

Computer simulation of pelagic production in Masfjorden, western Norway, and its consequences for production of released 0-group cod

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An ecosystem model including nutrients, phytoplankton, herbivores, two groups of pelagic carnivores, sublittoral gobies and 0-group cod is presented. The model is driven by solar radiation, temperature, freshwater run-off, and water exchange across the sill. The production of food for 0-group cod, such as sublittoral gobies, pelagic krill, prawns, and mesopelagic fish, is simulated. Simulations illustrate how the different compartments of the system are influenced by alterations in the forcing of the system. Water exchange, especially the renewal of sublittoral water, turned out to be the most important process determining the carrying capacity of young cod. The explanation is that the water renewal supplies the sublittoral habitat with zooplankton, which is utilized by the prey of young cod. Finally, effects of different cod release programmes are simulated and discussed.

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Introduction

During the last decade the value of the Norwegian fish harvest has been increasingly dependent on inshore waters. This is not because of an increased exploitation of natural fish stocks, but rather the result of fish cultivation. Areas with low wave action and reasonable water exchange offer excellent opportunities for intensive production of salmon in sea-cages. At present, there is an increasing attention to the possibility of a more extensive use of coastal areas, especially fjords, for fish farming (Ulltang, 1984). In contrast to intensive production, extensive cultivation utilizes the natural food chain. A small-scale version is the use of marine ponds in rearing fish larvae (Øiestad *et al.*, 1985), where the larvae feed on naturally produced zooplankton. When the larvae are some months old, however, more food is demanded than the pond can offer. The carrying capacity for the larvae is exceeded, and they must either be transferred to an intensive system or be released into a new environment with a higher carrying capacity. This latter alternative involves loss of human control and the actual outcome is given by the characteristics of the ecosystem. Furthermore, non-trivial legal aspects involving ownership and fishing regulations arise (Ørebeck, 1988), and from a commercial point of view the intensive technique has been preferable so far. This

does not mean, however, that sea ranching is not promising, and the present work is part of a project assessing its potential.

The outcome of sea ranching depends on the opportunities for growth and survival the ecosystem may offer the species under consideration. If a species succeeds in a particular system, the next question is how dense populations may be sustained without provoking a feedback resulting in decreased growth and survival. Fundamental knowledge about the species and the ecosystem under consideration is obviously required to answer these questions. Such knowledge may encompass important details of the behaviour of individuals as well as large-scale characteristics of the ecosystem (such as solar input, nutrient supply, and the circulation system). Important qualitative predictions about the species–system interactions may be drawn conceptually by trained ecologists. Quantitative predictions, however, depend on models where the variety of knowledge is combined in a common language. The present modelling efforts represent an early step in the assessment of factors determining the carrying capacity of a fjord. More precisely, it deals with the carrying capacity with respect to cod of age about one year. Field investigations (Salvanes, 1986a, b; Kaartvedt *et al.*, 1988; Aksnes *et al.*, 1989; Fosså, 1991; Nordeide and Salvanes, 1991) have identified fundamental properties

of the fjord, and a simple time-dependent pelagic model is formulated according to these findings. The purpose of this paper is to investigate the sensitivity of food availability (at different levels of the food chain) to dominating forcing functions. Furthermore, preliminary simulation experiments on cod release are presented in order to indicate upper limits of the carrying capacity for one-year-old cod.

The fjord

Masfjorden (Fig. 1) is separated from the outer fjord, Fensfjorden, by a 75 m deep sill. The length of the fjord is about 20 km and the width is on average 1 km. Total fjord volume is about $5.36 \times 10^9 \text{ m}^3$ and maximum depth is 494 m. The water masses of Masfjorden may be classified as: brackish water (0–3 m), intermediate water (3–75 m), and deep water (below sill depth) (Aksnes *et al.*, 1989). The layers above sill depth are

heavily influenced by advection. On the other hand, the deep water offers a non-advected environment, and is a habitat appropriate for local pelagic populations (Kaartvedt *et al.*, 1988; Aksnes *et al.*, 1989). Among these populations are carnivores feeding on herbivorous zooplankton (Giske *et al.*, 1990). The availability of the herbivorous zooplankton depends on the local production in the fjord and on the advective transport of herbivores across the sill (Aksnes *et al.*, 1989; Kaartvedt, 1991). Gobies, sublittoral fish species which are important food for young cod (Salvanes, 1986b), is another group dependent on the herbivores. A simplified conceptual model of the pelagic system in Masfjorden is illustrated in Figure 2, and the main components of the model will be explained below.

The model

The state variables of the model (Tables 1 and 2) are

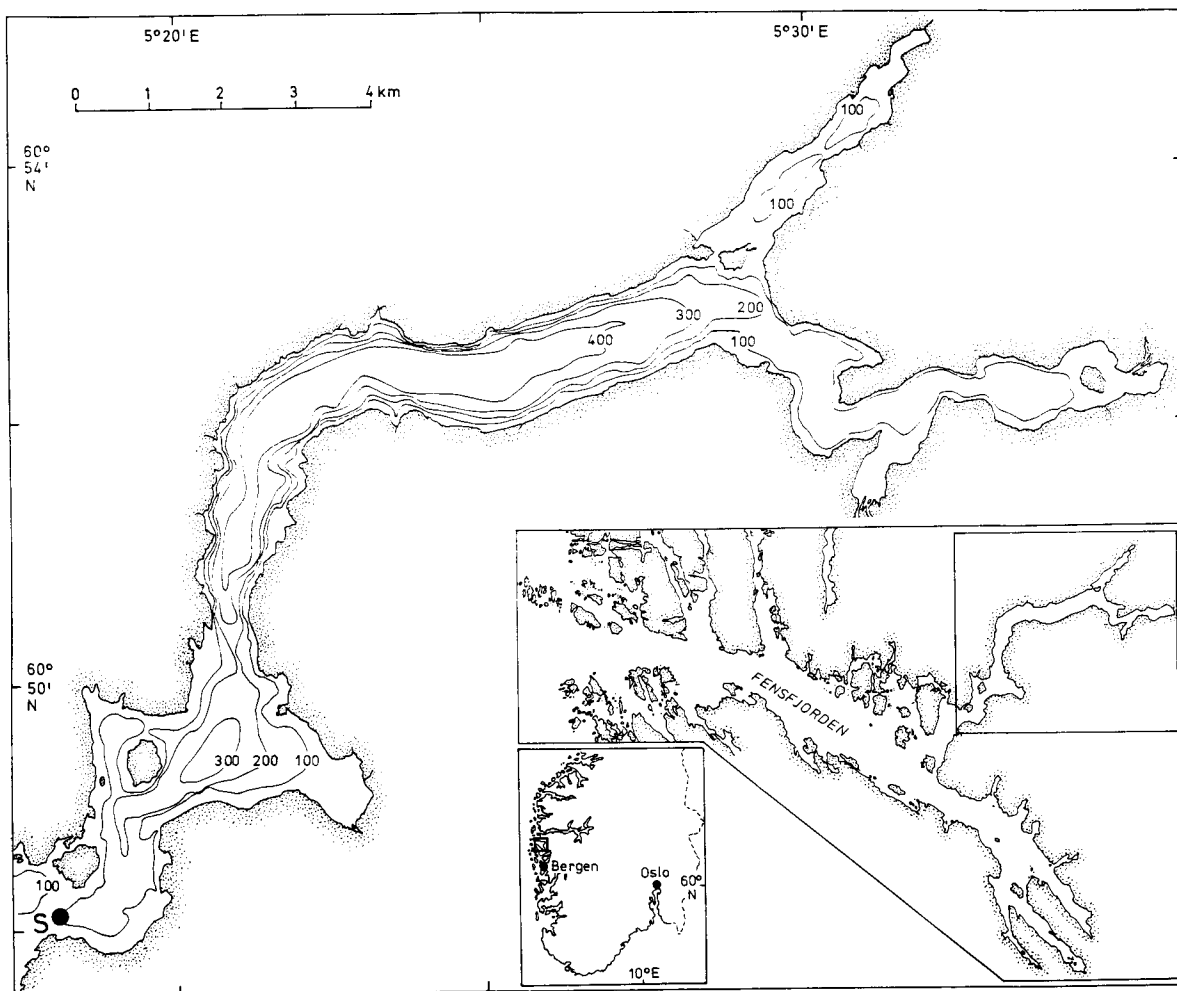


Figure 1. Map of Masfjorden. Location of the sill is indicated with an S.

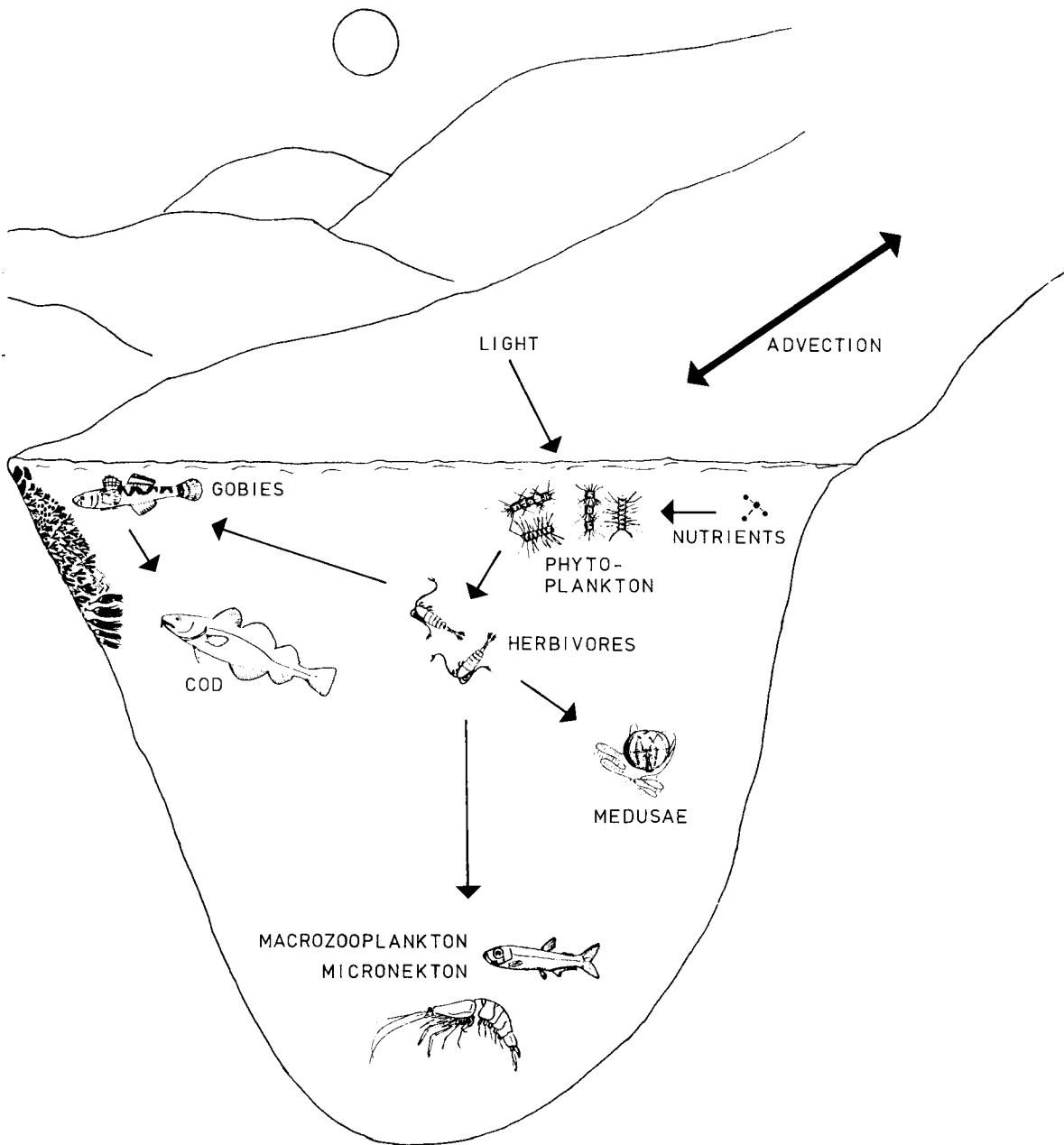


Figure 2. A simplified pelagic food chain of Masfjorden. The arrows indicate the dominant directions of the energy/mass transfers. In the text, medusae are referred to as the gelatinous zooplankton; macrozooplankton and micronekton are referred to as carnivorous zooplankton.

selected according to the conceptual model in Figure 2. These are nitrogen-nutrients, phytoplankton, herbivores, and the four carnivorous groups: gelatinous zooplankton, carnivorous zooplankton (macrozooplankton and micronekton), gobies, and young cod. All variables are basically expressed as $\text{mg nitrogen m}^{-3}$, but biomasses are transformed to common units (chl.

a , carbon and wet weight) by conversion factors (Table 3) in input and output operations.

In the model, the fjord is regarded as consisting of two habitats: the nearshore pelagic and the central pelagic. The volume of the nearshore pelagic is defined by the observed habitat of the gobies, and that of the central habitat as the difference between total fjord

Table 1. Definition of forcing functions (F_n), boundary conditions (B_n), and state variables (S_n). Monthly values for forcing functions, boundary conditions, and initial densities of state variables are given in Table 6. Definitions and values for the conversion factors between internal and input-output units are found in Table 3. 1 Ly day⁻¹ corresponds to 2.23 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Valiela, 1984).

Symbol	Definition	Input/output unit	Internal unit
F_1	Freshwater runoff	$\text{m}^3 \text{s}^{-1}$	day ⁻¹
F_2	Deep water convection	cm s^{-1}	day ⁻¹
F_3	Advection over the sill	cm s^{-1}	day ⁻¹
F_4	Water temperature	°C	°C
F_5	Surface radiation		Ly day ⁻¹
F_6	Photoperiod		dim.less
B_1	Nitrate in fresh water	$\mu\text{M NO}_3^-$	mg N m^{-3}
B_2	Nitrate in deep water	$\mu\text{M NO}_3^-$	mg N m^{-3}
B_3	Nitrate at the sill	$\mu\text{M NO}_3^-$	mg N m^{-3}
B_4	Phytoplankton at the sill	$\text{mg Chl } a \text{ m}^{-3}$	mg N m^{-3}
B_5	Herbivores at the sill	mg C m^{-3}	mg N m^{-3}
B_6	Gelatinous zooplankton at the sill	mg C m^{-3}	mg N m^{-3}
S_1	Nitrate	$\mu\text{M NO}_3^-$	mg N m^{-3}
S_2	Phytoplankton	$\text{mg Chl } a \text{ m}^{-3}$	mg N m^{-3}
S_3	Herbivorous zooplankton	mg C m^{-3}	mg N m^{-3}
S_4	Gelatinous zooplankton	mg C m^{-3}	mg N m^{-3}
S_5	Carnivorous zooplankton	mg C m^{-3}	mg N m^{-3}
S_6	Gobies	mg C m^{-3}	mg N m^{-3}
S_7	0-group cod	mg C m^{-3}	mg N m^{-3}

volume and volume of the nearshore. The gobies are assumed to feed on herbivores available in the nearshore habitat. These herbivores, however, are in exchange

Table 2. State equations. The processes are grazing/predation (G), production (P), respiration (R), sinking (Z), and mortality (M). Other symbols are explained in Table 1. Process equations are given in Table 4. Excretory release from gobies and codling is neglected in the nitrate equation (Equation 1). The advective term of herbivores (Equation 3) is omitted when photoperiod $F_6 < 0.4$ (approximately October through February).

$$(1) \quad \frac{\delta S_1}{\delta t} = R_3 + R_4 + R_5 + B_1 \times F_1 + (B_2 - S_1) \times F_2 + (B_3 - S_1) \times F_3 - P_2$$

$$(2) \quad \frac{\delta S_2}{\delta t} = P_2 - G_3 - Z_2 + (B_4 - S_2) \times F_3$$

$$(3) \quad \frac{\delta S_3}{\delta t} = P_3 - R_3 - M_3 + (B_5 - S_3) \times F_3$$

$$(4) \quad \frac{\delta S_4}{\delta t} = P_4 - R_4 - M_4 + (B_6 - S_4) \times F_3$$

$$(5) \quad \frac{\delta S_5}{\delta t} = P_5 - R_5 - M_5$$

$$(6) \quad \frac{\delta S_6}{\delta t} = P_6 - R_6 - M_6$$

$$(7) \quad \frac{\delta S_7}{\delta t} = P_7 - R_7 - M_7$$

with the herbivores of the central habitat. Renewal of the herbivores in the nearshore is assumed to be passive, and equal to the water renewal (c_9 , Table 3).

A vertical zonation of phytoplankton, herbivores, medusae, and carnivores is prominent at all seasons in the fjord (Kaartvedt *et al.*, 1988; Giske *et al.*, in press), and horizontal patchiness may also be important. In order to obtain realistic values of prey densities for the calculations of feeding rates in this spatial unresolved model, the inhabitants of the central pelagic habitat are compressed to a vertical layer of 30 m (c_2 , Table 3) termed "the actual feeding habitat". The thickness of this layer was scaled to the euphotic zone and observed sound scattering layers (Baliño, 1990; Giske *et al.*, 1990). With a mean fjord depth of 200 m, this compression leads to a seven times increase in densities of predators and prey in the feeding processes in the model relative to a regular distribution. However, the effect of this concentration is also influenced by the "half saturation" constants in the predation equations (Tables 4 and 5).

Gelatinous zooplankton were separated from other carnivores of the central pelagic habitat on the basis of their different methods of food intake. According to Kremer (1976), the feeding rate of filter-feeding gelatinous zooplankton can be characterized by a biomass-specific clearance rate independent of prey density (p_6 in Equation 10, Table 4). Also, in some of the simulation experiments we offer carnivores, but not gelatinous zooplankton, as an additional food source for codling.

The model is driven by radiation, day length, tem-

Table 3. Definition of constants and conversion factors. The factors are used in transformations between input–output units and internal units (see Tables 1, 4, and 7). The conversion factors are regarded as constants, although c_7 – c_{10} in nature are variable over different time scales.

Symbol	Definition	Unit	Value
c_1	Atomic weight of nitrogen		14
c_2	Depth of actual feeding habitat	m	30
c_3	Volume of actual feeding habitat	m^3	7.93×10^8
c_4	Volume of Gobidae/codling habitat	m^3	8.83×10^5
c_5	Vertical cross-sectional area of feeding habitat at sill	m^2	20 005
c_6	Bottom area of euphotic zone	m^2	2.62×10^7
c_7	C:N ratio of state variable	C/N	6
c_8	C:Chl <i>a</i> ratio	C/Chl <i>a</i>	50
c_9	Daily renewal of sublittoral water	day^{-1}	96
c_{10}	Sinking of phytoplankton	$m day^{-1}$	0.5

Table 4. Production (P), grazing/predation (G), sinking (Z), respiration (R), and mortality (M) process equations. The process equations are incorporated in the state equations in Table 2. Parameters (p_n) are given in Table 5 and constants (c_n) in Table 3.

	P_2 is calculated according to Kremer and Nixon (1978).
(8)	$P_x = G_x \times p_1 \times c_7^{-1}$, where $x = 3 \dots 7$
(9)	$G_3 = p_2 \times e^{(p_3 \times F_4)} \times c_7 \times S_3 \times (S_2 \times c_7 - p_4) \times (p_5 + S_2 \times c_7)^{-1}$
(10)	$G_4 = p_6 \times e^{(p_3 \times F_4)} \times c_7 \times S_4 \times c_7 \times S_3$
(11)	$G_5 = p_2 \times e^{(p_3 \times F_4)} \times c_7 \times S_5 \times (S_3 \times c_7 - p_4) \times (p_5 + S_3 \times c_7)^{-1}$
(12a)	$G_6 = \text{MIN}(A, B)$ where
(12b)	$A = p_2 \times e^{(p_2 \times F_4)} \times c_7 \times S_6 \times (S_3 \times c_7 - p_4) \times (p_5 + S_3 \times c_7)^{-1} \times F_6$
(12c)	$B = S_3 \times c_7 \times c_9 \times \delta t$
(13)	$G_7 = p_2 \times e^{(p_3 \times F_4)} \times c_7 \times S_7 \times (S_6 \times c_7 - p_4) \times (p_5 + S_6 \times c_7) \times F_6$
(14)	$Z_2 = S_2 \times c_{10} \times c_2^{-1}$
(15)	$R_3 = S_3 \times p_7 \times p_8 \times e^{(p_9 \times F_4)}$
(16)	$R_x = S_x \times p_8 \times e^{(p_9 \times F_4)}$, where $x = 4 \dots 7$
(17)	$M_3 = G_4 \times c_7^{-1} + G_5 \times c_7^{-1} + G_6 \times c_4 \times c_3^{-1} \times c_7^{-1}$
(18)	$M_6 = S_6 \times p_{10} + G_7 \times c_7^{-1}$
(19)	$M_x = S_x \times p_{10}$, where $x = 4, 5, \text{ and } 7$

perature, freshwater run off (and its nitrogen content), transport of nitrogen from deeper layers, and transport of nitrogen, phytoplankton, herbivores, and gelatinous zooplankton across the sill (Table 1, Fig. 2). Realistic values of radiation, day length, temperature, and freshwater run off were supported (next section). Realistic transport rates across the sill, however, were available only for short time periods, and the monthly values (Table 6B) used to force our model are based on ADCP measurements obtained irregularly over several years. Convection rate is calculated as the average velocity needed to explain the observed maximal vertical range of nutrient depletion over an annual cycle (own unpubl. data). While mortalities of phytoplankton, herbivores,

and gobies are dynamically represented, mortalities of the top predators of the model (carnivorous and gelatinous zooplankton and codling) had to be specified (Table 5).

FORTTRAN codes for the model are given by Aksnes and Giske (1989).

Forcing functions

Solar radiation and photoperiod

Surface radiation and photoperiod are computed according to a general model adaptable to any locality along the Norwegian coast. Given a geographical posi-

Table 5. A. Definitions of parameters. B. Parameter values. Q_{10} values (p_3 and p_9) are converted to natural logarithmic values per degree before use in the process equations. The lowering factor for winter respiration of herbivores p_7 is 1 (no reduction) when photoperiod $F_6 > 0.4$, and 0.2 otherwise. C. Sources for parameter values. Numbers refer to literature values (below) that have been transformed to scales and dimensions to fit the process equations. A ■ symbolizes that the parameter value is constructed on general ecological relationships (size, trophic level, and the ecosystem). An * is used on tuned parameter values.

	Symbol	Definition					Unit
A	p_1	Assimilation efficiency					dim. less
	p_2	Maximal grazing/predation rate at 0°C					day ⁻¹
	p_3	Q_{10} temperature rate constant for grazing/predation					°C ⁻¹
	p_4	Lower feeding threshold					mgC m ⁻³
	p_5	Michaelis-Menten half saturation constant for predation					mgC m ⁻¹
	p_6	Biomass-specific filtration rate at 0°C					m ³ mgC ⁻¹ day ⁻¹
	p_7	Respiratory activity in winter relative to summer					dim.less
	p_8	Maximal respiration rate at 0°C					day ⁻¹
	p_9	Q_{10} temperature rate constant for respiration					°C ⁻¹
	p_{10}	Natural mortality rate					day ⁻¹
		Herbivores	Gelatinous	Carnivores	Gobies	Codling	
B	p_1	.7	.8	.8	.85	.9	
	p_2	.0985		.075	.1	.05	
	p_3	2.95	1.7	2	2	1.4	
	p_4	5		0	0	100	
	p_5	50		150	10	1000	
	p_6		2.58×10^{-5}				
	p_7	.2 or 1					
	p_8	.03	.0064	.006	.006	.0017	
	p_9	1.8	3.5	3.2	3.2	2	
	p_{10}		0	.006	.0035	.004	
C	p_1	■	9	■	■	10	
	p_2	3,8		■	12	6	
	p_3	3,8	9	■	12	6	
	p_4	3		■	■	■	
	p_5	3		*	*	■	
	p_6		9				
	p_7	7					
	p_8	2,11	4,9	■	5	10	
	p_9	1	4,9	■	5	10	
	p_{10}		9	*	*	13	

1 Corner *et al.* (1967); 2 Dagg *et al.* (1982); 3 Frost (1987); 4 Gyllenberg and Greve (1979); 5 Hanson (1985); 6 Hawkins *et al.* (1985); 7 Hirche (1983); 8 Kiørboe *et al.* (1982); 9 Kremer (1976); 10 Lied (1983); 11 Miller and Landry (1984); 12 Parsons and Kessler (1987); 13 Pitcher and Hart (1982).

tion, a theoretical outer atmosphere radiation value is calculated and reduced to obtain the global surface radiation (Olseth and Skartveit, 1985, 1987). The reduction is made according to an empirical ratio between observed monthly surface radiation (for the selected position) and monthly outer atmospheric radiation. This relationship was based on the observations made over a 30-year period in different parts of Norway.

Temperature

Temperatures are based on measurements made over several years in Masfjorden (unpubl. data). Monthly values averaged for the upper 30 m were used as input.

Runoff water

The fresh water discharging into the fjord originates from a hydroelectric power plant and from natural

sources. Monthly data on the amounts of regulated freshwater supply were obtained from the administration of the power plant (Table 6). The amounts originating from other sources were calculated on the basis of regulated and non-regulated drainage areas and monthly runoff to the reservoirs in the regulated area.

Transport across the pelagic boundaries

Nitrogen nutrients are assumed to be transported from the deeper water into the euphotic zone with a specified year-averaged velocity (denoted convection, Table 6). The current across the sill (advection) is specified as monthly averages (Table 6B). The net exchanges of nitrogen, phytoplankton, herbivores, and gelatinous zooplankton depend on actual advection and actual content and biomass inside (dynamic) and outside (specified, Table 6) the system (Equations 1–4, Table

Table 6. A. Initial densities of state variables. Values are for 1 January. Data are averages of all measurements in the 0–30 m layer in December and January. Codling enter the model when they have become large enough to eat gobies (1 August, 20 mg C m⁻³). Densities of gobies and codling are in sublittoral habitat. Data on carnivores are from Kaartvedt *et al.* (1988) and densities of gobies are from Fosså (1991). B. Monthly values of forcing functions and boundary conditions. The values are given for the first day of each month. Values for other days are weighted means of the nearest two given values. Photoperiod F₆ is calculated for each day as the fraction of hours with daylight. See Table 1 for definitions of forcing functions and boundary conditions.

State variable		Value	I/O Unit
A	S ₁ Nitrate	5.6	μM NO ₃
	S ₂ Phytoplankton	0.05	mg Chl <i>a</i> m ⁻³
	S ₃ Herbivores	30.6	mg C m ⁻³
	S ₄ Gelatinous zooplankton	0.007	mg C m ⁻³
	S ₅ Carnivores	12.5	mg C m ⁻³
	S ₆ Gobies	952	mg C m ⁻³
	S ₇ Codling	0	mg C m ⁻³

Month	F ₁	F ₂	F ₃	F ₄	F ₅	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	
B	Jan	54.1	.00024	5	8.5	11	0	14	5.6	0.05	2.1	0.2
	Feb	51.4	.00024	5	7.5	32	0	14	4.5	0.1	0.7	0.2
	Mar	48.4	.00024	7	6.4	82	5	14	3.4	0.6	8.5	1.2
	Apr	47.3	.00024	10	3.9	135	5	14	1.2	0.6	58.2	2.0
	May	59.0	.00024	12	5.1	190	5	14	0.4	2.0	22.0	2.8
	Jun	46.8	.00024	10	7.1	180	5	14	3.8	0.4	58.3	2.2
	Jul	32.5	.00024	7	10.5	175	5	14	0.0	0.5	40.0	2.5
	Aug	36.1	.00024	7	13.0	135	5	14	0.0	0.7	35.0	2.0
	Sep	54.2	.00024	5	13.0	85	5	14	0.3	0.3	40.0	2.5
	Oct	56.7	.00024	4	13.4	40	5	14	0.5	0.7	47.5	1.3
	Nov	60.3	.00024	3	11.0	12	5	14	4.1	0.2	5.0	1.1
	Dec	56.3	.00024	8	10.2	6	5	14	6.0	0.1	2.1	0.1

2). Advection of herbivores is omitted in winter as they then stay in the non-advective deep water (Baliño, 1990; Giske *et al.*, 1990).

Processes

Primary production

Maximum growth rate of phytoplankton is made dependent on temperature according to the empirical relation given by Eppley (1972). This growth rate is then reduced in accordance with the prevailing nutrient and light conditions. Nitrogen uptake is expressed as Michaelis–Menten kinetics, and light limitation is expressed with a time-depth integrated version (Equation 14 in Kremer and Nixon, 1978) of the equation of Steele (1962). This version includes effects from self-shading and light acclimation. Primary production represents net production, and metabolic nitrogen loss is not explicitly represented in the model. Sinking of phytoplankton is assumed to occur at a constant rate (Table 3).

Herbivorous processes

The ration ingested is obtained from a maximum ration (temperature dependent), which is reduced by food-density dependent limitation. Below a certain threshold food concentration (p₄, Table 5) feeding ceases. Gross growth is calculated assuming constant assimilation

efficiency. Losses due to metabolism are expressed as a temperature-dependent power function. Reduced winter metabolism, as observed by Hirche (1983) and in own experiments (unpubl.), is represented by a separate parameter (p₇, Table 5).

Carnivorous processes

For carnivorous zooplankton, gobies and codling the feeding process is represented by a temperature-dependent maximum predation rate. This rate is reduced by the prevailing food availability according to a Holling type II (Holling, 1965) or Michaelis–Menten limitation term (Equations 11, 12b, and 13, Table 4). For gobies, a maximal predation rate is set equal to the rate of prey transport (i.e. herbivorous zooplankton) into the nearshore habitat (Equations 12a–c, Table 4). Gelatinous zooplankton is treated as passive filter-feeders, and a biomass specific filtration rate is the key parameter (p₆, Table 5). Assimilation efficiencies of all groups are set constant (p₁, Table 5), while the losses due to metabolism are temperature-dependent (Equations 15 and 16, Table 4).

Tuning of parameters

Those parameter values that are not based on own measurements are either obtained from relevant literature (Table 5C) or tuned. Among the tuned parameters,

the renewal rate of sublittoral water (c_9 , Table 3) turned out to be especially important. Unfortunately, we have not yet obtained realistic values for this parameter. Tuning was performed so that the modelled production of gobies corresponded with the estimated production of gobies (Fosså, 1991). Then we have assumed that the production of the sublittoral gobies is determined by the supply of their prey (herbivorous zooplankton). Furthermore, this supply is assumed to be entirely dominated by renewal of the sublittoral water. Other tuned parameters are the "half saturation" constants (of the feeding processes) for carnivores and gobies feeding on herbivores (p_5 , Table 5) and the natural mortality rates

for carnivores and gobies (p_{10} , Table 5). The tuning was accomplished by varying the parameters within reasonable limits such that the densities of the state variables at the end of the year were approximately equal to their initial values. No efforts, however, were made to fit the time solution of the state variables to observations.

Simulations

Three sets of simulations were performed (Table 7A). First, the effects of removing the primary production and different state variables were investigated. Second,

Table 7. Simulations. A. Descriptions of the three types of simulations performed (changes in state variables, in forcing functions, and cod release). B. Equations for diet choice of codling offered gobies and carnivores. In simulations with extended diet, codling will eat gobies (G_{GOB}) at maximal rate, while predation on carnivores (G_{CAR}) is restricted as shown in Equations 22a–c. G_{MAX} is the maximal predation rate for cod independent of prey density. C. Simulated effects of removing processes and state variables. Changes from basic run annual accumulated net production given as percentage of basic run: $100 \times (\text{Simulation} - \text{Basic})/\text{Basic}$.

Changes in state variables							
Primary production omitted							
Gelatinous zooplankton excluded							
Carnivores excluded							
Gelatinous zooplankton and carnivores excluded							
Codling excluded							
Both carnivores and gobies food for codling							
Boundary densities of herbivores changed							
A	Changes in forcing functions						
	Advection: 0, 5, 10, 15, and 20 cm sec ⁻¹ . Renewal of littoral water and convection changed accordingly						
	Convection: 0, 0.5, 2, and 10 times basic run rates						
	Runoff: 0, 0.5, 2, and 10 times monthly basic run rates						
	Temperature: monthly values changed -5, -2, -1, 1, 2, and 5°C compared to monthly basic run values						
	Cod release programme						
	Codling eating gobies and						
	Codling eating gobies and carnivores: 10 000, 50 000, 250 000 and 1 000 000 codling (60 g WW) released 1 January.						
	(20) $G_{MAX} = p_2 \times e^{(p_3 \times F_4)} \times c_7 \times S_7$						
	(21) $G_{GOB} = p_2 \times e^{(p_3 \times F_4)} \times c_7 \times S_7 \times (S_6 \times c_7 - p_4) \times (p_5 + S_6 \times c_7)^{-1} \times F_6$						
B	(22a) $G_{CAR} = \text{MIN}(A, B)$ where						
	(22b) $A = p_2 \times e^{(p_3 \times F_4)} \times c_7 \times S_7 \times c_4 \times c_3^{-1} \times (S_5 \times c_7 - p_4) \times (p_5 + S_5 \times c_7)^{-1} \times F_6$						
	(22c) $B = G_{MAX} - G_{GOB}$						
<hr/>							
	Simulation	S_2 Phyt	S_3 Herb	S_4 Gelat	S_5 Carn	S_6 Gob	S_7 Cod
	No primary production		-133.5	-2.0	-96.0	-45.0	-48.5
	No gelatinous zooplankton	0.2	0.3		-0.1	0.0	-0.1
	No carnivores	-2.0	-7.1	-0.4		27.4	12.1
	No gel. and carn.	-2.2	-7.4			27.5	12.0
	No codling	0.0	0.0	0.0	0.0	-4.9	
	Cod also eating carnivores	0.0	-0.1	0.0	1.2	18.0	1300.1
	Herb. at sill 0.1 × Basic	8.9	-58.7	5.2	-132.3	-47.5	-89.6
	Herb. at sill 10 × Basic	33.2	-97.1	-17.9	6548.0	172.5	38.7
C							

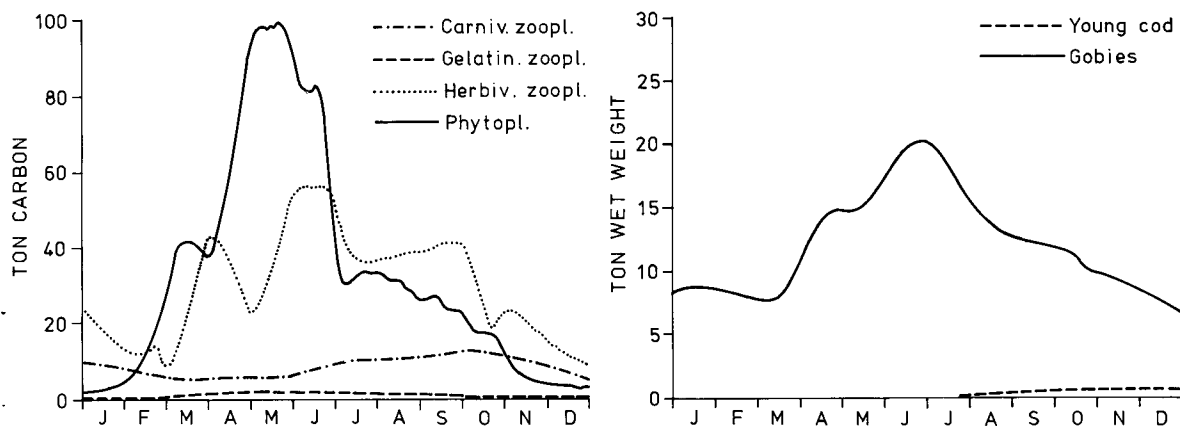


Figure 3. Standing stocks in Masfjorden from the basic run. Total biomasses in ton carbon (phytoplankton, herbivores, medusae, and carnivores) and in ton wet weight (gobies and codling).

changes in the values of the forcing functions were studied. The simulations were performed by changing one variable at a time. Changes in advection, however, were also combined with changes in convection and the rate of renewal of sublittoral water. With zero advection we assumed zero convection, and guessed a minimum renewal rate of sublittoral water of 3 day^{-1} . Other values of convection and sublittoral renewal were obtained by linear inter- and extrapolation of these extreme values and the values used in the basic run. This resulted in a sublittoral renewal rate close to 300 day^{-1} for the maximal advection rate of 20 cm s^{-1} . Finally, different cod release programmes were simulated. In these simulations codling were offered two sets of diets: "normal" (gobies) and "extended" (gobies and carnivorous zooplankton). In the extended diet simulations codling should prefer gobies, so predation on carnivores was upwards restricted to the difference between actual predation on gobies and the codling's feeding capacity (Equations 20 to 22 in Table 7B).

Results

Basic run

The time solutions of the biological state variables are given in Figure 3. The model was run for one year. Simulated net primary production of the fjord was $2341 \text{ ton C year}^{-1}$ (Table 8). This amounts to a net production of $90 \text{ g C m}^{-2} \text{ year}^{-1}$, which is normal for Norwegian coastal waters (Matthews and Heimdal, 1980). The nitrogen budget of the basic run (Table 9) shows that 2293 ton N was lost from the simulated system, while 2299 ton N was supplied, resulting in a 6 ton N increase at the end of the simulated year. Convection and land run off were responsible for the main net N-supply into the system, while advection was the

dominating process in regulating the total N-content of the system (Table 9).

Sensitivity to structural changes

The effects of removing processes and state variables are given in Table 7C. Total removal of primary production caused a negative production of herbivorous zooplankton, which means that the respiration/excretion exceeded the internal production for this group. Because of advective input of herbivores, however, there was still food available for higher trophic levels. Consequently, production of gobies and 0-group cod was only reduced to within 45 to 49% of the basic run. The present simulations indicate that codling are only moderately sensitive to alterations in the primary production of the fjord. Inclusion of carnivorous zooplankton in the diet of codling gave an increased production of 1300%. Boundary densities of herbivorous zooplankton seem to have an impact on the carrying capacities of most state variables. The effects are most pronounced for the pelagic carnivores, with a sixty-fold increase in production following a ten-fold increase in herbivore density at the sill.

Table 8. Annual accumulated net production (production respiration) of biological state variables from basic run. Values are for the entire fjord volume.

State variable	Annual net production
Phytoplankton	2340.9 t carbon
Herbivorous zooplankton	328.9 t carbon
Gelatinous zooplankton	-7.5 t carbon
Carnivorous zooplankton	14.6 t carbon
Gobies	15.0 t wet weight
0-group cod	0.7 t wet weight

Table 9. Yearly nitrogen budget obtained by the basic run simulation. All figures represent metric tonnes of nitrogen.

	Supply	Loss	Net
Runoff water	93		93
Convection of nutrient	311		311
Advection of nutrient	1453	1552	-99
Advection of phytoplankton	225	384	-159
Advection of herbivorous zooplankton	205	244	-39
Advection of gelatinous zooplankton	12	11	1
Sinking of phytoplankton		34	-34
Excretion of cod and gobies		1	-1
Mortality of carnivorous zooplankton		3	-3
Mortality of gobies and cod		1	-1
Faecal matter		63	-63
Sum	2299	2293	6
N-content of the simulated system	1 Jan 68	31 Dec 74	Change -6

Sensitivity to alterations in forcing functions

Sensitivities of production to alterations in the magnitude of advection across the sill (Fig. 4), convection of nutrients from below (Fig. 5), runoff water from land (Fig. 6), and temperature (Fig. 7) were investigated. Our results show that advection is a prerequisite for a large production of sublittoral fishes (gobies and codling), and that this production is stimulated with high advection levels. Surprisingly, production of pelagic carnivores was negatively influenced by strong advection. The production of this group, however, was clearly enhanced by increased nutrient input (increased convection and runoff). This increased input, however, did not facilitate any increased production of gobies and 0-group cod. Temperature increases seem to benefit the production of phytoplankton, herbivores, and gelatinous zooplankton, but reduce the production of carnivorous zooplankton, gobies, and codling. The opposite seems to be true for decreasing temperatures. It should be noted, however, that the changes were relatively moderate.

Simulated release of 0-group cod

The effect of releasing different amounts of codling into the system is given as codling biomass development the first seven months after release (Fig. 8A). After this time prey items other than those included in our model become important in the diet of cod (Salvanes, pers. comm.). With normal diet (gobies) the carrying capacity for young cod seems to be below 30 ton wet weight. A doubled capacity is indicated in the extended diet (gobies and carnivorous zooplankton) simulation (Fig. 8B).

Discussion

Basic run

The realism of a model is often judged by its ability to produce accurate time solutions of the state variables. This requires accurate measurements not only of the state variable, but also of the forcing functions and boundary conditions. Such monitoring is expensive and has not yet been included in the present project. The forcing of our basic run is based on available measure-

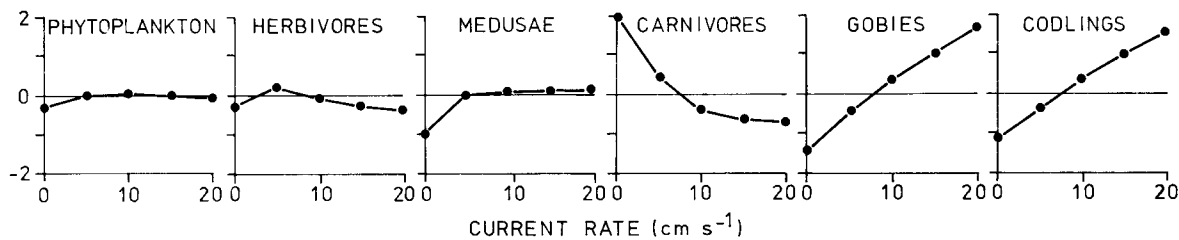


Figure 4. Simulations of dependency of production on changes in advective regime, given as different constant water transport rates across the sill (Table 7A). Y-axes are deviations from the basic run net annual accumulated production as a fraction of the basic run $((\text{Simulation} - \text{Basic Run}) / \text{Basic Run})$. A doubling of production will give 1, half basic run production will give -0.5, and values below -1 show negative net annual accumulated production in the simulation experiment.

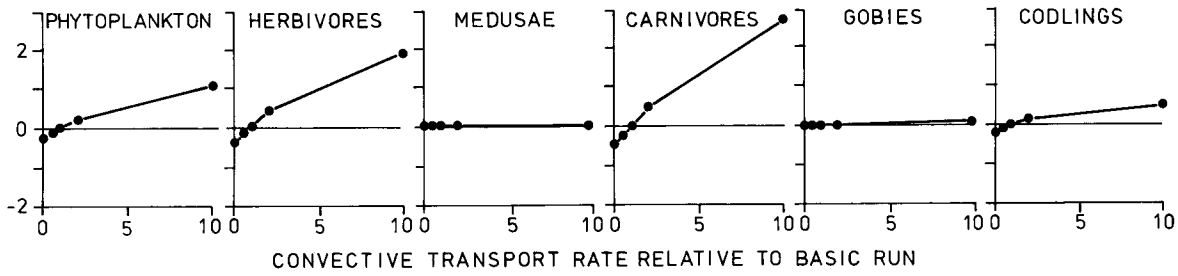


Figure 5. Simulations of dependency of production on changes in convective regime. X-axis is multiplication factor of convection relative to F_2 in Table 6B (see Table 7A). Y-axis as in Figure 4.

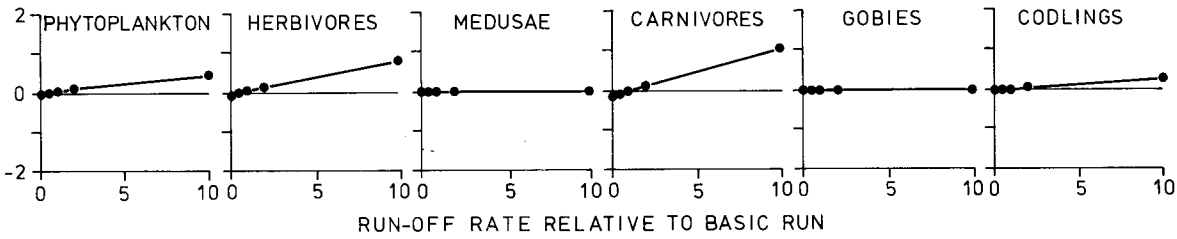


Figure 6. Simulations of dependency of production on changes in freshwater runoff. X-axis is multiplication factor of runoff relative to F_1 in Table 6B (see Table 7A). Y-axis as in Figure 4.

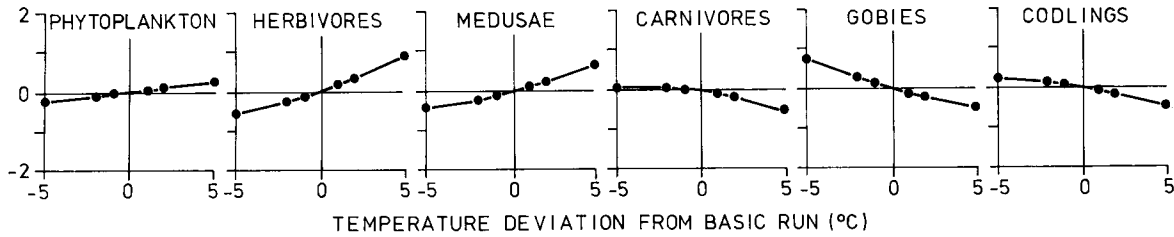


Figure 7. Simulations of dependency of production on changes in temperature regime. X-axis is difference from basic run temperature (Simulation-Basic). Temperatures that in simulations would fall below 0°C are adjusted to 0°C . Y-axis as in Figure 4.

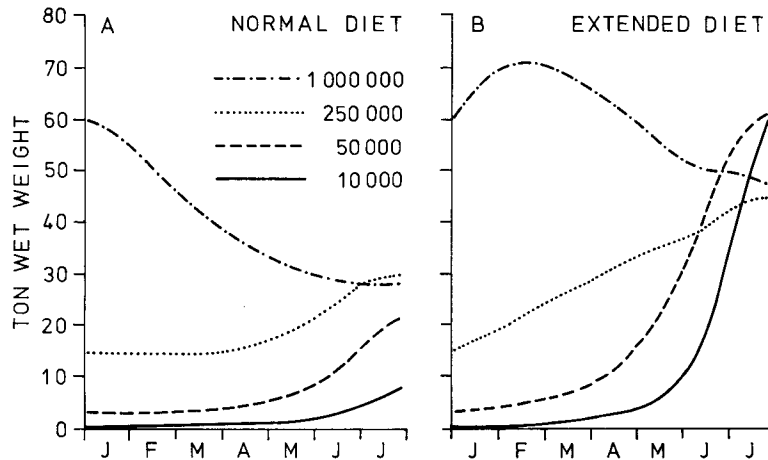


Figure 8. Simulations of release of codling. Different numbers of 60 g WW codling are released on January 1. A. Normal diet (sublittoral gobies). B. Extended diet (sublittoral gobies and pelagic macroplankton and micronecton) (see equations in Table 7B).

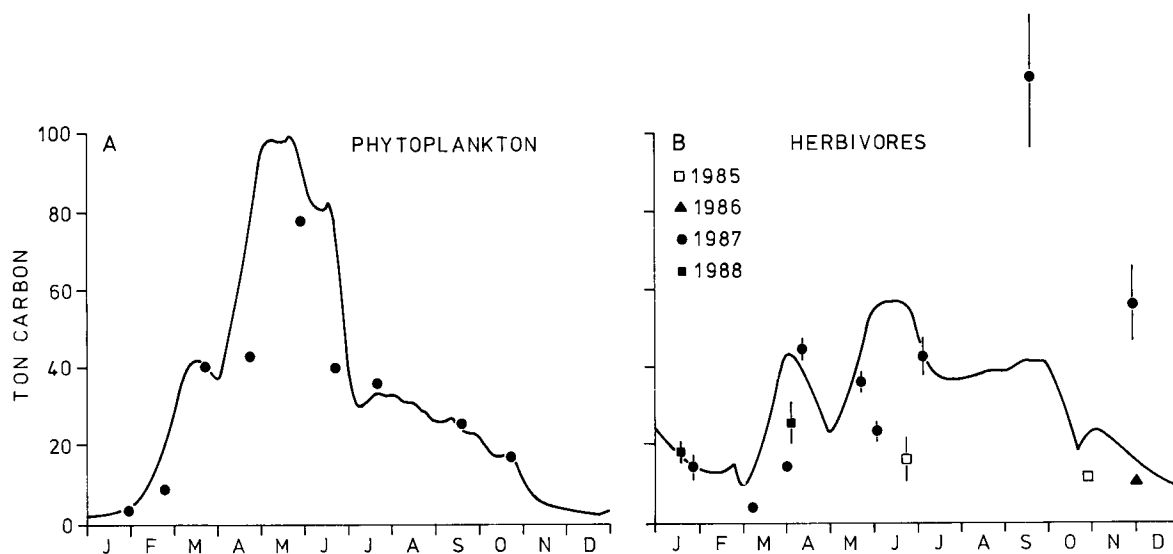


Figure 9. Comparison of model output and cruise measurements. A. Phytoplankton. All field data are from 1980 (Institute of Marine Research, Bergen). B. Herbivores. Field estimates are based on Juday net (180 μ m) hauls. Vertical bars are 95% confidence intervals.

ments undertaken sporadically during several different years. Hence, the basic run represents a biased average situation rather than a specific year. Nevertheless, in Figure 9A we have plotted measurements of phytoplankton standing stock in Masfjorden together with the time solution of the basic run. There is a surprisingly good fit between the model results and field measurements, taking into account that no efforts were made to fit the time solution of the model to observations.

Available estimates of herbivorous zooplankton biomass are plotted together with the model results in Figure 9B. Here, the fit is not impressive due to considerable year to year variations in the measurements. Aksnes *et al.* (1989) concluded that the amount of herbivorous zooplankton in Masfjorden is dominated by advective processes rather than by internal production. These advective processes are mainly dependent on a variable wind regime along the west coast of Norway. Such variability in the wind regime is likely to propagate into the herbivorous level and thereby give rise to yearly fluctuations like those observed in Figure 9. This means that monitoring of the advective forcing and the herbivorous boundary biomass is necessary if a meaningful comparison between observations and model prediction is to be made. Contrary to zooplankton, the much higher growth rate of phytoplankton makes this group influenced more by internal production than by advection (Aksnes *et al.*, 1989). This decreased dependency on advective forcing may explain the better fit obtained for phytoplankton.

Sensitivity to structural changes

Of the simulations performed, production of codling

was most sensitive to an extension of their diet (Table 7C). Inclusion of carnivorous zooplankton in their diet caused a more than ten-fold increase in cod production during the first autumn. Furthermore, Figure 8B indicates that an extended diet also increases the carrying capacity for cod during the next seven months. This gives rise to the question: why do codling in Masfjorden not feed on the pelagic macrozooplankton and micro-nekton? Such feeding behaviour has been observed in fjords of northern Norway (Wiborg, 1948; Percy *et al.*, 1979; Falk-Petersen and Hopkins, 1981; Klementsens, 1982; dos Santos and Falk-Petersen, 1989). A more pelagic mode of feeding may involve an increased risk of predation, since the free water masses do not offer the same shelter as the sublittoral habitat. The sublittoral habitat may be preferable, therefore, as long as it supplies codling with enough food. This food supply may be exceeded by the demand when large amounts of released cod enter the fjord. A prey shift may be induced, but the consequences are uncertain. The new food demand may be satisfied, but it may also lead to increased predator exposure and thereby to increased mortality.

Advection and renewal of littoral water seem to be extremely important for gobies and codling. An increased water renewal in the sublittoral habitat increases prey availability for the gobies. This points out the need for knowing the mechanisms governing water renewal on scales of tens of metres in upper nearshore water. Generally speaking, the relationship between gobies and herbivorous zooplankton is a relationship between a stationary predator and advected prey. According to Aksnes *et al.* (1989) and Kaartvedt (1991) this relationship may be an important charac-

teristic of fjord ecology. Advection of prey may increase the carrying capacity for a stationary predator considerably, and this mechanism may be utilized in fjord ranching. Theoretically, one could expect the best result by releasing a stationary species that utilizes advected prey directly.

While increased advection and renewal rate enhanced production of gobies, production of pelagic carnivores decreased (Fig. 4). We believe this to be an artefact of the model. The nitrogen budget (Table 9) shows that advection across the sill represented a net loss of herbivorous zooplankton (39 ton N). This means that the zooplankton content of the fjord in our run is on average richer than the boundary biomass outside the sill. Therefore, advection will decrease the standing stock of zooplankton in the fjord. We have, however, no field measurements that support this. Some of our measurements (Aksnes *et al.*, 1989) indicate the opposite: more zooplankton is transported into the fjord by advection than out of the fjord. The vertical profile of both currents and zooplankton is decisive for the net effect of advection, and this is not realistically represented in our present depth integrated version. The dependence on advection for the carrying capacity of carnivores is, however, clear from the simulations of changes in boundary densities of herbivorous zooplankton (Table 7C). A ten-fold increase in boundary densities of zooplankton will lead to a continual net supply, while a ten-fold decrease will create a continual loss (Equation 3, Table 2). In the first case, production of carnivores was more than 60 times higher than basic run; in the second case the annual production was negative.

Both gobies and pelagic carnivores depend on herbivorous zooplankton and therefore must be regarded as competitors. The competition is likely to increase as the renewal of sublittoral water increases; this competition contributes to the decline in pelagic carnivorous production at high renewal levels (Fig. 4). In the basic run we see that the production of gobies is enhanced by 27% when pelagic carnivores are removed (Table 7C). In the model, gobies do not compete with other groups in their local habitat, and no other top predators than codling eat gobies. Our production estimates for gobies and 0-group cod, therefore, represent the production for the food chain: herbivorous zooplankton–sublittoral zooplankton predator–sublittoral top predator, when the renewal rate of sublittoral water is assumed to be about 100 day^{-1} (C_9 , Table 3).

Simulated release of 0-group cod

The simulations of different cod release programmes do not take competitors of codling into consideration. Salvanes (1986b) found that codling competed with pollack, saithe, and poor-cod over two-spot goby and sand goby. In accordance with this, the cod production obtained in our simulations represents upper limits. Our

estimates of a capacity of 50 000 to 250 000 codling are within the actual recruitment estimated in Masfjorden (Salvanes, unpubl.). This indicates that our model underestimates an upper limit, which is reasonable since our model predicts that more herbivores are advected out of the fjord than into the fjord (Table 9, contrary to observations by Aksnes *et al.*, 1989). Furthermore, the renewal parameter is tuned so that the production of gobies (without competitors) equals the estimated production of gobies (Fosså, 1991). The realized production of gobies, however, is most probably depressed by their competitors. If so, our renewal parameter chosen for the basic run may be underestimated.

Released cod with extended diet had a much better growth than cod with normal diet (Fig. 8). This indicates a food shortage in the sublittoral habitat during winter and spring, which could have been avoided or reduced had codling been able to utilize pelagic carnivores, as observed in fjords of northern Norway. As suggested above, however, other factors (such as predation on codling) may hamper young cod in utilizing pelagic food resources. An ecological difference between northern and southern Norway may exist in this respect.

Future work

As the different constituents of an ecosystem are patchily distributed, the importance of representing spatial dimensions seems obvious. Spatial representation, however, requires knowledge about the spatial behaviour of the constituents. This causes no immediate problems for the physical–chemical variables such as temperature and nitrate, nor does the behaviour of phytoplankton (sinking and swimming) need introduce intractable problems. At the herbivore and higher levels, however, serious gaps of fundamental knowledge about behaviour exist. This limits the realism of spatially resolved models, and such models cannot develop at a higher rate than the acquisition of knowledge about the mechanisms governing the spatial behaviour of the constituents. The problem is, of course, not solved by removing the spatial dimensions and aggregating the constituents into a common time dimension. This is true because the rate of the processes is ultimately coupled with the actual spatial structure of the system. Most important is the feeding process, which is continuously dependent on the distribution and density of both prey and predator. The outcome of the feeding processes will directly affect energy flow through the system and thereby the time solution of the state equations. In the present model we have introduced a nearshore and a central habitat in order to obtain more realistic densities of gobies and codling. An “actual feeding habitat” within the central habitat was also assumed in order to obtain more realistic densities of predators and prey. Such adjustments are hardly sufficient, and the present feeding representations should be substituted with

mechanistic formulations (Clark and Levy, 1988; Huntley, 1988).

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