Review of ecosystem models of fjords; new insights of relevance to fisheries management

Anne Gro Vea Salvanes

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Fjords on the west coast of Norway contain small ecosystems that have similar physical and biological processes as large oceanic ecosystems. Hence, they are ideal experimental facilities. However, ecosystems are complex and hard to analyse. Ecosystem modelling may overcome parts of these difficulties. A major benefit from model development is that it allows a mathematical framework to be used to integrate large amounts of field data with ecological theory. This paper reviews Norwegian ecological fjord models and discusses predictions from these models in view of results obtained from other parts of the world and for management of ecosystems. Fundamental processes in ecosystems are predation, competition, migration and behavioural interactions among individuals at various trophic levels, coupled with their response to environmental variability. Ecological modelling combines information from field and experimental studies with theory, and gives ecological insight of indirect or direct relevance for fisheries management. However, due to the complex world and the lack of unified theory that formulates explicitly how events at the individual level influence population dynamics, no model combines environmental and behavioural processes in a food-web context where fish are involved. Simplifications exist and various model types have been developed. It has been claimed that rather than developing a single all-encompassing model, one may end up with a series of partial models each of which can be used to predict answers to one or a few "what-if" questions. The models developed for the fjord ecosystems of Norway have evolved along this line. All these models can be classified as bottom-up and subdivided into i) multispecies ecosystem models; ii) hydrographical drift models for early life stages and iii) life history models comprising age-structured Leslie matrix population models, and static and dynamic optimisation models of behaviour. This paper gives an overview of the main ideas behind the models and the major results on how environmental variability and human impact affects production of fish at higher trophic levels, as demonstrated through simulation experiments. The relevance of this for fisheries management is commented on and it is suggested that results and ideas from ecosystem models for fjord studies should be utilized as input in population models for fish populations of large marine ecosystems, and thus indirectly contribute to improvement of management strategies.

Anne Gro Vea Salvanes, University of Bergen, Department of Fisheries and Marine Biology, PO Box 7800, N-5020 Bergen, Norway.
E-mail: anne.salvanes@ifm.uib.no

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INTRODUCTION

Fisheries vary in economic return due to pronounced variability at all life stages of fish. Stochastic events, which generate spatial and temporal variations in the environment that propagate from plankton to fish (Huse & al. 2002), and human influence (Beverton & Holt 1957), generate changes in species' interactions, behaviour, spatial distribution, abundance, reproduction, growth and mortality and the availability of fish to the fishermen.

Much attention has been paid to natural recruitment variability in fish populations (Hjort 1914; Beyer & Laurence 1980; Fiksen & Folkvord 1999) and to human influence (Beverton & Holt 1957; Beverton & al. 1984; Stokes & al. 1993) as important regulators of the sizes of fish populations. During recent years there has been an increasing tendency to analyse the variability in sizes of fish populations as a consequence of fundamental properties of the ecosystem (Southward & al. 1975; Hollowed & al. 1987; Peterman 1987; Peterman & Bradford 1987; Sharp 1988; Aebisher & al. 1990; Hermann & al. 1996; Anderson & Piatt 1999). As such, in a study on the low level of fish production in the Irish Sea, Brander & Dickson (1984) suggested that causal relationships should be sought at the plankton level.

Ecosystem simulation models are useful to investigate possible environmental impacts on fish populations

(Parsons & Kessler 1987; DeAngelis & Cushman 1990; Giske & al. 1991; Salvanes & al. 1992, 1995). Aksnes & Lie (1990) initiated the development of ecological models, that also assume oceanographical and meteorological factors as driving forces (bottom-up models) for a shallow sill fjord. Between this fjord and the coast there was low water exchange due to a small cross sectional sill area. Local freshwater runoff had therefore a significant influence on vertical structure and seasonality of the fjord system. Such dynamics are typical in fjords where the fresh water runoff largely exceeds advective transport across the sill (Aksnes & Lie 1990; Kaartvedt & Svendsen 1990; Kaartvedt & Nordby 1992). In addition, run-off quantities influence the visibility regime for animal groups. They also have a decisive role in determining whether jellyfish or mesopelagic fish will dominate the pelagic ecosystem of west Norwegian fjords (Eiane & al. 1999).

Zooplankton, fish and jelly distribute as behavioural responses to environmental cues and to interactions with other organisms. Specification of such issues in models adds a further complexity. As yet no model handles both environment and behaviour in a food-web context at the fish level. Models including fish either exclude behaviour, or dynamic interactions between fish species. Others may assume a constant environment and ignore behaviour. Recent reviews of models that link environment and behaviour of "average" fish are provided by Giske & al. (1998a, 1998b) whereas Grimm (1999) and Huse & al. (2002) reviews individual-based models. A single-species ecological model (bottom-up) has been developed for capelin by Giske & al. (1992a, 1992b, 1998b), Fiksen & al. (1995) and Huse & Giske (1998) for large oceanic ecosystems. This model excludes dynamic interactions with other fish. The model predicts that fluctuating environmental factors propagate through the marine food chain via the spread of plankton, and that this in turn influences recruitment, growth, mortality and horizontal migration behaviour of capelin.

Other models developed for large ecosystems are top-down multispecies approaches that assume a constant environment and do not specify any fish behaviour. Ecological studies on the Georges Bank of the North-West Atlantic were the first to use a multispecies approach and that attempted to quantify predation and starvation in the commercial fish stocks (Grosslein & al. 1980; Sissenwine 1984; Sissenwine & al. 1984). Later, models were developed as tools for predicting consequences of human influence on fish populations, and for suggesting management options. Most existing multispecies models (MSVPA (Sparre 1991); ECOSIM (Walters & al. 1997); ECOPATH (Christensen 1995); the work of Bax & Eliassen (1990); MULTSPEC (Tjelmeland & Bogstad 1998) or the aggregated version AGGMULT; and the SYSTEM model (Hamre & Hatlebakk 1998)) are top-down models developed for interacting fish stocks of large ecosystems such as the Barents Sea, North Sea and the Norwegian Seas. Predation and top-down control in a constant environment is the fundamental element in these and the models do not specify any effects of environmental fluctuations or behaviour (Rødseth 1998). Predation is quantified by assuming that the total food supply is divided between populations proportionally to their biomass.

Modelling depend on data that have to be collected through extensive field studies. Fjords on the west coast of Norway are ideal experimental facilities and ecological modelling is a good tool for obtaining insights into general ecological questions of indirect or direct relevance for fisheries management. Also of benefit are their ease of access, their small size and the lower cost of field studies. The fjords have open access to coastal waters through advective exchange of water masses across sills with large cross-sectional areas (Svendsen 1980; Aksnes & al. 1989; Aure & al. 1996; Asplin & al. 1999). An oceanographic simulation model developed by Klinck & al. (1981b, 1981a) demonstrates clearly the dynamic control of fjord circulation by the offshore-wind driven coastal current. It shows that alongshore wind, through Ekman-flux, causes a net volume exchange in a fjord.

Detailed fjord studies have therefore been conducted and questions raised were of relevance for fisheries management. Masfjorden, western Norway, was chosen as the fjord site where intense scientific activity was connected to a large-scale cod enhancement experiment[1]. The aim was to test if releases of captive-bred juvenile cod may buffer year-to-year variations in recruitment to the local fisheries and elevate the overall cod production

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[1] The aim was to integrate large amounts of field data within a single framework for use in the evaluation of the possibilities for cod enhancement. Cod enhancement was launched as a way to manage commercial fish stocks through the increase of fish production in productive near-shore areas by adding large numbers of hatchery reared juveniles. After release to the sea these hatchery fish could eat natural food at no cost instead of being reared intensively and fed expensive food pellets. It was the claimed successful pacific salmon ranching combined with the decreasing value of the Norwegian fishery seen early in the 1980s which gave birth to the renewed idea that cod enhancement could have an economic benefit. Enhancement work had earlier (1870-1970) been attempted via release of larvae (e.g. (Shelbourne 1964; Salvanes & al. 1994), and recently genetically marked larvae (Kristiansen & al. 1997). Small-scale releases of juveniles (Svåsand & al. 2000) were conducted after mass-production techniques of rearing fish to juvenile size had been developed (Øiestad & al. 1985), but Masfjorden was chosen for a large-scale release experiment.

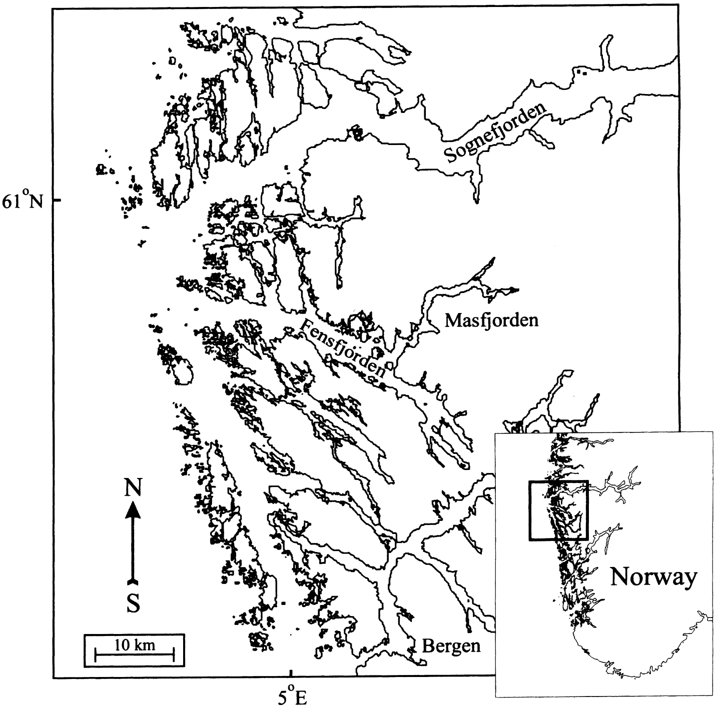

Fig. 1. Location of Masfjorden on the west coast of Norway.

in coastal waters. Various types of bottom-up models for studying general ecological questions of relevance for fisheries management have been developed. The studies include both field work and modelling of oceanography (Aksnes & al. 1989, Asplin & al. 1999), field studies on plankton and fish (Kaartvedt & al. 1988; Aksnes & al. 1989; Giske & al. 1990; Fosså 1991; Baliño & Aksnes 1993; Fosså & al. 1994; Nordeide & al. 1994; Rasmussen & Giske 1994; Salvanes & al. 1994; Kristoffersen & Salvanes 1998; Eiane & al. 1999; Suneetha & Nævdal 2001; Suneetha & Salvanes 2001), behaviour models of copepods and fish (Aksnes & Giske 1990; Giske & Aksnes 1992; Aksnes & Giske 1993; Rosland & Giske 1994; Salvanes & al. 1994; Fiksen & Giske 1995; Giske & Salvanes 1995; Rosland & Giske 1997; Giske & Salvanes 1999) and bottom-up dynamic ecosystem models with trophic interactions between fish species, but omitting behaviour (Aksnes & al. 1988; Giske & al. 1991; Salvanes & al. 1992; Salvanes & al. 1995; Salvanes & Baliño 1998). I start with a description of Masfjorden as representative of a typical west Norwegian fjord. Reviews of major results from ecosystem modelling follow with further discussion of hydrodynamic modelling and life-history models and finally a discussion of the new insights derived from this and the literature showing the relevance of these fjord studies to fisheries management.

THE WEST NORWEGIAN FJORD ECOSYSTEM

Masfjorden (Fig. 1), represents typical west Norwegian topography. It is ca 22 km long, 0.3-1.5 km wide, with a maximum depth of 494 m, and is separated from the outer Fensfjorden and the coast through an outlet, which has a 75 m deep sill. The water masses of Masfjorden may be classified as brackish between 0 and 3 m depth, intermediate, found between the brackish water and the sill depth of 75 m; and deep water found below the sill depth (Aksnes & al. 1989). Advection of the intermediate water masses is to a large extent meteorologically driven and the upper and lower parts move in opposite directions so linking fjord and coastal water masses. Winds along shore and from the south generate downwelling, and wind from the north gives upwelling (Klinck & al. 1981a, 1981b). Downwelling transport extends deeper and generates a larger volume flux than does upwelling (Asplin & al. 1999).

The local and almost nonmigratory population of coastal cod is the main species of Masfjorden of economical interest and this population supports a small local fishery with an annual yield of between 3.3 and 9.6 tonnes, which forms from 12-35 % of the estimated cod biomass (Salvanes & Ulltang 1992). Other commercial species include spurdog (5 tonnes), ling (*Molva molva*) and some tusk (*Brosme brosme*), haddock (*Melanogram-*

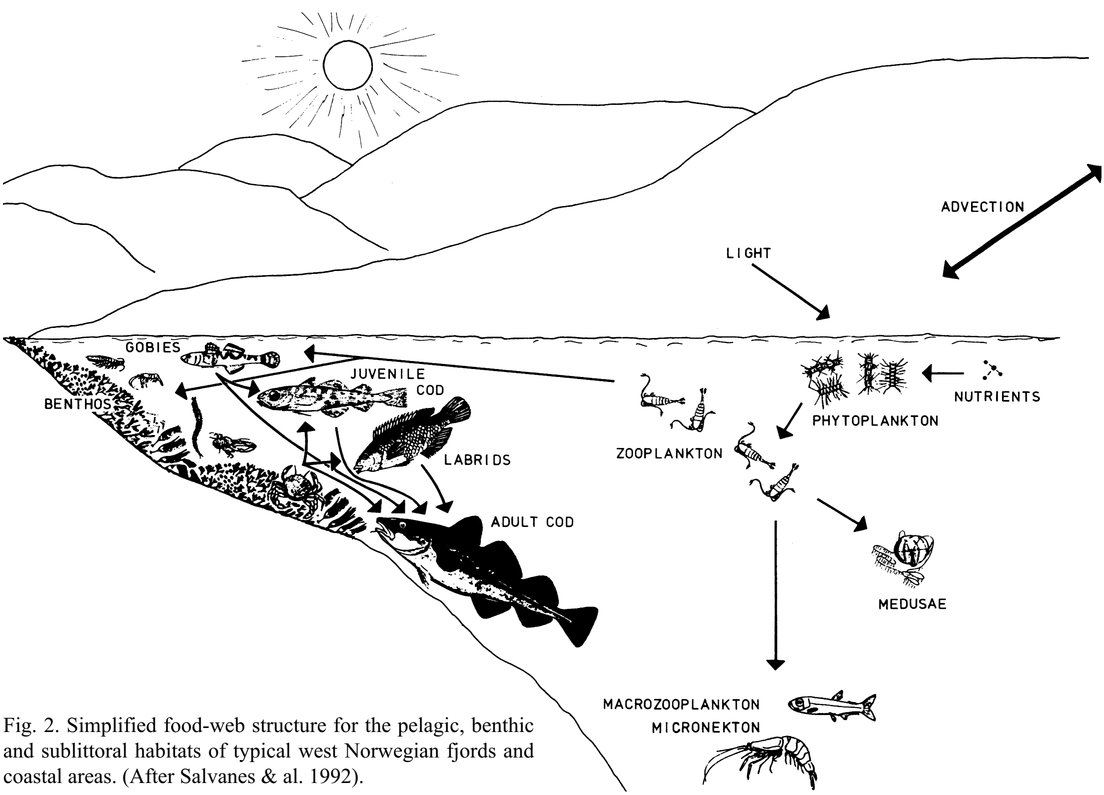

Fig. 2. Simplified food-web structure for the pelagic, benthic and sublittoral habitats of typical west Norwegian fjords and coastal areas. (After Salvanes & al. 1992).

mus aeglefinus), pollack (*Pollachius pollachius*) and saithe (*P. virens*) (Salvanes 1986).

The trophic position of cod in the fjord ecosystem is illustrated in Fig. 2. Juveniles settle at a depth of 0-20 in summer and early fall and remain there locally until maturation (Salvanes & Ulltang 1992). Field data shows that 20 % mature at age 2 years, 52 % at age 3 and 82 % when 4 years and older. Other highly abundant fish populations are the gadids pollack, saithe, poor-cod (*Trisopterus minutes*), four species of labrids (Labridae) and the two-spotted goby (*Gobiusculus flavescens*) (Fosså 1991; Salvanes & Nordeide 1993). Cod and pollack are the main top predators and they have shown intra- and interspecific diet overlap and cannibalism (Nordeide & Fosså 1991; Salvanes & Nordeide 1993). Newly settled juvenile cod eat mostly gobies, older fish take mostly labrids and benthic crustaceans. The productivity of gobies depends on advective transport of zooplankton from the coastal waters (Giske & al. 1991; Salvanes & al. 1992).

Of no immediate economical interest, although of indirect and fundamental significance for the overall ecosystem productivity, are phytoplankton and highly abundant pelagic animals such as zooplankton, mesopelagic fish, shrimps, prawns and jellyfish (Kaartvedt & al. 1988; Aksnes & al. 1989; Giske & al. 1990; Martinussen 1991; Rasmussen & Giske 1994; Goodson & al. 1995; Eiane & al. 1999; Salvanes & Kristoffersen in press).

ECOSYSTEM MODELLING

Models with increasing complexity as far as the representation of fish and food-web structure were developed along with field data accumulated. The field measurements were used for initial values for state variables and for parameters representing the forcing functions. All versions (Aksnes & al. 1988; Giske & al. 1991; Salvanes & al. 1992; Salvanes & al. 1995; Salvanes & Baliño 1998) were time resolved (time step = 15 min) bottom-up simulation models in which central topographical, meteorological, physical and biological characteristics were integrated to analyse the impact of environmental forcing on the carrying capacity for fish in fjord ecosystems. The earliest versions use biomass as the internal unit, whereas Salvanes & Baliño (1998) changed the unit to individuals. In the Salvanes & al. (1992; 1995) model the fjord is divided into 3 main compartments: the central pelagic, the sublittoral, including gobies and 0-group cod and the benthic habitat ranging from the shore down to a depth of 20 m. As a simplification it was assumed that all wild

0-group cod, including those that were released, settled into the sublittoral habitat on 1 August, so accounting for the knowledge that the cod move into deeper habitats with increasing age. The range of the benthic habitat matched observed depth ranges for 1, 2 and 3 year old and older cod and of labrids and benthos.

The model version in Salvanes & al. (1992) was developed further by Salvanes & Baliño (1998) to include: i) 2 year old and older pollack as a top predator; ii) an improved density-dependent feeding rate of the fish by changing the formulae describing the feeding rate so that it was constrained by an optimum and a maximum temperature; iii) age-dependent fishing mortality distributed evenly through the year; and iv) a change of the internal unit from biomass to the numbers of average sized individual. This was done because biomass is a drawback for the expression of mortality and predation rates at higher trophic levels than phytoplankton.

Competition and cannibalism were modelled by specifying the prey types each predator group could consume. The feeding rate (G) was calculated for each time step and is formulated dynamically according to the Michaelis-Menten equation (Holling 1966), but modified to incorporate more than one prey type for trophic levels above gobies by Salvanes & al. (1992). For a predator with a density, B_{pred}, that eats more than one prey type, the feeding rate upon a prey type with a density B_{prey} was expressed as:

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

where $1/n\sum_{i=1}^{n} K_i$ represents the average half saturation constant K for the n prey and $\sum_{i=1}^{n} B_i$ the total density for all prey types included in the diet of the predator. The G_{max} expresses the maximum feeding rate, depending on optimal temperature for feeding in cod and of environmental temperature during each time step (see Salvanes & Baliño 1998 for further details). G_{max} is also adjusted for assimilation, excretion and respiration rates. The half saturation constant is a composite function of maximum feeding rate that is restricted by handling and digestion of prey at high density. It also depends on encounter rate, which in turn depends on cruising speed, visual range, prey size, prey density, prey visibility, which is reflected by the availability of refuges, and optical properties of the water column (Aksnes & Giske 1993). It is not a trivial task to obtain reasonable estimates of the half saturation parameters and so approximations were used. We estimated half saturation constants from growth rates derived from field experiments assuming that the growth rate is linearly related to feeding rate (for further details, see Salvanes & al. 1992).

The model version in Salvanes & al. (1992) was evaluated by comparing the simulated total annual accumulated diet composition for each predator group with independent data obtained from field studies. The diet compositions predicted by the model were similar to those observed from field data (Fig. 3). The extended model of Salvanes & Baliño (1998) was further evaluated through a comparison of the simulated average individual fish growth with field estimates of growth. Also the predicted and observed growth in weight through a year were close to each other.

Predictions from the ecosystem model

Advection has major effect on carrying capacity

The models predicted that zooplankton availability was a key factor for the regulation of carrying capacity of fish in the open fjord ecosystems of western Norway (Fig. 4). The simulations in Salvanes & al. (1995) also showed that it was not local production, but drifting zooplankton advected into the fjord that determined the availability. The amount of zooplankton available for transport depends on the biological processes that determine the zooplankton availability such as reproductive potential, growth and mortality, in addition to regional wind conditions and distance from the coast. The plankton density varies seasonally, and in periods with high availability, the amount advected can largely exceed the local production (Salvanes & al. 1995). Because much of the zooplankton are consumed by gobies and other fish which could potentially fall prey to the cod, the cod production on the coast and in the fjords will indirectly benefit from primary and secondary production from a much larger area than the local habitat alone.

Gobies experience good food conditions and higher productivity when the advective supply of zooplankton is high. A major implication of these model predictions for cod enhancement is that large-scale releases of juveniles should preferably be conducted in years with better than average zooplankton availability at the release site. Hence, the simulation experiments did not, generally, predict positive effects of cod enhancement. In Salvanes & al. (1992) it was stressed that given that zooplankton advection was so important for fish productivity in fjords, a vital scientific goal would be to evaluate the production potential for a specific year early enough to decide whether releases of juveniles could be profitable. This required further research on the physical forces and the events that have an effect on advective transport. Aksnes & al. (1989) hypothesised that meteorological variability influences advective transport of zooplankton into the fjords. Physical modelling (Asplin & al. 1999) supported this hypothesis. It was shown that non-local wind-driven transport generates exchange of water between the coast and the fjords. A review on this material is covered in the section *Hydrodynamical mod-*

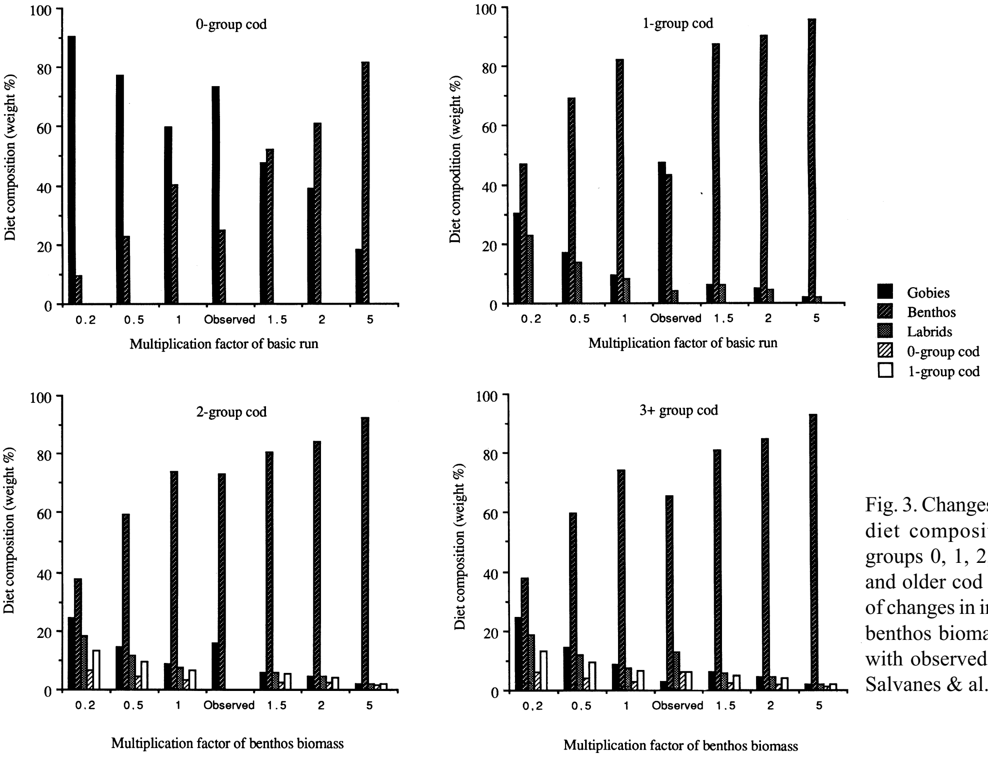

Fig. 3. Changes in simulated diet composition of age-groups 0, 1, 2, and 3 years and older cod as a function of changes in initial value of benthos biomass compared with observed diets. (After Salvanes & al. 1992)

elling of water transport between coast and fjord. These findings imply that there are uncertainties in the carrying capacity for fish in west Norwegian fjords in accordance with stochastic variation in the climatic conditions that generate regional wind conditions on the coast. This is what originally led to the question reviewed in the section, which was: What are the "enhancement potentials for unknown carrying capacities ?"

Fjord-coast gradients; data support model predictions

The simulations presented by Salvanes & al. (1995) predicted a higher carrying capacity for fish on the outer coast than in the inner fjords (Fig. 5A). The prediction is confirmed by data on zooplankton and fish. Published data on *Calanus finmarchicus*, the dominant species in the zooplankton biomass of west Norwegian coastal waters show a strong gradient with high densities in the

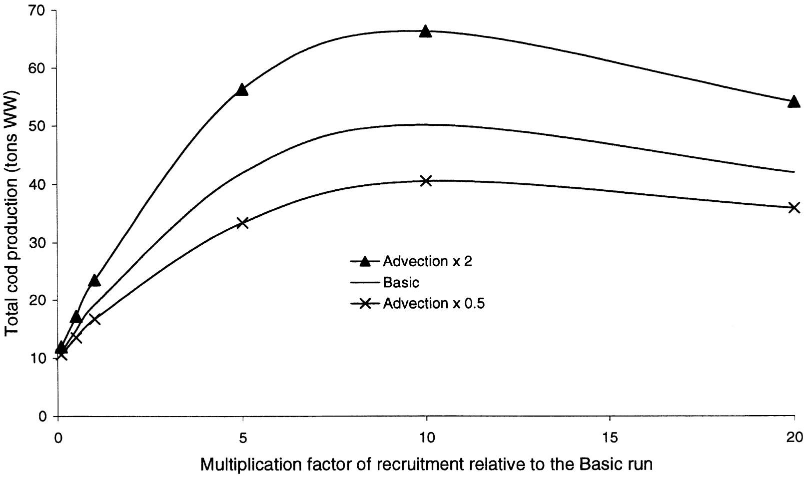

Fig. 4. Simulated production curves for the entire cod population in Masfjorden as a function of recruitment relative to observed average recruitment for three advection rates (After Salvanes & Baliño 1998).

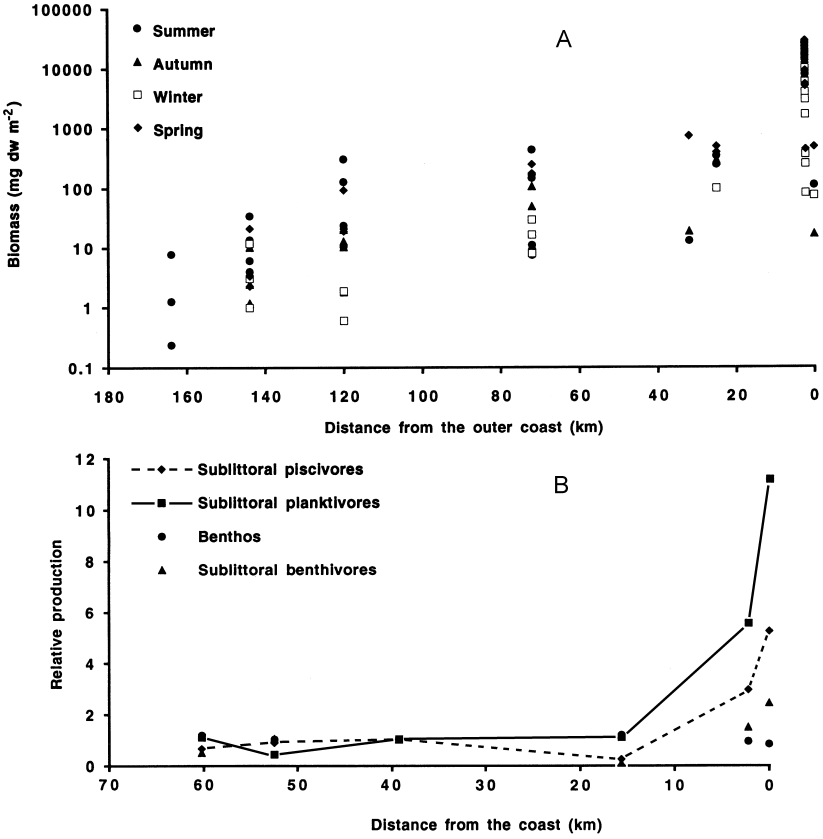

Fig. 5. A. Simulated yearly production for five west Norwegian fjords located at different distances from the fjord (After Salvanes & al. 1995). B. The density of *Calanus finmarchicus*, the dominating zooplankton in Norwegian waters, as a function of the distance from the coast (Redrawn from Salvanes & al. 1995).

outer coastal areas and lower densities in the innermost localities (Fig. 5B). Moreover, the cod from Masfjorden 40 km inland from the coast had a lower growth rate than cod from Øygarden on the outer coast (Fig. 6). Also, the fish biomass per area was higher on the coast than in Masfjorden (Svåsand & al. 1998). The difference is a result of higher advection rates of water masses rich in zooplankton at the coast than in the fjord, and that the advection become damped with increasing distance from the coast (Klinck & al. 1981b). Empirical estimates show that the production of cod was 2.8 tonnes km^{-2} yr^{-1} in Øygarden and 0.9 tonnes km^{-2} yr^{-1} in Masfjorden (Svåsand & al. 1998), but the natural mortality on 1 year old cod was higher in Øygarden than in Masfjorden (2.0 yr^{-1} in Øygarden and 1.5 yr^{-1} in Masfjorden) due to cropping by additional avian top-predators like cormorants and shags (Otterå & al. 1999).

Local phytoplankton is more or less constant along the gradient, except for the high phytoplankton production in the fjord at the greatest distance from the coast (Fig. 7). This is due to the greater local freshwater runoff, low advective transport of zooplankton from the coast and thus low grazing (Fig. 8). Similar dynamics has been documented for other fjords where freshwater runoff dominates over advection as a physical forcing (Aksnes & Lie 1990; Kaartvedt & Svendsen 1990; Kaartvedt & Nordby 1992).

Density-dependent predation and cannibalism limit fish production

Simulation experiments presented in Salvanes & Baliño (1998) showed that biological processes within the ecosystem also affected the production potential for cod. When food availability was limited, possibly as a result of restricted rates of advection, density-dependent predation in cod became a factor. It was caused by mediating competition for gobies into cannibalism particularly in years of high juvenile recruitment. In the simulations, recruitment was varied from zero up to 20 times the observed average for 0-group cod and with low, average and high advection rates. This gave a cod production that was positively correlated with advection and which increased with recruitment levels up to a maximum around 10 times the average cod recruitment. At higher levels of recruitment, production was damped because energy was lost between trophic levels or diverted into predators of young cod.

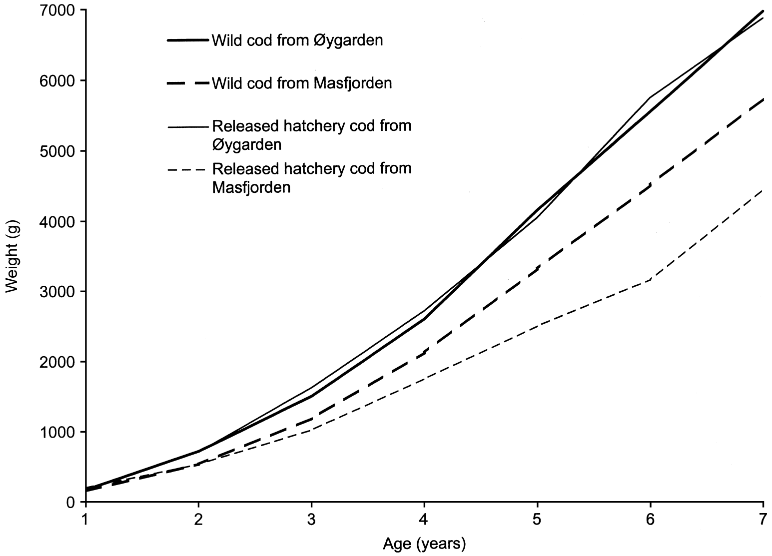

Fig. 6. Weight at age for wild cod from Øygarden at the coast and from Masfjorden 40 km from the coast.

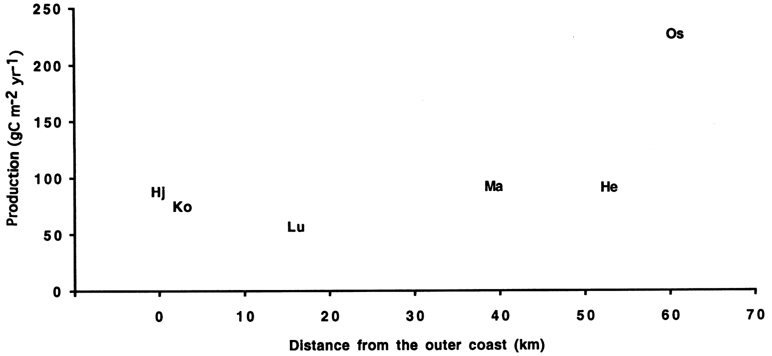

Fig. 7. Simulated phytoplankton production (gC m^{-2} $year^{-1}$) for six west Norwegian fjords (Hjeltefjorden (Hj), Korsfjorden (Ko), Lurefjorden (Lu), Masfjorden (Ma), Herdlefjorden (He), and Osterfjorden (Os)) located at various distances from the outer coast (After Salvanes & al. 1992).

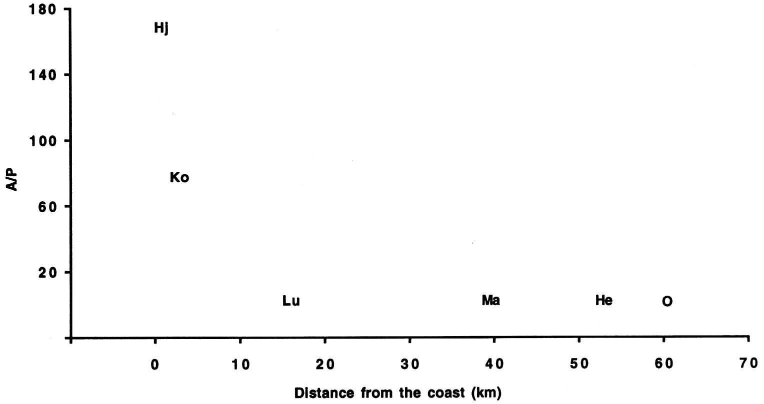

Fig. 8. Simulated yearly zooplankton advection relative to local production (A/P) for six west Norwegian fjords (Hjeltefjorden (Hj), Korsfjorden (Ko), Lurefjorden (Lu), Masfjorden (Ma), Herdlefjorden (He), and Osterfjorden (Os)) located at various distances from the outer coast (After Salvanes & al. 1992).

Marginal effect of fishing mortality predicted from the ecosystem model

Simulation experiments (Salvanes & Baliño 1998) showed that the short-term effects of fishing on the growth and survival of cod were marginal compared to the effect of advection. The model predicted that if cod were fished with a moderate fishing mortality rate (F = 0.28 yr^{-1}) the pollack would consume one tonne less of juvenile cod and therefore grow at a somewhat slower rate (c.f. table 2 of Salvanes & Baliño 1998).

Limitations of the modelling

Although the ecosystem modelling for west Norwegian fjords provided new insight on major causal relationships in coastal ecosystems, the models developed have their limitations. They express simplifications of environmental stochasticity and cannot at present be used to estimate long-term stable yields of cod. Moreover, since the environment fluctuates and because genetic characteristics vary among individuals, individual variation in behaviour and behavioural responses to internal and external cues, seen as variations in growth, survival, reproduction and migration, are likely to influence ecosystem dynamics. Tank experiments on cod demonstrated individual behavioural variation (Hart & Salvanes 2000) that was associated with genetic factors (Salvanes & Hart 2000). At present there is, however, no unified theory that formulates explicitly how events at the individual level influence population dynamics (Persson & al. 1997; Grimm 1999), and it is difficult to transfer experimental observations from the laboratory directly to effects on population dynamics. Experiments may provide valuable input data for models, but they can also be used to evaluate model predictions. Further research should utilize this and examine the consequences of individual variation for population processes. Along with the development of increasing computer power (Huse & al. 2002) it will be possible to develop individual based models and use these for simulation experiments for this purpose.

HYDRODYNAMICAL MODELLING OF WATER TRANSPORT BETWEEN COAST AND FJORD

The simulation presented in Asplin & al. (1999) is a supplement to, and an extension of, the ecosystem models developed for an idealised food-web structure of Masfjorden. Predictions from the ecosystem model (Aksnes & al. 1988; Giske & al. 1991; Salvanes & al. 1992; Salvanes & al. 1995), field measurements of advection rates (Aksnes & al. 1989), and the model approach developed by Klinck & al (1981b), formed the basis for 3D physical modelling of the water transport between the coast and the fjords. In the ecosystem models, advection was included as a forcing function, but they simplified advection to a bordering forcing function that changed monthly, but with no depth resolution. The reason for this simplification was that the focus was on the effect of biological and external factors on the dynamics of biological processes and species interactions within the ecosystem. In Asplin & al. (1999) the realism of advective transport between coast and fjords was taken further and studied in isolation from the ecosystem model. 3D numerical simulation experiments were used to demonstrate that short-term events of non-local wind-generated coastal upwelling and downwelling influence water exchange. The wind regimes used as model input are frequently observed on the coast of Norway. Wind stress on the coastal ocean was the only forcing of the model and no local wind was specified within the fjords. See Asplin & al. (1999) for further details.

The model is a three-dimensional, primitive equation, time-dependent, σ-coordinate, ocean circulation model (the Bergen Ocean Model (BOM), Berntsen & al. (1996). The model domain consisted of a rectangular fjord topography, which was idealized by keeping fjord sizes and distances from the coast resembling real topography of Masfjorden and Fensfjorden, through which Masfjorden is connected to coastal waters of western Norway.

Northern and southern winds generate opposite direction of advective transport

The simulation experiments predict that coastal winds from the north cause upwelling and transport the upper water layer out from fjords. Winds from the south cause downwelling and transport the upper layer inwards (Fig. 9). The transport is rapid and about 50 % of the upper water layer may be replaced within 1-2 days. Simulations using real topography confirm this pattern (Asplin pers. commn). The predictions from the 3D model imply that if strong winds from the south occur frequently, advection will transport planktonic organisms into the fjord. This may increase the carrying capacity for planktivorous fish if the time of high advection coincides with the time of high density of zooplankton in coastal waters (Asplin & al. 1999). In contrast, frequent strong winds from the north may flush the surface layers out from the fjord. This implies a reduced production potential for planktivorous organisms and may also – if this wind direction is strong and prevailing – reduce the retention of locally spawned fish eggs and larvae. Frequent shifts between wind directions could cause exchange of early life stages between neighbouring fjords and thus enhance genetic exchange and similarities between fjords. Although advection can influence the amount of recruits that settle in a fjord, this does not mean that advective transport is the only factor that determines the recruitment level. Density-dependent cannibalism and predation will put additional constraints on whether a year class that is large at settlement continues to be large also at older ages.

LIFE-HISTORY MODELS

Enhancement potentials for unknown carrying capacities

In Salvanes & al. (1992) it was stressed that one should evaluate the production potential for a specific year early

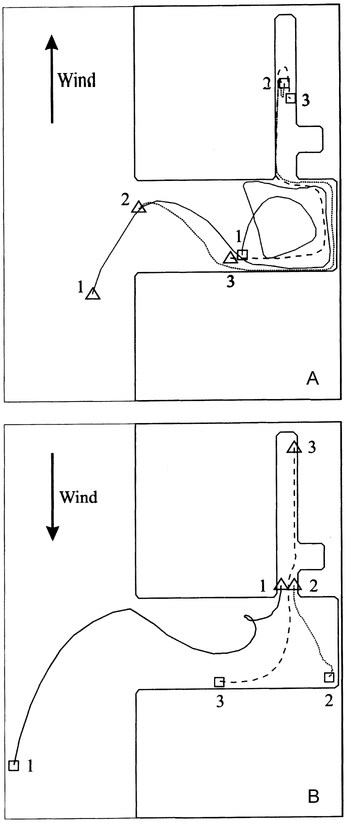

Fig. 9. Advection of passive particles (identified by numbers) in the surface layer for (A) the down-welling simulation experiment (wind from south) and (B) the upwelling experiment (wind from north). Open triangles refer to start positions and the squares to end positions of particles 72 h later (After Asplin & al. 1999).

enough to decide whether releases of juveniles could be profitable. However, since advection of zooplankton is fundamental for fjord productivity, and since Asplin & al. (1999) showed that the zooplankton renewal is determined by stochastic events such as regional wind conditions, which is linked to climate, the previous goal needs a revision. It is not trivial to predict effects of stochastic events so it will therefore not be possible to know exactly the biomass of zooplankton that become transported between the coast and fjords. The research goal should therefore be modified to evaluate whether large-scale releases of juvenile cod can have a positive effect on cod biomass given the uncertainty of the carrying capacity of fish in the fjords. Giske & Salvanes (1999) adopted this approach. They compared long-term enhancement potentials using simulation experiments that included "unknown" and "known" variable carrying capacity. They developed an age-structured life history model for cod using a Leslie-matrix (Leslie 1945; Aksnes 1988). Average-sized individuals represented each age group. The recruitment and carrying capacity were specified as stochastic variables and the mortality was frequency-dependent so as to mimic the effects of density-dependent cannibalism. All environmental impacts were modelled through their effect on survival, whereas fecundity was kept constant for any environmental condition.

The model was parameterised using data on cod from Masfjorden. Population developments through 150 years were simulated for the three situations: i) no cod releases; ii) yearly release of a fixed number of cod given unknown carrying capacity and iii) releases of an amount of cod that matched the carrying capacity given that the carrying capacity was known each year. The time unit was one year.

The simulations show that "perfect" releases that matched a known carrying capacity maintained the population at a much higher level than if a fixed number were released (Fig. 10) (Giske & Salvanes 1999). If we do not have the necessary information needed to release an amount of juveniles that match the fluctuating carrying capacities and instead decide to release a fixed number of juvenile cod, or if we only can predict that the following year will be good or bad, then releases of juveniles will not enhance the cod population. The extra fish released will be lost due to the limited carrying capacity and frequency-dependent cannibalism.

STATIC OPTIMIZATION

Vertical distribution versus diet

Giske & Salvanes (1995) discuss the assumptions underlying optimal foraging theory where most effort has been put into predicting diet selection (Shoener 1987; Gilliam 1990) for benthic and littoral fish, such as cod, that partition the time between feeding and hiding. They stress that the situation is different for pelagic animals. Giske & Salvanes (1995) combine the model of how light influences prey detection in fish (Aksnes & Giske 1993; Aksnes & Utne 1997), optimal foraging theory (Stephens & Krebs 1986), and the theory of prey digestion (Bromley 1994). They showed that the extra gain in growth achieved by a selective diet in the pelagic habitat could not balance the increased mortality risk associated with feeding in a well illuminated area where conditions were suitable for choosing between prey. Giske & Salvanes (1995) conclude that pelagic planktivores should be depth-selective in order to maximise their fitness, as diet selection would be too costly.

The findings of Giske & Salvanes (1995) are highly relevant for *Maurolicus muelleri* that is the fish species that dominate the pelagic habitat of west Norwegian fjords. Field studies of Masfjorden report two dense layers of *M. muelleri* that undertake pronounced diurnal

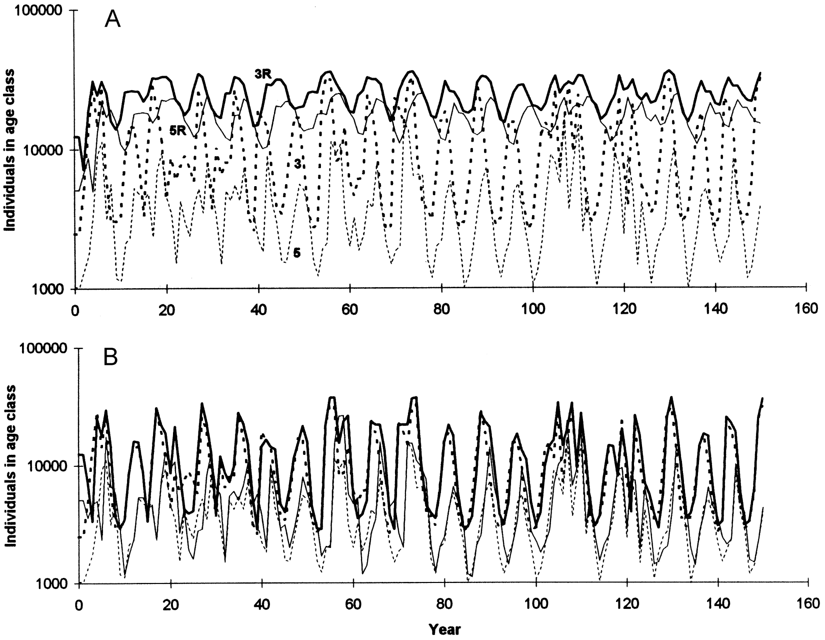

Fig. 10. Simulated abundance of age group 3 (bold lines) and 5 (weak lines). Continuous lines represent the abundance for scenarios of juvenile releases and the dotted lines represent the abundance without any release. A. Effect of releases of a number of juveniles that match an assumed known carrying capacity. B. Effect of releases of a fixed number of juveniles assuming that carrying capacity is unknown (After Giske & Salvanes 1999).

vertical displacements (Giske & al. 1990) with a migration speed of up to 90 m h^{-1} (Baliño & Aksnes 1993). Baliño & Aksnes (1993) also show that the winter depth distribution of these layers followed isolumes (light intensity 0.2 and 0.006 $\mu E\ m^{-2}\ s^{-1}$, respectively for the upper and lower layer), thus demonstrating the importance of light as a cue for the onset of vertical migration. They utilized a 120 kHz echosounder and a QSP-160 quantum sensor to investigate continuously the dynamics of the *M. muelleri* layers. Cloud cover reduced light and this was followed by corresponding upward migration (Fig. 11).

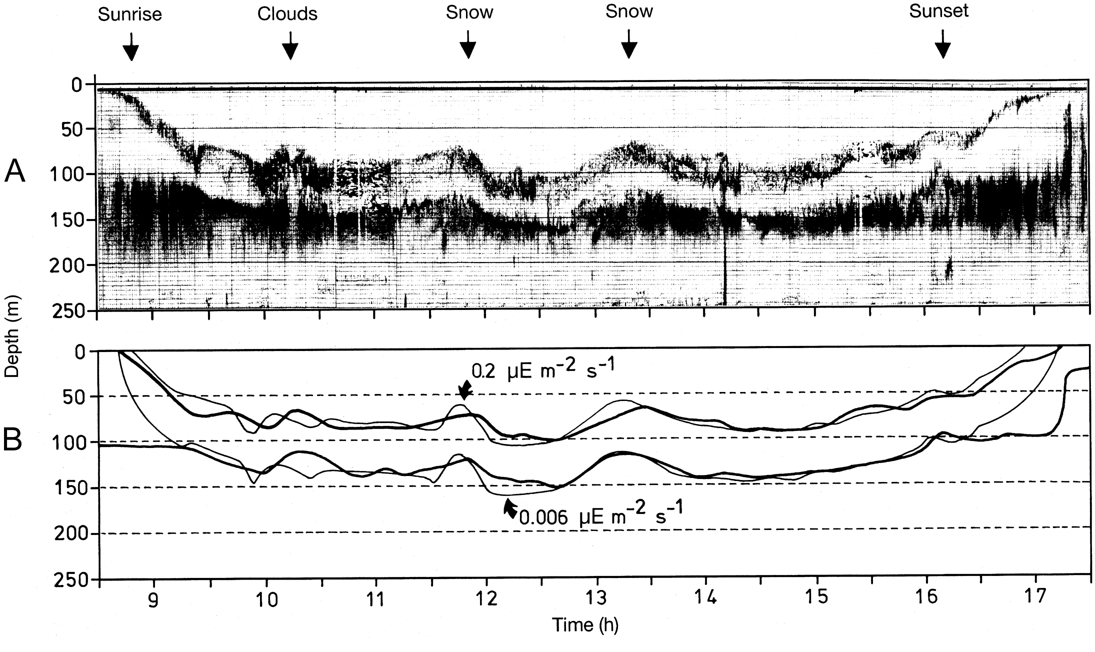

Fig. 11. Typical sound scattering layers of *Maurolicus muelleri* in January 1988. A. 120 kHz echograms recorded during daytime. B. Contours of the upper borders of layers I and II together with isolumes (After Baliño & Aksnes 1993).

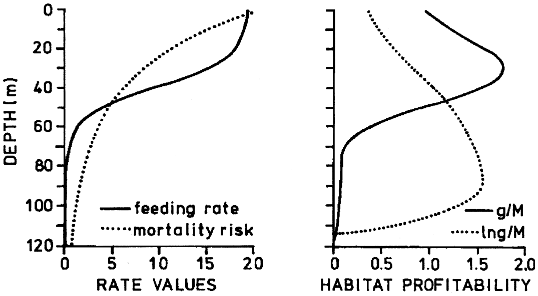

Fig. 12. Habitat profitability of fish. Juveniles may use extra growth to shorten time to maturation (After Giske & Aksnes 1992).

The two depth layers of *M. muelleri* actually separate juvenile and adult fish; juveniles in shallow water and adults deeper down. Giske & Aksnes (1992) showed theoretically that life history theory (Aksnes & Giske 1990) could be used to predict differences in risk-acceptance associated with feeding for juvenile and adult fish. Giske & al. (1998b) summarize the main results of these studies. They show that juveniles are more risk-prone in an attempt to shorten their generation time than are adults where feeding is only likely to enhance fecundity. Giske & Aksnes (1992) show that while the optimal trade-off for juveniles is to minimize *g/M,* adults should minimize *ln(g)/M* (Fig. 12).

Giske & Aksnes (1992) tested this hypothesis on *M. muelleri* in Masfjorden. Interestingly, they found that adults had so low a feeding rate they lost weight in winter. They argue that this is not consistent with any model of life history theory, as a negative growth rate cannot produce offspring (Giske & al. 1998b). Juveniles had high growth rates so feeding conditions were good. Giske & Aksnes (1992) concluded that adults seemed to maximize the probability of overwintering survival. This is also predicted from dynamic optimization models of *M. muelleri* (Rosland & Giske 1994); see later section).

The fitness of cod in relation to fishery and environmental fluctuations

Long-term effects were studied of various fishing patterns on fitness measured as a potential contribution to future generations from small, average and large cod year classes (Salvanes & Baliño 1998). The instantaneous rate of increase *r,* which is the population growth rate, was chosen as a measure of fitness. This proxy for fitness is often used for age-structured populations (Roff 1992). For an iteroparous life history the following is assumed; i) that selection maximizes *r*; ii) that individual somatic growth can be expressed by a von Bertalanffy growth curve; iii) that fecundity is proportional to body weight; and iv) that the survival from birth, set at spawning time until the entry to age 1 year indicates the recruitment level to the population. A high survival during its first year of life represents the result of good environmental conditions during the pelagic stage and low mortality risk after settlement. This generates large year-classes. Poor environmental conditions give low survival in early life and result in small year-classes. It is also assumed that natural mortality decreases with increasing age. The time step of the model is 1 year. The Euler-Lotka equation in Roff (1992) is modified to incorporate age-dependent mortality:

$$1 = \sum_{a=\alpha}^{\infty} qW_{\infty}\left(1 - e^{-k\left(\alpha - a_0\right)}\right)^3 p_1 p_\alpha e^{-ra} \qquad (2)$$

where fecundity is expressed by the von Bertalanffy equation based on weight times *q* which is relative fecundity which is expressed as eggs g^{-1} female, discounted for the sex ratio and was derived from Kjesbu & al. (1996). Salvanes & Baliño (1998) used this approach for an idealised situation when cod was allowed to mature also at age 1 year. In the present paper, I modify this approach and discount the fecundity for observed proportion mature at each age (0 % at age 1; 20 % at age 2; 52 % at age 3 and 80 % at age four years and older). W_∞ is the asymptotic weight estimated from data, *k* the rate at which an individual approaches the asymptotic size and a_0 the intersection point of the growth curve with the x-axis. The $p_\alpha = \prod_{a=1}^{\alpha-1} e^{-\left(M_a + F_a\right)}$ refers to the probability of surviving from age 1 until the start of maturation age α. p_1 is taken as the probability of surviving from the egg stage until settlement, a value derived from Sundby & al. (1989), and also through the 0-group until the start of age group 1 (Salvanes & Ulltang 1992). M_a is instantaneous natural mortality rate at age *a* predicted from the ecosystem simulation model for 1-group ($M_1 = 0.59$) or assuming the traditional $M = 0.2$ for cod that are 2-years old and older. One set of conditions for a moderate fishery is simulated by parameterising the model with fishing mortality F_a for age *a* as estimated for cod from Masfjorden by Salvanes and Ulltang (1992); $F_1 = 0.05$; $F_2 = 0.14$; $F_3 = 0.28$; $F_{4+} = 0.64$ yr^{-1}. Another set of conditions with high *F*s is used to explore the effect of high fishing intensity, and utilizes the estimated *F* for North Sea cod (Daan & al. 1994). The solution of the equation with respect to α is found by iteration using the SOLVER module of Excel, for selected combinations of entry ages to a moderate fishery as observed in Masfjorden and an intensive fishery set at the same level as for the North Sea. The model used low and medium growth rates and low, medium and high survival probabilities for the first year (p_1).

The Euler-Lotka equation parameterised for Masfjorden cod predicts that the fitness increases with decreasing maturing age down to age 2-years, which is the

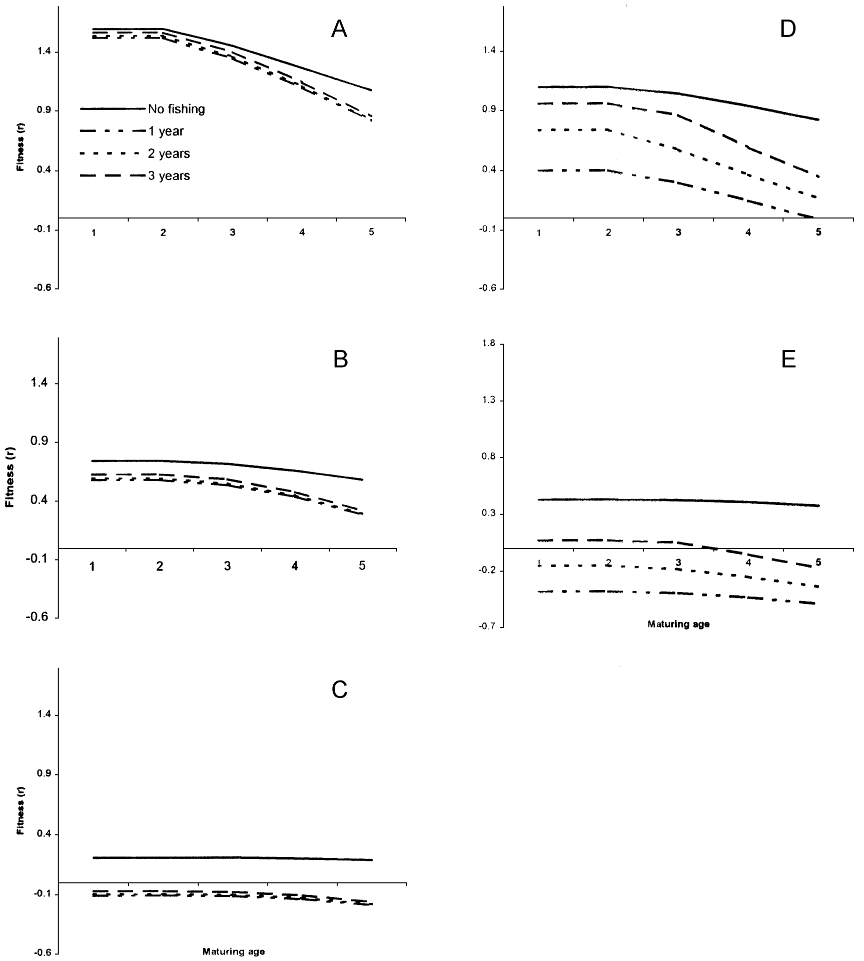

Fig. 13. The fitness of (A) large, (B) average and (C) small year classes of cod for different entry age to the fishery for average growth and a moderate fishery. D. The fitness of a large year class for high fishing intensity (all F = 1.0.) and strong density dependent growth (low *k*) for different entry age to the fishery. E. The same *F* and *k* as for graph *e*, but for average year-class size.

earliest observed maturing age for wild cod in the fjord. Low, medium and high survival probabilities from birth and to one year old can be interpreted as resulting in small, medium and large cod year-classes. The predictions show that if fishing mortality is moderate, the fitness of medium and large year classes will be positive even though one-year-old cod is fished upon (Fig. 13A & B). Medium and large year classes will therefore contribute to population growth under a moderate fishery on juveniles. A small year class will, however, only be able to contribute positively to population growth rate ($r > 0$) if it is not fished upon (Fig. 13C).

Although medium sized year classes tolerate a moderate fishing pressure well and provide sufficient replacement spawners, it is predicted that they cannot contribute to positive population growth if the fishing mortality is as high as in the North Sea ($F = 1.0$) (Fig. 13E). Year classes heavily fished as 1 and 2 year olds will soon disappear from the population and will not be able to produce sufficient replacement spawners through their life time. Only a year class that is originally large will be able to contribute positively to population growth ($r > 0$; Fig. 13D). These predictions imply that in an iteroparous species that is heavily fished, it will be the large year classes that become responsible for producing sufficient replacement spawners that keep population size at high levels.

Optimal timing of juvenile releases

Also based on life history theory, the optimal timing of habitat shifts was used as an analogy to study the optimal timing for release of cod juveniles under the evalu-

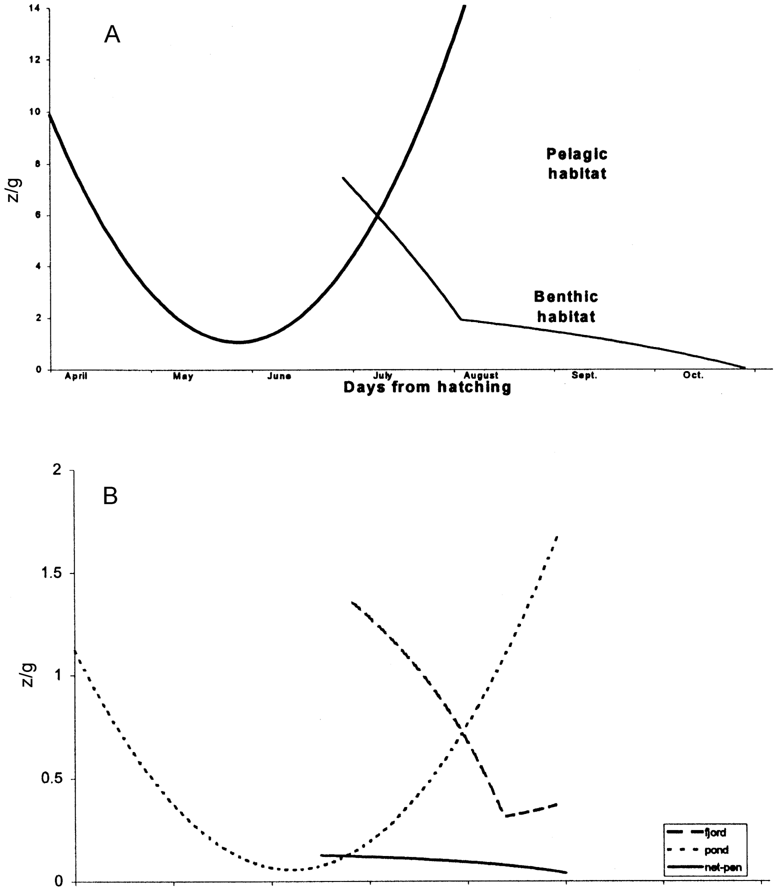

Fig. 14. Mortality per growth ratio for cod in the (A) pelagic (left) and benthic habitat (right). B. production pond for cod juveniles (left), benthic habitat (right) and net-pen (bottom) (After Salvanes & al. 1994).

ation of the possibilities for cod enhancement (Salvanes & al. 1994). During their first year of life, wild cod undergo a morphological change or metamorphosis during the larval period when they are 1.5 months old. Subsequently the cod settle into the nearshore benthic habitat at 0-20 m depth. As pelagic larvae the cod feed on zooplankton, but after settlement they switch to feeding on gobies and benthic crustaceans that are larger prey. Mortality on pelagic stages is mainly a result of predation from large crustaceans, pelagic fish and jellyfish (Hunter 1984), whereas mortality on newly settled cod in Masfjorden is due to predation from larger gadids such as cod and pollack (Salvanes & Nordeide 1993). In the pelagic habitat there is no shelter for the larvae, while macroalgae serves as shelter for juveniles within the shallow nearshore habitats of the west Norwegian fjords.

In Salvanes & al. (1994) the theoretical framework from evolutionary ecology and the optimal timing of habitat shifts (Werner & Gilliam 1984) was also applied to field data on cod. Data-sets were available for cod from four different habitats: i) the natural pelagic; ii) the pond used to rear juveniles; iii) net-pens used for juvenile on-growth and iv) the shallow benthic habitat in Masfjorden. For these four habitat types time dependent instantaneous growth rates (g_t) and mortality rates (z_t) were estimated. According to Werner & Gilliam (1984) juvenile fish maximise their fitness by staying in the habitat where mortality rate per growth rate is minimal. A habitat shift would be favourable when the function describing z_{tA}/g_{tA} in habitat A intersect the z_{tB}/g_{tB} in the alternative habitat B, where t refers to time and indirectly to size. The model predictions of cod's natural shift from pelagic to benthic was consistent with field observations (Fig. 14A), and the intuitively realistic outcome that net-pens are better habitats than both the pond and the benthic habitat of the fjord from June/July, indicated a valida-

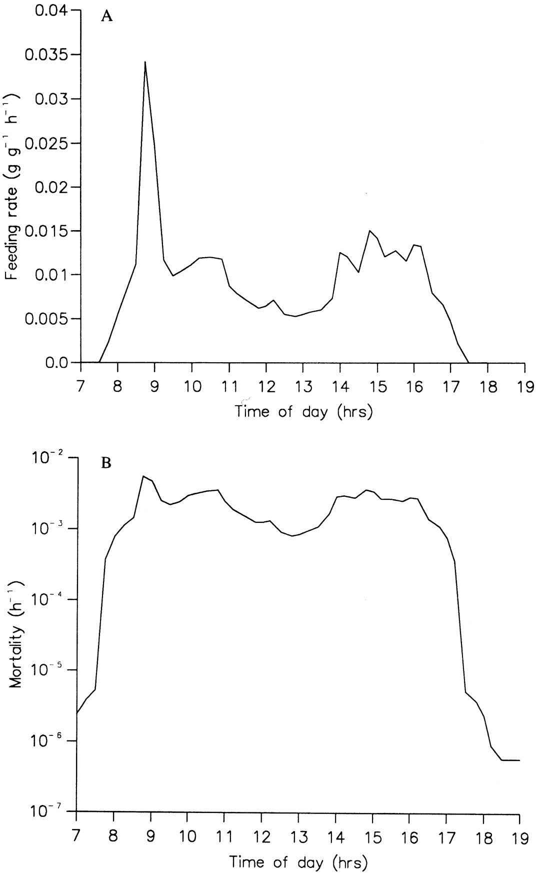

Fig. 15. Daytime pattern in (A) average feeding rate (g g^{-1} h^{-1}) and (B) average mortality risk (h^{-1}) for juveniles in the basic run of the model of Rosland & Giske (1994).

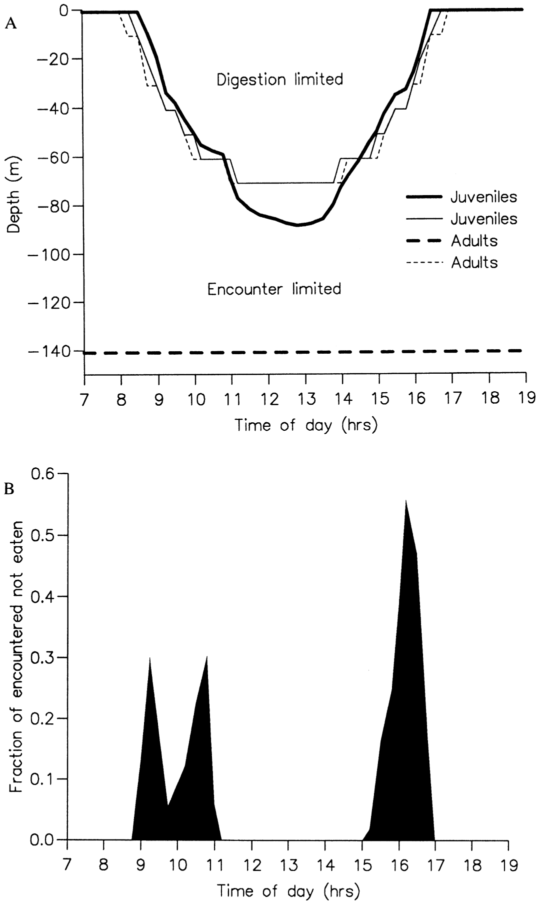

Fig. 16. A. Mean depths (thick lines) of juvenile and adult fish. Thin lines mark the depths where feeding rate shifts from digestion to encounter limitation. B. Fraction of food encountered by juvenile fish in the different time intervals which was not eaten as a result of stomach limitation (After Rosland & Giske 1994).

tion of the life-history approach (Salvanes & al. 1994). The result from the analysis indicate that the optimal timing for release will generally be after cod have reached a size at which they settle to the benthic habitat in fjords (Fig. 14B).

DYNAMIC OPTIMIZATION

Dynamic optimisation models integrating effects of gradients of the external environment on motivation and feeding have been developed for pelagic organisms of Masfjorden (Rosland & Giske 1994; Rosland 1997; Rosland & Giske 1997), and for studying the causes of diel vertical distribution of juvenile and adult *Maurolicus muelleri*. The juveniles and adults were offered the same environment, but the fitness function, defined as the relationship between growth over 24 h. Juveniles were given high pay-off for growth, while the reward for adults were almost equal as long as they did not risk short-term starvation (Giske & al. 1998b). The model calculates the optimal depth at which feeding opportunities are balanced against mortality risk. The fitness reward gained by feeding is weighted against the danger of being eaten by a predator (Rosland & Giske 1994). Predictions of vertical distribution correspond well with observations of *M. muelleri* in Masfjorden, and the assumption of age differences in mortality-feeding trade-offs appeared realistic. Results predict crepuscular feeding activity (Figs 15 & 16) of the juveniles, and distribution of zooplankton seemed to be the most important environmental factor regulating the adult depth position during the winter months in Masfjorden.

The model is developed further in Rosland & Giske (1997) for a pelagic fish living in a seasonal environ-

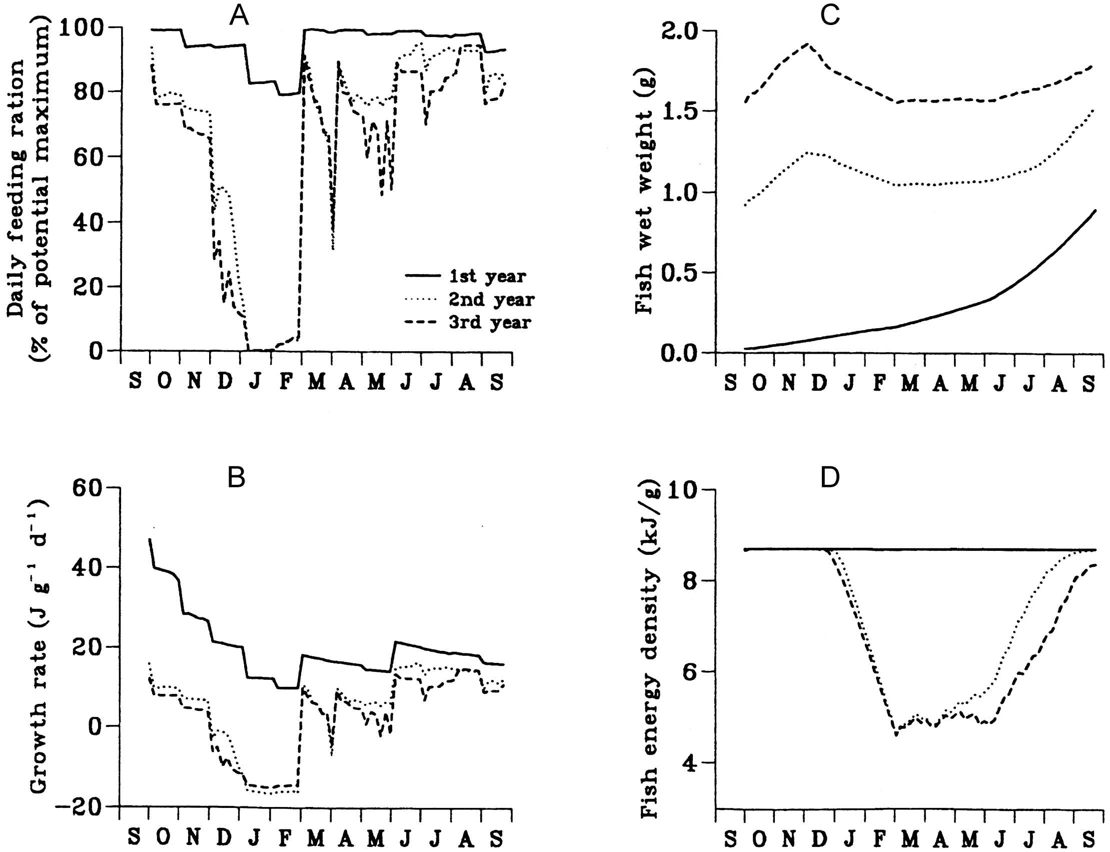

Fig. 17. Time distribution of: (A) average individual daily feeding ration as a percentage of maximum potential food consumption capacity; (B) average individual weight-specific growth rate as energy intake per unit body weight (J g^{-1} day^{-1}); (C) average individual fish weight (g wet weight); (D) average individual energy density (kJ g^{-1}). The different lines represent the same cohort in the first (solid), second (dotted) and third (dashed) year (After Rosland & Giske 1997).

ment. The optimal strategies predicted by the model depended on fish weight, energetic state and seasonal environment factors (Fig. 17). Seasonal factors and changes in energetic state had little influence on small fish, but had a high impact on large individuals (Rosland & Giske 1997). No reproduction occurred in winter and during this part of the year, large fish can minimize visual predation risk by staying at a depth with low light intensity but the cost was a low feeding rate and negative energy budget. For the spring, summer and autumn, the model predicted that large fish should stay at a depth that provided feeding rates necessary to rebuild energy reserves lost in winter so as to provide sufficient energy for reproduction and somatic growth.

The same principles as those used when studying vertical migration of the non-commercial *Maurolicus muelleri* in Masfjorden (Aksnes & Giske 1990; Giske & Aksnes 1992; Rosland & Giske 1994; Giske & Salvanes 1995) were then utilized by Huse & Giske (1998) in developments of population models for capelin in the Barents Sea. In the modelling of the trade off of growth versus mortality risk for *M. muelleri* it was assumed that it experienced light gradients in the vertical habitat of Masfjorden, but Huse & Giske (1998) modified the trade-off along a horizontal gradient assuming that capelin experienced gradients in temperature and food. From this the model predicted horizontal migrations of capelin.

DISCUSSION

Field studies may reveal patterns at a given time and place. Laboratory investigations may isolate effects of single causes. A major benefit from modelling is that it allows a mathematical framework to be used to integrate large amounts of field data with processes hypothesised to be present and compatible with published ecological theory. Models can be used for simulation experiments. These may help to identify the most important processes and species interactions and they allow studies of extreme "what if" situations and combinations of variables not yet experienced. Model predictions can also later be tested using new data from field observations or from experiments.

Ecosystems are complex. Fundamental processes are predation, competition, migration and behavioural interactions among individuals at various trophic levels, coupled with their response to environmental variability. Due to the complex world and the lack of a unified theory that formulates explicitly how events at the individual level influences population dynamics (Persson & al. 1997; Grimm 1999), no model combines environmental and behavioural processes in a food-web context where fish are involved. Simplifications exist and various model types have been developed. Giske & al. (1998) claim that rather than the development of a single all-encompassing model, one may end up with a series of models, each of which can be used to predict answers to one "what-if" question. The models developed for the fjord ecosystems of Norway have evolved along this line. A classification of models has been into those labelled top-down that is driven by predation and assumes a constant environment and those called bottom-up where dynamic environmental effects are important and are propagated from the bottom to the top of the food chain. In addition, versions of these two either can exclude environmental factors as dynamic variables or include them.

We may classify model approaches discussed in this review into a) top-down multi-fish species models for large ecosystems (Grosslein & al. 1980; Sissenwine 1984; Sissenwine & al. 1984; Sparre 1991; Christensen 1995; Hamre & Hatlebakk 1998; Tjelmeland & Bogstad 1998); b) single-species bottom-up behaviour models for large-ecosystems (Giske & al. 1992a; Fiksen & al. 1995; Giske & al. 1998b; Huse & Giske 1998); c) bottom-up multispecies models for small fjord ecosystem (Aksnes & al. 1988; Aksnes & Lie 1990; Giske & al. 1991; Salvanes & al. 1992; Salvanes & al. 1995; Salvanes & Baliño 1998); d) hydrographic fjord models dealing with environmental variables and small drifting organisms (Svendsen 1980; Klinck & al. 1981b; Klinck & al. 1981a; Asplin & al. 1999) and e) bottom-up life-history models (Aksnes & Giske 1990; Giske & Aksnes 1992; Rosland & Giske 1994; Salvanes & al. 1994; Giske & Salvanes 1995; Rosland 1997; Rosland & Giske 1997; Giske & Salvanes 1999). Details on the c, d and e models are provided above, and below I discuss the main new general ecological findings and their relevance for fisheries management in the context of those mentioned under a and b as well as other relevant studies.

New ecological insight

A major conclusion from the fjord ecosystem model is the effect of non-local wind-generated advection of zooplankton between the coast and the fjord. Its effect was propagated further up the food-web and had severe indirect influences on the productivity of cod populations (Giske & al. 1991; Salvanes & al. 1992; Salvanes & al. 1995; Salvanes & Baliño 1998). It is important to note that positive effects from advection will be damped because populations consist of several age groups and biological interactions, such as predator-prey relationships, will occur causing energy to be dissipated between trophic levels. The interactions will also strengthen negative effects of advection if net-transport of zooplankton is directed out of the fjord.

One benefit of the fjord ecosystem approach, as compared with the Georges Bank (Grosslein & al. 1980) or the MULTSPEC model for the Barents Sea (Tjelmeland & Bogstad 1998), is the small area studied. Masfjorden made it possible to gather basic data with which model predictions could be tested. Another benefit is that environmental impact was included dynamically in the process formulate. Empirical estimates presented in Svåsand & al. (1998) confirms higher production and individual growth for cod on the coast (Øygarden) than in Masfjorden 40 km inland from the coastal current (Fig. 6). Also, independent data on diet for cod confirmed that predicted diet composition, from a dynamic food-web model, was realistic (Fig. 3). A larger proportion of the production on the coast was, however, lost due to higher predation risk from avian predators (Otterå & al. 1999). Hence, the fishery yield did not increase proportional to the gross productivity.

The multispecies approach utilised on Georges Bank was used to quantify empirically a snapshot of the energy budget (Sissenwine 1984). Results show that fish consume most of their own production (61-93 %), and that fish production was 1.2-2.1 % of particulate primary production. In the case of exploring ecosystem changes, this type of analysis needs to be repeated. This is a result of the empirical nature of the work. The MULTSPEC model for the Barents Sea (Tjelmeland & Bogstad 1998), is a dynamic model that was utilized to quantify diet consumption of cod and marine mammals when taking into account predation and competition. A major drawback of the model was the assumption of a constant environment. The effects of dynamic environmental changes could not be studied. Competition was modelled by assuming that total food supply is divided between the stocks proportional to the stock biomass. Some model predictions for cod growth and capelin recruitment have been evaluated against abundance indices from surveys and the VPA for age groups 1-3 (Tjelmeland & Bogstad

1998). Whether these really are independent data is uncertain, as much of the data utilized as input for the MULTSPEC model would also be input for the VPA model. Input data for the Masfjorden ecosystem model and independent data for model evaluation were much easier to have control over.

The new aspect predicted from the hydrographical model was the rapid exchange of water between the fjords and the coast that was generated by non-local regional wind forcing (Asplin & al. 1999). The major strength of this modelling was the confirmation of the main conclusion of the ecosystem simulation model that advection of zooplankton was important for cod production (Aksnes & al. 1988; Aksnes & al. 1989; Giske & al. 1991; Salvanes & al. 1992; Salvanes & al. 1995; Salvanes & Baliño 1998). Hence, these modelling approaches complement each other. Nevertheless, because it is impossible to quantify stochastic events that regulate regional wind conditions, it will also be impossible to obtain quantitative predictions for cod enhancement potentials. This was demonstrated in the simulation experiments of Giske & Salvanes (1999). They show that cod releases do not result in cod enhancement when the uncertainty in carrying capacity was unknown (Fig. 10).

Wind forced interactions between physical processes and zooplankton were also modelled for the Georges Bank ecosystem (Lewis & al. 1994). Model predictions suggest that high winds during winter can cause significant replacement of the bank water mass with surrounding waters and that the exchange causes a major reduction of the zooplankton population and zooplankton and phytoplankton production over the bank. Werner & al. (1996) took this approach further. They studied trophodynamic and advective influences on Georges Bank larval and cod populations. They found that around 20 % of eggs and larvae spawned over the bank were lost due to advection. Werner & al. (1996) concluded that the larvae that were most likely to remain over the bank also were those inhabiting the most favourable feeding regions as they had the highest growth rates. Hence, climatic effects could also, through their impact on circulation processes, affect the plankton stages of fish populations and thus represent one cause of recruitment variability.

Recruitment variability was pronounced between the few years studied in Masfjorden and empirical estimates of the year class size of 6-8 month old cod varied between 15 000 and 178 000 individuals (Salvanes & Ulltang 1992). There is generally large recruitment variation in marine fish populations as demonstrated for the North Sea cod by O'Brien (2000). In the fjords of western Norway cod eggs and larvae inhabit the upper advective 50 m depth layer. Under strong southerly winds net-transport of water masses will be in to the fjords (Asplin & al. 1999), whereas frequent strong northerly winds may "drain" the fjords for locally produced early life stages of fish, if the buoyancy and the capability of vertical displacements make them unable to counteract outward transport. There is some evidence for transport of batches of larvae of mesopelagic fish (*Maurolicus muelleri*) out of Herdlefjorden under periods with strong northerly winds (Gundersen 1997), but there is a lack of field data that quantify advective transport of egg and larvae in the west Norwegian fjords. Hence, model predictions of quantitative particle transport are not yet tested for these areas. For the Baltic Sea simulation experiments that predict larval transport from a 3D eddy-resolving baroclinic model agreed well with field observations (Voss & al. 1999). Predicted typical retention and dispersal situations corresponded well with field data, supporting the conclusion from the simulation experiment of Asplin & al. (1999).

Another climatic effect on cod recruitment has been demonstrated using data for North Sea cod. O'Brien & al. (2000) show an inverse correlation between recruitment to 1 year old and surface temperature based on a 30 year long data series. The functional relationship between the temperature and the cod recruits was, however, not explored. It might be that the temperature signal could be associated with changes in the drift patterns of the egg and larval cod stages and that these early life stages in years with high temperature drift to sub optimal nursery areas or to areas with high predation risk.

The importance of environmental gradients for behavioural trade-offs and their impact on spatial distributions was also demonstrated through the model simulation experiments for fish in Masfjorden. Light is a common stimulus for the vertical displacements and acts as a controlling, initiating and orientation cue during migration (Childress 1995). The ratio between mortality risk and feeding rate in fish, which locate their prey and predators by sight, tend to be at minimum at intermediate light levels. Thus, migration during dawn and dusk may extend the time available for visual feeding while minimising the predation risk, the so-called "antipredator-window" (Clark & Levy 1988; Rosland & Giske 1994). Towards the Polar Regions in summer the nights become less dark, and the optimal vertical distribution for catching prey and avoiding predators will be altered. For example, *M. muelleri* in the northern Norwegian Sea changed from daily vertical migration behaviour to schooling as winter changed to summer (Kaartvedt & al. 1998). Such behaviour serves as an alternative antipredator strategy during feeding sessions in the upper illuminated and productive water masses.

The importance of light as a major stimulus for diel vertical migration was tested using *M. muelleri* from Masfjorden as a model organism (Giske & Aksnes 1992;

Aksnes & Giske 1993; Baliño & Aksnes 1993; Giske & al. 1994; Rosland & Giske 1994; Giske & Salvanes 1995; Rosland 1997; Rosland & Giske 1997; Salvanes & Kristoffersen in press). Ontogenetic differences in daytime levels were observed. In winter and spring, juveniles were found in separate Sound Scattering Layers (SSL) above the adults. During daytime, mesopelagic fish can adjust their vertical position to accommodate fluctuating light intensities caused by changes in cloudiness and precipitation. The adjustment of the daytime depth levels of the SSLs thus suggests that vertically migrating mesopelagic fish tend to follow isolumes, at least over short time periods (Fig. 11). During a 24 h cycle in the summer the estimated light intensity at the depth of *M. muelleri* have been observed to change by 3 orders of magnitude (Baliño & Aksnes 1993).

RELEVANCE FOR FISHERIES MANAGEMENT

The simulation experiments for the ecosystem and the cod population of Masfjorden involve topics of relevance for fisheries management. Although short-term effects of a moderate, non-selective fishery ($F < 0.5$ yr^{-1}) predicted only marginal effects on growth and survival of cod, the long-term effect predicted from the Euler-Lotka model indicated clear effects of fishing on the population growth rate (Fig. 13). Only slight reduction in the growth of predators on juvenile cod and slightly increased growth of the cod surviving the fishery through more food gained per individual was predicted from the ecosystem model. However, the one-year time horizon of the model was too short for obtaining realistic long-term effects on population dynamics of changes in the fishery.

The management consequences predicted from the modified Euler-Lotka equation (Fig. 13) and the Leslie-Matrix approach (Giske & Salvanes 1999) provided long-term predictions of population growth rates. Giske & Salvanes (1999) concluded that a cod population could not be managed by releasing juveniles to fill the gap between large and small year-classes because of the uncertainty in productivity caused by a variable environment combined with frequency-dependent cannibalism. The long-term effect of fishing depicted in Fig. 13 suggests that the age-specific fishing mortality is important. If the fishery is intensive on juveniles, their year classes may become unable to produce sufficient replacement spawners. Only large year classes appeared to be able to tolerate a high fishing pressure. Since the data show that most year classes are average or small (see e.g. fig. 1 of O'Brien & al. 2000) these results suggest that a long-term yield from local cod populations requires low or moderate fishing intensity on juveniles to maintain populations. In the few years when a large year class dominates the population, fishing boats could perhaps also fish when these are immature. It might be that frequency-dependent cannibalism on year classes born 1-2 years after large ones, function as a way of dampening fluctuations in the populations.

Some limitations of the analysis of long-term effects on fishing need mentioning. It was assumed that the fished individuals had the same fitness as those that die naturally. A fishery has, however, the potential to influence the evolution of fish populations (Stokes & al. 1993). For example a fishery such as gillnetting, uses passive gear, can selectively remove the most active fish and individuals that grow with the highest rate (Beverton & al. 1984). This could lead to a population that in the long-term changes to consist of small individuals. An active fishery such as trawling can select other parts of a fish population such as the less active and the juveniles. Because individual variation in behaviour is influenced by genetic variation (Salvanes & Hart 2000) it is likely that individuals that escape a fishing gear may have genetic characteristics that deviate from the average individual of the population. Except for several papers and literature cited in Stokes & al. (1993), Heino (1988), Walsh & Morgan (1998) and Law (2001) such issues are nearly absent in the fisheries literature. We should expect future research on these issues along with developments of individual-based models that accounts for genetic variations (Huse & al. 2002).

Salvanes & al. (1994) showed that optimal release time was generally after cod settled in the near shore benthic habitat. This result contradicts the results expected from the nearly 100 years long cod-hatchery period. Millions of one-week-old yolk-sac larvae hatched in hatcheries were released into the sea with the hope of improving cod recruitment and stabilising population sizes (Shelbourne 1964). However, the mortality was extremely high on these young stages at 23 % per day for the first 10 days and 12 % per day for the next month (Kristiansen & al. 1997). Few individuals of large cohorts of yolk sac larvae would survive until settlement.

The modelling experiments on vertical migration of fish tested for the non-commercial *Maurolicus muelleri* of Masfjorden have shown relevance for fisheries management issues (Giske & al. 1998b). Also species of commercial interest undertake vertical migrations, and understanding the causes of migration will be essential for evaluating the quality of features such as the acoustic target strengths used in acoustic surveys (Godø & Michalsen 2000). Acoustics surveys are used to estimate stock sizes for fisheries management purposes. For example, the Norwegian herring undertake diel vertical migration (Huse & Korneliussen 2000). Also cod migrate vertically, but less frequently on a diurnal basis (Arnold & Greer Walker 1992; Arnold & Holford 1995; Godø & Michalsen 2000), and there have been observed differences between populations such as those from the North Sea and the Irish Sea (Righton & al. 2001). To improve the ability to predict effectiveness of fisheries management, the understanding of why and when vertical migration occurs in cod would be needed.

It has been demonstrated that insights into general ecological questions of relevance for fisheries management can be obtained from fjords, which are ideal for field observations, field experiments and for modelling because they are small and have similar physical and biological processes, as do large oceanic ecosystems. Moreover, field studies are less costly in small fjords than in large ecosystems. Longer-term studies should utilise fjords as "experimental facilities" to learn more marine ecology and to explore effects of different management strategies in further detail. Results and ideas from such studies could then be utilized as input in population models for fish populations of large marine ecosystems, and thus indirectly contribute to improvement of management strategies. For example, the modelling approach used to study causes of vertical migration in mesopelagic fish (Aksnes & Giske 1990; Giske & Aksnes 1992; Rosland & Giske 1994; Giske & Salvanes 1995) was also used by Huse & Giske (1998) for modelling horizontal migration of capelin from the Barents Sea.

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