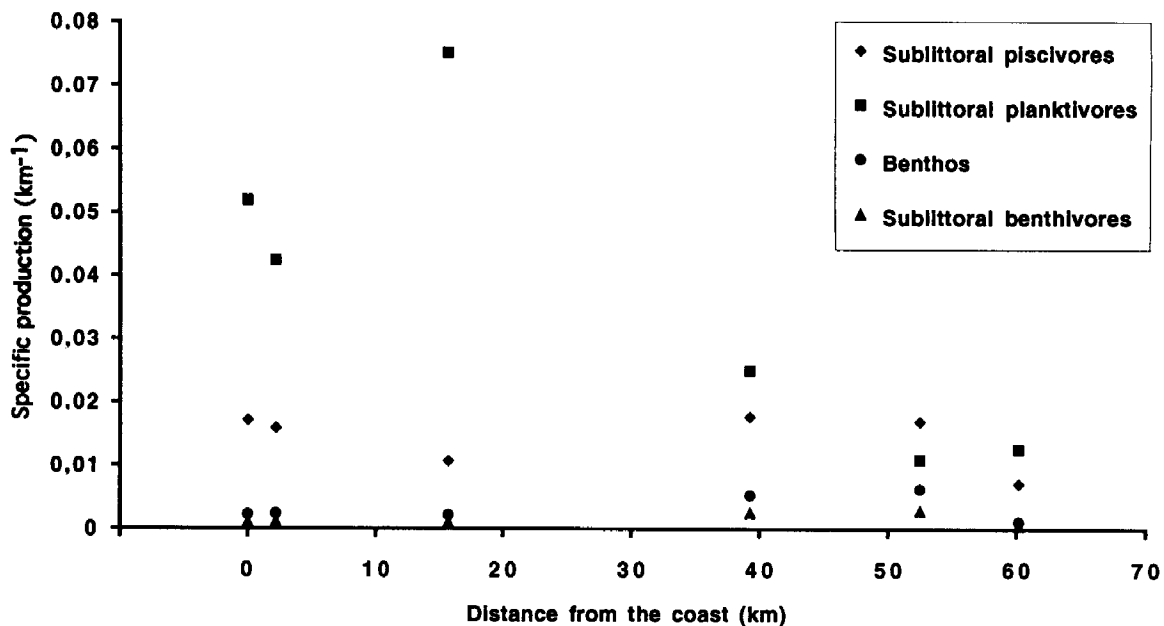
and Eliassen (1990) and Christensen and Pauly (1992). However, these approaches do not focus on environmental variability and are therefore less applicable for analyses incorporating forcing functions depending on complex coastal topography and variable meteorological and oceanographic conditions which propagate into ecosystems via influence on the primary production and through zooplankton advection (Wickett, 1967; Colebrook, 1978; Koslow *et al.*, 1987; Aksnes *et al.*, 1989; Mackas, 1992; Pace *et al.*, 1992; Sameoto and Herman, 1992; Baranovic *et al.*, 1993). For Masfjorden, it has

been demonstrated from field studies and modelling that zooplankton advection may have a strong impact on fish recruitment and production (Aksnes *et al.*, 1989; Fosså, 1991; Giske *et al.*, 1991; Kaartvedt, 1991; Salvanes *et al.*, 1992).

The earlier published data on *Calanus finmarchicus*, but also recent studies (Båmstedt, pers. comm.) demonstrate a strong gradient, with high concentration at the outer coastal areas and low concentrations at the innermost localities. This gradient spans several orders of magnitude. The model also indicates a higher fish

production in the outer relative to the inner coastal areas. According to the model, the high production in the outer areas depends on advected biomass as the local phytoplankton and zooplankton is more or less constant along the gradient. Actually, the highest phytoplankton production ($>200 \, g \, cC \, m^2 \, year^{-1}$) was calculated for the innermost fjord, Osterfjorden. Its high primary production, compared with the other fjords, is mainly a result of low zooplankton grazing pressure due to low advection. Hence, at the spatial scale we are analysing, there is no correlation between simulated potential fisheries yield and local primary production. This contradicts the conclusions of Nixon (1988), who reported a positive correlation between published data on fishery yield and primary production when including many coastal ecosystems around the world. From our study, we can conclude that there is no correlation with local zooplankton production, as long as the advective component dominates the zooplankton renewal. This will not necessarily be the case for the innermost and/or more enclosed coastal areas where production on higher trophic levels depends on a much larger degree on the local primary and secondary production.

During spring, high but variable amounts of *C. finmarchicus* are advected into coastal areas of western Norway (Matthews *et al.*, 1978; Aksnes *et al.*, 1989). Such variability would first of all affect regions strongly dependent on advective supply and to a lesser extent areas dependent on local production. Hence, we should expect that yearly fluctuations (which means a variable fishery yield) would be more pronounced in exposed areas than in more enclosed areas (a constant, but low yield).

The study fjords are situated at the west coast of Norway. The coastal current transports coastal surface water northwards, and intermediate water masses in the fjords are frequently exchanged with Atlantic water from the Norwegian Sea via the Norwegian Deep. The simulations indicate that in most of these coastal areas, advection of zooplankton outweighs local production. Fjords with shallow sills preventing renewal of the intermediate water or estuaries clearly separated from oceanic water may, however, have a much higher dependency on local secondary production. Nixon (1988; his figure 6) found high correlation between phytoplankton production and fish harvests in coastal areas and concluded that trophic efficiency was high. The same conclusion may also have been drawn by comparison of fish and primary production at the western coast of Norway. By taking advective transport of oceanic zooplankton into consideration, however, this apparently high efficiency is dramatically reduced. This means that the coastal fish production benefits from the

primary production over a much larger area than the local habitats of the fish stocks, and that variability in the transport processes (often associated with meteorology and large-scale circulation patterns) will rapidly affect the fish stocks.

The simulation indicates that while growth prospects for individuals at lower trophic levels vary with the distance from the coast, potential for growth seems largely unaffected by the distance from the coast for the sublittoral piscivores (e.g. cod). This indicates that, for immigration of a new sublittoral piscivore to a habitat, it does not matter whether the habitat is situated close to the outer coast or far from it. A consequence for stock enhancement may be that a small-scale release of sublittoral piscivores will be equally productive in most coastal areas, while the outcome of a large-scale release will be strongly dependent on distance from the coast. Furthermore, the outcome may be high, but variable, in the outer coastal areas as the carrying capacity depends on fluctuating advective processes. In the inner areas, local production contributes relatively more to the carrying capacity and the outcome may therefore be more constant although lower.

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APPENDIX

Equations for forcing functions (advection, convection and freshwater run-off), processes [grazing (G), respiration (R), mortality (M) and production (P)] and state variables (nutrients, phytoplankton, zooplankton and higher trophic groups) of the simulation model. For further details see Giske *et al.* (1991) for trophic levels from phytoplankton to gobies and Salvanes *et al.* (1992) for higher trophic levels. A list of symbols is provided.

Forcing functions
Advection:

$$F = AD_{sill}(a_{sill}/v_{adv}) \qquad (A1)$$

Convection:

$$C = C_{deep}(a_{surface}/v_{adv}) \qquad (A2)$$

Freshwater run-off:

$$FR = RUN/v_{adv} \qquad (A3)$$

Process equations

Grazing on one prey (zooplankton, medusae, sublittoral planktivores, sublittoral benthivore):

$$G = \frac{G_{max} \cdot e^{\lambda \cdot T}(B_{prey} - B_{prey,thr})}{K + B_{prey} - B_{prey,thr}} B_{pred} \qquad (A4)$$

Grazing on more than one prey (littoral planktivore):

$$G = \frac{G_{max} \cdot B_{prey}}{\dfrac{1}{n} \cdot \sum_{i=1}^{n} K_i + \sum_{i=1}^{n} B_i} B_{pred} \qquad (A5)$$

where *i* refers to prey type
Production:

$$P = G \cdot A \qquad (A6)$$

Respiration for higher trophic levels:

$$R = r_{max0} \cdot e^{\lambda \cdot T} \cdot B \qquad (A7)$$

Mortality for zooplankton:

$$M_{zoo} = G_{gel} + G_{pel} + G_{sub} \cdot \frac{v_{sub}}{v_{pel}} \qquad (A8)$$

Mortality for higher trophic levels:

$$M_{prey} = \sum_{pred=1}^{m} G_{pred} \qquad (A9)$$

State equations
Nutrients:

$$\frac{dN}{dt} = R_{zoo} + R_{gel} + R_{car} + N_{fresh}RUN$$
$$+ (N_{deep} - N)C_{deep}$$
$$+ (N_{sill} - N)AD_{sill} - P_{phyt} \qquad (A10)$$

Phytoplankton:

$$\frac{dB}{dt} = P_{phyt} - G_{zoo} - Z_{phyt} + (B_{sill} - B)AD_{sill} \qquad (A11)$$

For zooplankton and medusae:

$$\frac{dB_{fjord}}{dt} = P - R - M + (B_{sill} - B_{fjord}) \cdot F \qquad (A12)$$

Renewal of zooplankton in the sublittoral habitat:

$$\frac{dB_{zoo,sub}}{dt} = RW_{sub}B_{zoo,fjord} \qquad (A13)$$

For higher trophic levels:

$$\frac{dB}{dt} = P - R - M \qquad (A14)$$

Symbol	Meaning	Unit
G_{max}	Maximum grazing rate at 0°C	s^{-1}
λ	$\ln Q_{10}/10$, where Q_{10} is the temperature rate constant for grazing	$°C^{-1}$
T	Water temperature	$°C$
v_{adv}	Volume of advective layer	m^3
$a_{surface}$	Surface area	m^2
a_{sill}	Cross sectional area at the sill	m^2
AD_{sill}	Advection over the sill (monthly average)	$cm\ s^{-1}$
F	Renewal rate according to advection	s^{-1}
C_{deep}	Deep water convection (monthly average)	$cm\ s^{-1}$
C	Deep water convection rate	s^{-1}
RW_{sub}	Renewal rate of sublittoral water*	s^{-1}
RUN	Freshwater run-off (monthly average)	$m^3\ s^{-1}$
FR	Freshwater renewal rate	s^{-1}
N_{fresh}	Nutrients in fresh water	$g\ m^{-3}$
N_{deep}	Nutrients in deep water	$g\ m^{-3}$
N_{sill}	Nutrients above sill	$g\ m^{-3}$
B	Density	$g\ m^{-3}$
B_{pred}	Density of predator	$g\ m^{-3}$
B_{prey}	Density of prey	$g\ m^{-3}$
$B_{prey,thr}$	Lower grazing threshold	$g\ m^{-3}$
K	Half-saturation constant for feeding	$g\ m^{-3}$
P	Production	$g\ m^{-3}\ s^{-1}$
A	The fraction of food intake assimilated	$-†$
R	Respiration	$g\ m^{-3}\ s^{-1}$
Z_{phyt}	Sinking of phytoplankton	$g\ m^{-3}\ s^{-1}$
r_{max0}	Maximum respiration rate at 0°C	s^{-1}
M_{zoo}	Mortality of zooplankton	$g\ m^{-3}\ s^{-1}$
G_{gel}	Grazing by medusae	$g\ m^{-3}\ s^{-1}$
G_{pel}	Grazing by pelagic planktivore	$g\ m^{-3}\ s^{-1}$
G_{sub}	Grazing by sublittoral planktivore	$g\ m^{-3}\ s^{-1}$
G_{zoo}	Grazing by zooplankton	$g\ m^{-3}\ s^{-1}$
v_{sub}	Volume of sublittoral habitat	m^3
v_{pel}	Volume of pelagic habitat	m^3
B_{sill}	Density of phytoplankton or zooplankton at the sill	$g\ m^{-3}$
B_{fjord}	Density of phytoplankton or zooplankton within the fjord	$g\ m^{-3}$

*This parameter is tuned to obtain similar simulated and empirically estimated production of planktivores, which is dominated by gobies (Fosså, 1991; Giske *et al.*, 1991).
†Dimensionless.

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