OPTIMAL RESPONSES TO ENVIRONMENTAL AND PHYSIOLOGICAL CONSTRAINTS: EVALUATION OF A MODEL FOR A PLANKTIVORE

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A numeric model for the life history of the mesopelagic planktivore *Maurolicus muelleri* is tested for sensitivity to different parameter values. The model is based on stochastic dynamic programming with decision variables for habitat choice (depth) and energy allocation (between somatic or reproductive growth). The model includes sub-models to represent the foraging, mortality and growth processes. The parameters that induce large changes in most variables are those related to foraging and visual predation risk. By inducing changes in the strategic habitat choices, they have a large impact on other processes like growth, survival and reproduction. The other parameters tested generally have local impact (e.g. on weight or survival), with less impact on other variables of the model. Seasonality in prey abundance and larval survival both have to be present for the model to predict the seasonal strategies observed for *M. muelleri* in Norwegian fjords. Size dependent factors in the prey encounter, predation and growth processes may explain the observed differences amongst different sized groups of the fish. The strategies predicted for different seasons and size groups of fish, however, are very dependent on the ratio between food abundance and visual predation risk. Size dependent processes in general seem important to understand the selective forces that shape the observed life history patterns of the fish.

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INTRODUCTION

This paper presents a sensitivity analysis on a model for the life history of a mesopelagic planktivorous fish. The dynamics of a population of mesopelagic fish is simulated from a model (ROSLAND & GISKE 1997) based on Stochastic Dynamic Programming (MANGEL & CLARK 1986, 1988; HOUSTON et al. 1988) with a detailed representation of the biological processes. A basic assumption underlying the model is that individuals are able to adapt to the environment, and that they live to maximise their fitness (here: net reproductive rate) under the given conditions.

Changing parameters and variables of the model may give insight into how the environmental variables influence the individual and the population, and how the fish may optimally respond to different environmental conditions. The analysis also gives an indication of how sensitive the model is to changes in different parameters.

The model simulates a population of the mesopelagic planktivore *Maurolicus muelleri* living in a fjord of western Norway. Vertical distribution, growth, feeding, mortality and reproduction of *M. muelleri* have been studied by several authors (LOPEZ 1979; GJØSÆTER 1981; CLARKE 1982; YOUNG & BLABER 1986; YOUNG et al. 1987; WEISS et al. 1988; GISKE et al. 1990; GISKE & AKSNES 1992; MELO & ARMSTRONG 1991; PROSCH 1991; IKEDA 1994; RASMUSSEN & GISKE 1994; GOODSON et al. 1995; BJELLAND 1995; SALVANES & STOCKLEY 1996) and therefore, the life history and ontogeny are relatively well documented for this species.

The diel vertical distribution of *M. muelleri* was also modelled for a winter situation by ROSLAND & GISKE (1994) with a stochastic dynamic programming model with a relatively fine time resolution (15 minute time intervals). The time horizon of the model covered only a diel cycle, and therefore it was not possible to link fitness directly to lifetime reproduction and survival.

By modelling the whole life cycle of the fish, it is possible to calculate the optimal strategies (habitat choice and energy allocation) based on lifetime survival and reproduction. Such a model therefore includes the basic life history variables (survival and reproduction), as well as state dynamics and time dependent variability accounted for by stochastic dynamic programming.

THE MODEL

The central processes of the model are listed in Table 1 and a declaration of the parameters and variables are given in Table 2. Complementary details of the processes in the model are given by ROSLAND & GISKE (1994) and ROSLAND & GISKE (1997), where the last paper presents a basic run of the present model. More detailed descriptions of the models for growth and visual prey encounter are also given in HEWETT & JOHNSON (1992) and AKSNES & GISKE (1993), respectively.

The fish can choose between a set of habitats (z) at different depth positions and light intensities. Due to

Table 1. The basic equations of the model (parameter and variables are declared in Table 2). Note that the visual range (r_z) represent *M. muelleri* in Eq. 1 and its predators in Eq. 6. The indexes x and i indicates the new value of the variable under feeding level x or energy allocation strategy i.

Number	Process (unit)	Equation
(1)	Prey encounter rate (g d^{-1})	$p_z = p(r_z \sin q)^2 \nu N_z w_p \kappa_t$
(2)	Maximum food consumption rate (g d^{-1})	$C_z = \alpha \omega^\beta f_u(u_z) f_\kappa(\kappa_t, \sigma)$
(3)	Food consumption rate (J d^{-1})	$c_x = x q_p \dfrac{C_z}{X}$
(4)	Probability that fish will be consuming food at level x at depth z	$\lambda_z(x) = \left[\left(\dfrac{p_z}{C_z} X \right)^x \exp\left(\dfrac{p_z}{C_z} X \right) \right] \Big/ x! \quad x \in \{0, X\}$
(5)	Growth rate (J d^{-1})	$g_x = c_x \left(1 - k_f - k_e \left[1 - k_f \right] \right) - R(\omega)$
(6)	Survival probability over a time interval	$S_z = \exp\left[-\tau \left(\kappa_t k_v r_z^2 + k_n \omega^{-0.25} \right) \right]$
(7)	Weight of a ripe batch of oocytes (g)	$w_b = \begin{cases} 0 & \text{for } \delta < D \\ 0.05\omega & \text{for } \delta = D \end{cases}$
(8)	Number of oocytes in a batch	$b = \dfrac{w_b}{w_o}$
(9)	State change in total energy content (J) over a time interval (t)	$\varepsilon_x = \varepsilon + \tau g_x - w_b q_o$
(10)	State change in fish weight (g) over a time interval (t)	$\omega_x = \begin{cases} \omega & \text{if } \varepsilon_x \le q_f \omega \\ \dfrac{\varepsilon_x}{q_f} & \text{if } \varepsilon_x > q_f \omega \end{cases}$
(11)	State dynamics for the age of the developing oocytes (t)	$\delta_i = \begin{cases} 0 & \text{if } \delta = 0 \text{ and } i = 0 \text{ or } \delta = D \\ \delta + \tau & \text{if } \delta = 0 \text{ and } i = 1 \text{ or } 0 < \delta < D \end{cases}$
(12)	The fitness of the fish at time t at states ω, ε and δ	$F(\omega, \varepsilon, \delta, t, T) = \max_{z,i} \left\{ S_z \sum_{x=0}^{X} \lambda_z(x) \left(F(\omega_x, \varepsilon_x, \delta_i, t+1, T) + bL_t \right) \right\}$

vertical gradients in prey density and water temperature these variables have unequal values in the different habitats. Within each habitat, however, the light intensity is constant during daytime.

Prey encounter rate (p_z) is a visual process and is represented as a function of the visual range (r_z), visual field angle (θ), swimming speed (v) of the fish and prey density (N_z) in the habitat (Eq. 1 in Table 1). The equation is multiplied by prey weight (w_p) and daylength (κ_t) to express prey encounter rate in weight units per day. The visual range (r_z) is a function of light intensity, water turbidity, prey size, prey contrast and the visual sensitivity threshold of the predator's eye (AKSNES & GISKE 1993).

The growth rate of the fish depends on prey encounter rate and physiological factors such as food consumption rate and food processing rate. The maximum food consumption capacity (C_z) is defined as a function of fish weight (ω) and water temperature ($f_u(u_z)$) and feeding ration ($f_\kappa(\kappa_t, \sigma)$) (Eq. 2 in Table 1). Feeding ration is calculated as the number of stomachs evacuated (i.e. potential for food consumption) during a period of day light (κ_t) given a stomach evacuation rate (σ), relative to a situation with 24 hours of daylight (i.e. $f_\kappa(\kappa_t, \sigma) \mu \kappa_t/\sigma$). Stomach evacuation is calculated by an exponential model (JOBLING 1981).

Food consumption rate (c_x) is a fraction of maximum food consumption rate (C_z) (Eq. 3 Table 1), with a

Table 2. Description of the variables used in Table 1 (UD refers to unpublished data).

Name	Description (unit)	Value	Based on data from
α	consumption parameter (g d^{-1})	0.16	Ikeda (1996), Hewett & Johnson (1992)
β	consumption exponent	0.75	Schmidt-Nielsen (1983), Hewett & Johnson (1992)
κ_t	daylength as a fraction of 24 hours	0-1	Skartveit and Olseth (1988)
θ	visual field angle (degrees)	30	Aksnes & Giske (1993)
σ	stomach evacuation rate (d^{-1})	2.7	Rasmussen and Giske (1994)
τ	duration of time interval (d)	5	-
ω	structural fish weight (g wet weight)	0.01-4.00	-
D	oocyte ripening time (τ)	3	-
$f_\kappa(\kappa, \sigma)$	daylength effects on consumption	0-1	-
$f_u(u_z)$	temperature effects on consumption	0-1	Hewett & Johnson (1992)
i	energy allocation rule	0 or 1	-
k_e	excretion coefficient	0.10	Rudstam (1989)
k_f	egestion coefficient	0.16	Rudstam (1989)
k_n	non-visual mortality coefficient (d^{-1})	$2.6 \cdot 10^{-3}$	-
k_v	visual mortality coefficient (d^{-1})	0.22	Rosland & Giske (1994)
L_t	larval survival	-	Lopez (1979), Schultz (1993)
N_z	prey density (ind. m^{-3})	10-680	Giske et al. (1991), UD
q_f	energy density of fish (J/g)	8685	Anonymous (1977)
q_o	energy density of oocytes (J/g)	4700	Ikeda (1996)
q_p	energy density of prey (J/g)	2500	Vijverberg & Frank (1976)
$R(\omega)$	respiration rate (J/d)	-	Ikeda (1996), Hewett & Johnson (1992)
r_z	visual range (m)	-	Aksnes & Giske (1993)
T	total number of time intervals	292	-
t	index for time interval	1-T	-
u_z	water temperature	4.82-12.68	UD
v	swimming speed (m/d)	1 fish length s^{-1}	Eggers (1977)
w_o	oocyte mass (g wet weight)	$1.4 \cdot 10^{-4}$	Melo & Armstrong (1991)
w_p	prey wet mass (g wet weight)	$1.4 \cdot 10^{-4}$	UD
X	maximum feeding intensity	10	-
x	level of feeding intensity	0-J	-
z	depth index	1-30	-

Poisson distributed probability (λ_z) with expectation equal to prey encounter rate divided by maximum food consumption capacity (p_z/C_z) (Eq. 4 in Table 1). Food consumption rate (c_x in Eq. 3) is multiplied by energy density of the prey (q_p) in order to express food consumption rate in energy units per day.

The net growth rate (g_x) (Eq. 5 in Table 1) depends on the food consumption rate (c_z), fraction egested (k_f), fraction excreted (k_e) and on the size and temperature dependent respiration rate ($R_z(\omega)$).

Survival probability (S_z) depends on visual predation rate and non-visual mortality rate (Eq. 6 in Table 1). Visual predation rate is a function of the predators visual range (r_z), and it is only functional during the period of daylight (κ_t). Non-visual mortality rate is a size dependent function (McGurk 1986).

The weight of a batch of oocytes (w_b) is calculated as a constant fraction of the structural fish weight (ω) (see lower line in Eq. 7 in Table 1). However, batch spawning cannot take place before the oocytes are ripe, and unless developmental age (δ) is equal to the ripening age for the oocytes, batch weight is set equal to zero (see upper line in Eq. 7 in Table 1). Batch fecundity (b) is calculated by dividing batch weight (w_b) with individual oocyte weight (w_o) (Eq. 8 in Table 1). Batch fecundity is size dependent due to the weight dependent batch weight (Eq. 7 in Table 1).

The dynamic state variables represent structural fish weight (ω), total energy content of the body (ε) and the age of a batch of developing oocytes (δ). The state dynamics of the variable tracking total body energy (ε) depend on the growth rate (g_x) and the amount of energy lost in reproduction (Eq. 9 in Table 1). Energy lost in reproduction is calculated by multiplying batch weight (w_b) with the energy density of oocytes (q_o).

The state dynamics of the structural fish weight (ω) depend on total body energy (ε) (Eq. 10 in Table 1). Structural fish weight (ω) may be considered as fish length expressed in weight units. Fish length is converted to fish weight by a weight-length regression established by Rasmussen & Giske (1994). It is assumed that there is a standard value for energy density (q_f) characterising a fish in a good energetic condition. Multiplying structural weight (ω) with energy density (q_f) gives a standard value of total energy content corresponding to each structural weight (ω). Structural fish weight can only increase if the new value of total energy content (ε_x in Eq. 9 in Table 1) exceeds the standard value for total body energy corresponding to the structural fish weight. If total energy content decreases below the standard value for total energy the fish is assumed to respire fat, i.e. structural weight remains unchanged (Eq. 10 in Table 1). If total energy content (ε) is less than the standard total energy content, the fish

has to resume the standard level of total energy before structural weight growth can continue (Eq. 10 in Table 1).

The state variable tracking the age of an oocyte batch (δ) depends on several factors (Eq. 11 in Table 1). The initiation of a batch is controlled by the fish (index i), but once production of a batch is initiated the process is irreversible and the fish cannot terminate the process, i. e. it continues until the batch is ripe ($\delta = D$) and spawned.

The fitness function is formulated as the net reproductive rate. The fitness ($F(\omega,\varepsilon,\delta,t,T)$) of a fish at a given state ($\omega,\varepsilon,\delta$) at a given time ($t$) is the sum of oocytes spawned added the future expected state dependent fitness of the mother ($F(\omega_x,\varepsilon_x,\delta_x,t,T)$). The value of oocytes are not equal throughout the year, but vary seasonally according to a variable (L_t) representing survival probability of larvae.

It is seen from the equations that prey encounter rate (p_z), food consumption capacity (C_z), visual mortality ($k_v r_z^2$) are functions of the habitat (z). Non-visual mortality ($k\omega^{0.25}$) is a habitat independent function, but may be controlled through weight growth.

THE SENSITIVITY ANALYSIS

According to Jørgensen (1988), the sensitivity to changes in a parameter value can be measured as the relative change in model output (V) divided by the relative change in parameter value (p). The equation of Jørgensen (1988) is modified here in order to get equal measures of sensitivity for all values of input parameters and model output variables.

The variables V_1 and V_2 in Eq. A represent the model output variables for two runs with parameter settings p_1 and p_2, respectively. In Eq. A, V_1 always represents the run with smallest output value ($V_1 \leq V_2$), and p_x always represents the smallest of the parameter values (p_1 or p_2) corresponding to the model output variables (V_1 and V_2):

$$U_x = \left(\frac{V_1 - V_2}{V_1}\right) \bigg/ \left(\frac{p_1 - p_2}{p_x}\right) \quad \text{given} \quad V_1 \leq V_2 \qquad \text{Eq. A}$$
$$\text{where} \quad p_x = \min(p_1, p_2)$$

$U_x = 0$ if the model output is insensitive to changes in the parameter value ($V_1 = V_2$). The sign of U_x indicates positive or negative correlation between parameter values and model output, and the absolute value of U_x

shows the strength of the sensitivity. When $-1 < U_x < 1$, then other processes dampen the effects from changes in the parameter value.

The physiological parameters tested for sensitivity (Tables 3; 4) are food consumption parameter (α in Table 2), stomach evacuation rate (σ in Table 2), developmental time of the oocytes (D in Table 2) and energy density of the oocytes (q_o in Table 2). The environmental variables tested for sensitivity (Tables 3; 4) are prey density(N_z in Table 2), individual prey weight (w_p in Table 2), water temperature (u_z in Table 2), non-visual mortality risk (k_n in Table 2) and visual predation risk (k_v in Table 2). For the sensitivity runs, changes in prey density and temperature involve changes in the overall values only, while the seasonal profiles (relative difference in the seasonal values) of the variables are unchanged.

The seasonality profiles in larval survival, prey density and temperature (three lower rows in Table 3) were also changed, but the sensitivity index (U_x) for these

runs was not measured, as they did not involve changes in single parameter values.

Measuring sensitivity to parameter changes is done by focusing on some essential model output variables: net reproductive rate, cumulative individual fish weight (over life), survival and habitat choice (light intensity in selected habitat) during the first, second and third year. The model results (V_p) for the different parameter values are given as fractions of the basic run (V_b) in Table 3 (i. e. V_p/V_b), while the sensitivity (U_x from Eq. A) is given in Table 4.

RESULTS

Physiological processes

Changes in the parameters for oocyte developmental time (D), energy density of oocytes (q_o) and stomach evacuation rate (σ), all have relatively moderate effects on the model output (Table 3). The sensitivity indexes are also less than one (Table 4) for all variables tested,

Table 3. The results from the different runs (V_p) given as fraction of the basic values (V_b). The three lower rows involve no changes in single parameter values, and therefore no value is given in column two.

Variable	Changed with factor	Net reproductive rate	Cumulative fish weight	Annual survival during the three years			Annual light intensity in the habitat during the three years		
				1st	2nd	3rd	1st	2nd	3rd
Development time of oocyte	0.33	2.260	0.687	1.030	0.892	0.887	1.000	1.320	1.490
	2.00	0.550	1.190	1.010	0.985	1.040	0.996	0.935	0.849
Energy density of oocytes	0.50	1.090	1.170	1.000	0.995	1.030	0.998	0.925	0.874
	2.00	0.862	0.799	1.010	0.957	0.936	1.000	1.150	1.280
Stomach evacuation	0.50	1.090	1.060	0.961	0.992	0.982	1.000	0.936	0.997
	2.00	0.697	0.761	1.090	0.974	1.050	0.994	1.250	1.120
Consumption capacity	0.67	0.157	0.111	0.972	0.783	0.820	0.938	2.500	2.900
	1.50	2.950	2.440	1.040	1.050	1.060	0.716	0.462	0.555
Prey density	0.25	0.138	0.237	0.327	0.195	0.144	2.180	4.410	6.910
	0.50	0.372	0.471	0.561	0.541	0.472	1.590	1.820	2.570
	2.00	2.280	1.650	1.700	1.570	1.780	0.586	0.619	0.483
	4.00	4.460	1.990	2.490	2.350	2.960	0.301	0.354	0.218
Individual prey weight	0.50	0.373	0.470	0.561	0.542	0.471	1.590	1.830	2.590
	2.00	2.280	1.650	1.700	1.570	1.780	0.586	0.621	0.482
Non-visual mortality	0.25	5.290	0.832	6.110	2.890	2.490	0.808	1.050	1.020
	0.50	2.840	0.939	3.090	1.950	1.840	0.915	1.000	0.971
	2.00	0.173	0.948	0.129	0.280	0.289	1.050	1.070	1.220
	4.00	0.012	0.932	0.002	0.025	0.016	1.160	1.130	1.630
Visual mortality	0.25	4.490	1.980	2.480	2.460	2.980	1.340	1.470	0.923
	0.50	2.290	1.660	1.710	1.590	1.810	1.200	1.280	0.983
	2.00	0.375	0.466	0.558	0.528	0.455	0.773	0.969	1.380
	4.00	0.133	0.224	0.324	0.185	0.130	0.537	1.140	1.780
Water temperature	0.67	0.221	0.157	1.090	0.958	0.955	0.842	1.900	2.430
	1.50	1.430	1.690	0.828	0.648	0.628	1.070	0.982	0.919
Seasonal larval survival		3.170	0.927	1.030	0.796	0.743	1.010	1.310	1.350
Seasonal prey distribution		1.780	1.490	1.250	0.742	0.640	0.525	0.898	1.010
Seasonal temperature		1.450	1.560	0.918	0.821	0.911	1.020	0.850	0.756

i.e. the changes in model output are less than the changes in parameter values. Fish weight and net reproductive rate are the most sensitive variables, while survival and habitat choice are less affected by changes in these parameters (Tables 3; 4).

Food consumption capacity (α) is the exception in having a strong influence on model results (Table 3). The sensitivity indexes (Table 4) indicate a strong effect even for small changes in this parameter, and largest effects for reductions of the parameter (Table 4). The strong effects from changes in this parameter rely on its strong influence on fish weight (Fig. 1B), which in turn affects size dependent factors like feeding rate, mortality risk, fecundity and habitat choice (Table 3). High food consumption capacity (i. e. high growth potential) enables the fish to restrict feeding to favourable seasons (Fig. 1A) with high food abundance (spring and summer). It is profitable to avoid feeding in the winter because of the low food abundance which makes growth costly in terms of visual predation risk.

The reduced winter mortality is partly countered by increased visual predation risk in the summer (Fig. 1C), due to higher feeding potential and feeding rates at this time (Fig. 1A). Total annual survival is, therefore, at about the same level as in the basic run (Table 3). The large increase in fish weight and fecundity, however, increases the net reproductive rate (Table 3) and the value of future reproductions (Fig. 1D) compared to the basic run.

Reduced food consumption capacity reduces the growth potential and the flexibility for seasonal feeding. The fish has to keep feeding rates higher in the winter (Fig. 1A) to avoid starvation and to support energy for oocyte production during the following year. Seasonal patterns in mortality are less clear (Fig. 1C). Peaks in mortality are evident in the winter, partly because reduced prey abundance makes feeding more costly, and partly because the fish stays in more illuminated waters to increase feeding rate (Table 3). Annual survival is less than in the basic run (Table 3), and com-

Table 4. The sensitivity index (U_x in Eq. 1) for the different runs involving changes in single parameters. The sensitivity index measures the relative difference in model output relative to the relative difference in parameter value.

| Variable	Changed with factor	Net reproductive rate	Cumulative fish weight	Annual survival during the three years			Annual light intensity in the habitat during the three years		
				1st	2nd	3rd	1st	2nd	3rd
Development	0.33	-0.619	0.224	-0.012	0.060	0.062	0.000	-0.158	-0.241
time of oocyte	2.00	-0.819	0.189	0.008	-0.015	0.045	-0.004	-0.070	-0.177
Energy density	0.50	-0.094	-0.168	-0.001	0.005	-0.034	0.002	0.081	0.145
of oocytes	2.00	-0.160	-0.251	0.014	-0.045	-0.069	0.000	0.149	0.284
Stomach	0.50	-0.086	-0.059	0.040	0.008	0.019	-0.002	0.068	0.003
evacuation	2.00	-0.434	-0.314	0.092	-0.027	0.046	-0.006	0.247	0.118
Consumption	0.67	10.900	16.200	0.058	0.561	0.445	0.135	-3.050	-3.860
capacity	1.50	3.910	2.890	0.077	0.098	0.117	-0.795	-2.330	-1.600
Prey	0.25	2.090	1.070	0.687	1.370	1.990	-0.393	-1.140	-1.970
density	0.50	1.680	1.120	0.782	0.850	1.120	-0.590	-0.817	-1.570
	2.00	1.280	0.649	0.703	0.569	0.776	-0.706	-0.615	-1.070
	4.00	1.150	0.329	0.498	0.451	0.655	-0.774	-0.609	-1.200
Individual	0.50	1.680	1.130	0.784	0.845	1.120	-0.589	-0.825	-1.590
prey weight	2.00	1.280	0.655	0.703	0.565	0.780	-0.706	-0.610	-1.080
Non-visual	0.25	-1.430	0.067	-1.700	-0.629	-0.497	0.079	-0.015	-0.006
mortality	0.50	-1.840	0.064	-2.090	-0.955	-0.836	0.093	0.000	0.030
	2.00	-4.780	-0.055	-6.740	-2.570	-2.460	0.053	0.067	0.215
	4.00	-26.700	-0.024	-154.000	-13.000	-20.000	0.052	0.042	0.210
Visual	0.25	-1.160	-0.328	-0.494	-0.485	-0.661	-0.113	-0.157	0.028
mortality	0.50	-1.290	-0.663	-0.713	-0.592	-0.806	-0.195	-0.282	0.017
	2.00	-1.670	-1.150	-0.792	-0.894	-1.200	-0.294	-0.032	0.381
	4.00	-2.180	-1.150	-0.696	-1.470	-2.240	-0.287	0.045	0.259
Water	0.67	7.140	10.900	-0.184	0.089	0.095	0.380	-1.820	-2.900
temperature	1.50	0.860	1.380	-0.415	-1.090	-1.190	0.147	-0.037	-0.176
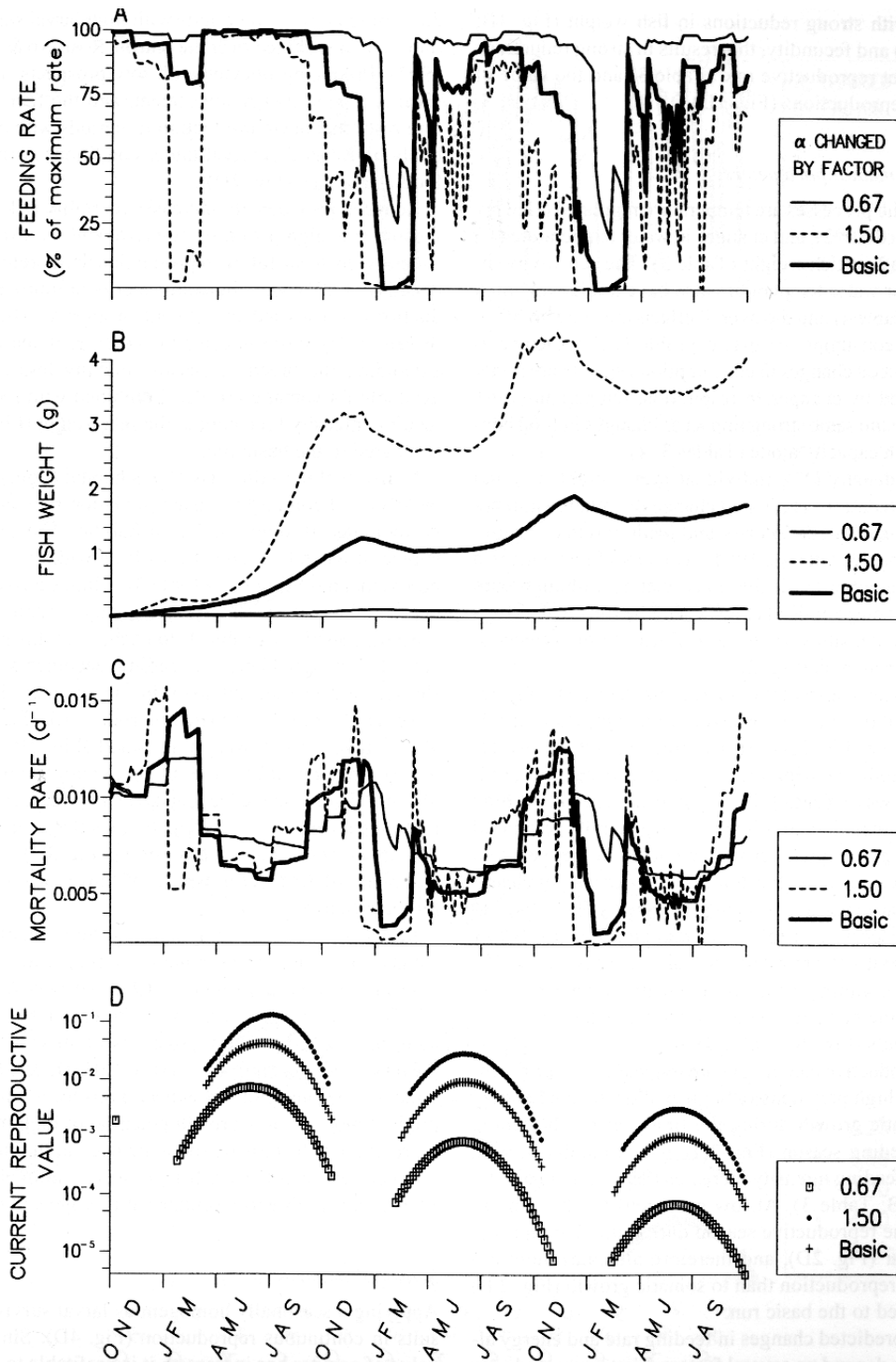
Figure 1. Average seasonal values in: A: feeding rate as percentage of maximum potential food consumption rate (100*c_x/C_z in Table 1) B: fish weight (g), C: mortality rate (d^{-1}) and D: current reproductive value, for basic run and for variations in the food consumption capacity (changed with the factor given in the figure legend)

bined with strong reductions in fish weight (Fig. 1B; Table 3) and fecundity, this results in strong reductions in the net reproductive rate (Table 3) and the value of future reproductions (Fig. 1D).

Environmental parameters

Metabolic processes are temperature regulated (HEWETT & JOHNSON 1992), and changes in water temperature (u_z) clearly affect fish weight (Table 3). The sensitivity indexes for water temperature also have a relatively high value (Table 4) and the overall effects are comparable to those of consumption capacity (Table 3). Since temperature induced changes in consumption capacity are partly countered by changes in respiration, temperature does not have the same strong impact as changes in food consumption capacity alone (Tables 3; 4).

Prey density (N_z), individual prey weight (w_p) and visual predation risk (k_v) all change the relationship between visual predation risk and feeding rate (μ/f ratio; cf. WERNER & GILLIAM 1984). The model responds in a similar manner to all these parameters, although with different magnitude (Tables 3; 4). The runs with different prey densities are used to illustrate the effects of these parameters (Fig. 2).

The seasonal patterns in feeding rate generally resemble those in the basic run, although some differences exist (Fig. 2A). At low prey density the fish reduces feeding during the first winter, because mortality risk when feeding (μ/f) is too high to allow high growth rates. Feeding intensity is generally less in all seasons at low prey density compared to the basic run (Fig. 2A), due to high μ/f ratios, and fish weight clearly shows large variations with prey density (Fig. 2B; Table 3). Because of relatively higher μ/f ratios at low prey density, the mortality risk also increases (Fig. 2C; Table 3), although feeding intensity is generally less than in the basic run. High prey density has the opposite effects (Fig. 2C; Table 3).

Reproductive patterns are also dependent on prey density. At high prey density the fish allocate more energy to somatic growth during the first year by shortening the breeding season (Fig. 2D), which combined with higher feeding intensity increases fish weight markedly (Fig. 2B; Table 3). At low prey density, the fish extends the reproductive season during the first and second year (Fig. 2D), and therefore allocates more energy to reproduction than to somatic growth (Fig. 2 B) compared to the basic run.

The predicted changes in feeding rate and energy allocation depend on several factors. First, increased prey density reduces the mortality risk when feeding (i.e. low μ/f ratio), making growth less costly. Large size also increases fecundity and enables the fish to produce more oocytes in periods with high larval survival (normally distributed over the season, ROSLAND & GISKE 1997). Producing oocytes with low prospects of survival is a poor energy investment, and the fish therefore restricts oocyte production to periods with a relatively high larval survival under conditions with high food abundance (Fig. 2D).

Reduced prey density increases mortality risk when feeding (i.e. high μ/f ratio). Survival and the expected fitness gain from future reproduction is therefore reduced (Fig. 2D), and allocating energy to future reproductions is a wasted investment of energy. The fish, therefore, lay more oocytes in the current season by expanding the breeding season, making less energy available for somatic growth. Combined with reduced feeding intensity this reduces the fish weight (Fig. 2B) compared to the basic run.

Non-visual mortality risk (k_n) is habitat (light) independent and contrary to visual predation risk, can not be regulated through choice of habitat. The optimal choice of habitat actually varies little with changes in non-visual mortality risk (Table 3), while survival and net reproductive rate shows large changes (Table 3) and a strong sensitivity (Table 4) to changes in this parameter. The winter check in feeding becomes slightly shorter, and feeding intensity in the summer slightly lower at increased non-visual mortality risk (Fig. 3A). The changes in fish weight are small (Fig. 3B; Table 3), and are a result of different energy allocation (Fig. 3D) and changes in the feeding intensity (Fig. 3A). Similar to the changes in prey density, the allocation of energy to somatic or reproductive tissue (Fig. 3D) changes as a result of different prospects of future survival and reproduction.

Larval survival (L_t) is assumed to be normally distributed over the season in the basic run, with a maximum around mid June (SCHULTZ 1993; ROSLAND & GISKE 1997), and oocytes laid far from the optimal hatching date, therefore, have low prospects of survival. It is, however, evident from Figs 1B, D; 2B, D; 3B, D that under conditions with low expectations from future reproductions (i. e. low growth potential or high mortality risk) the fish starts reproducing even in the first autumn at very small sizes. It is, however, unlikely that *M. muelleri* is able to reproduce at this age and size.

Seasonal patterns

Applying a seasonally homogenous larval survival results in continuous reproduction (Fig. 4D). Since the value of oocytes has increased, it is profitable to invest energy into current reproduction rather than to somatic weight, and the fish begin breeding in the first autumn.
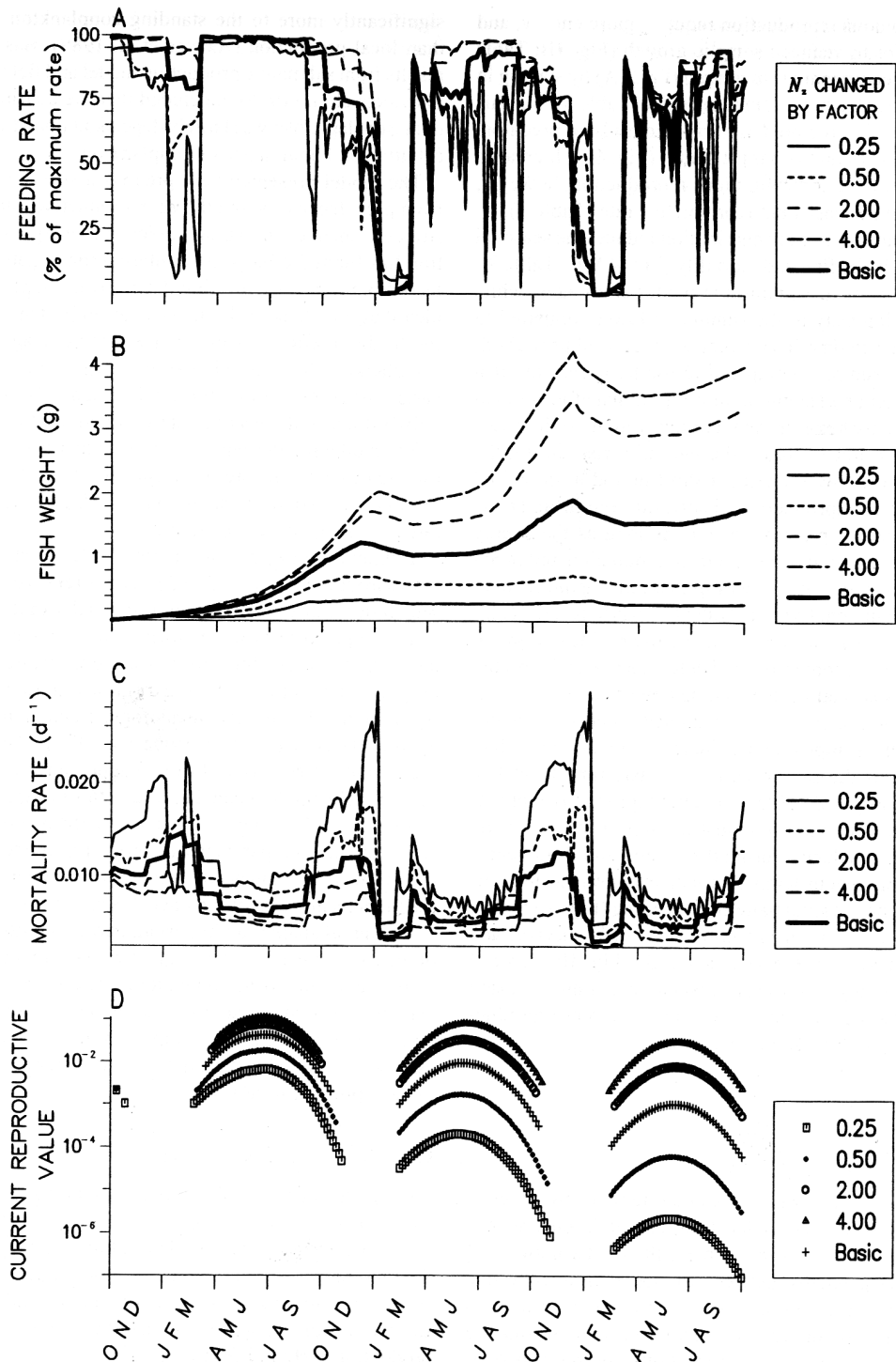
Figure 2. Average seasonal values in: A: feeding rate as percentage of maximum potential food consumption rate ($100*c_x/C_z$ in Table 1) B: fish weight (g), C: mortality rate (d^{-1}) and D: current reproductive value, for basic run and for variations in the prey biomass (changed with the factor given in the figure legend)

Continuous reproduction requires more energy, and is paid for by reduced somatic growth (Fig. 4B; Table 3). The feeding rate is increased (Fig. 4A) by staying in habitats with a higher light intensity (Table 3), but this also increases the predation risk from visual predators during the second and third winter (Fig. 4C). Increased larval survival and continuous reproduction, however, results in increased net reproductive rate (Table 3).

A homogenous prey distribution reduces the seasonal patterns in feeding and mortality (Figs 4A, C; Table 3). The fish feed throughout the winter at all ages, while feeding intensity in the summer is lower compared to the basic run (Fig. 4A). Because of reduced prey abundance in summer, compared to the basic run, the fish compensate by staying in more illuminated water (Table 3). This helps in maintaining a high feeding rate (Fig. 4A), but increases the mortality risk during the summer (Fig. 4C). During a short period in the initial phase of the reproductive season both feeding and mortality rates drop (Figs 4A, C). As long as the energy reserves can support both oocyte production and metabolic demands, this is a way of maximising the chances of reproduction. Eventually the fish has to resume feeding again to avoid starvation and to provide energy for continued reproduction, and enters habitats with higher light intensity and better feeding opportunities (Fig. 4A) later in the summer. The fish allocate energy to oocytes during the summer, and switches to somatic growth in the end of the season as in the basic run. Total fish weight (Fig. 4B; Table 3) and net reproductive rate increase at a homogenous distribution (Table 3), while survival is reduced during the second and third year.

A homogenous temperature distribution has little effect on the seasonal patterns in feeding (Fig. 4A), mortality (Fig. 4C), reproduction (Fig. 4D), survival and habitat choice (Table 3). Fish weight (Fig. 4B; Table 3) and fecundity increase at constant temperature causing net reproductive rate (Table 3) and current reproductive values (Fig. 4D) to increase.

DISCUSSION

Population effects

Net reproductive rate represents life time reproductive success of the fish under different conditions. Within the range of values tested here, the model indicates a strong dependence between the net reproductive rate and variables, such as non-visual (k_n) and visual (k_v) mortality risk and prey density (N_z) (Table 3), that are related to the processes of mortality and prey encounter.

Advective processes are important for the transportation of zooplankton into fjords, and may contribute significantly more to the standing zooplankton stock than local production (AKSNES et al. 1989). Based on results from a dynamic production model and field data, SALVANES et al. (1995) concluded that the distribution of mesopelagic fish was largely dependent upon the distribution and abundance of zooplankton.

The model presented here predicts a strong impact from prey density (N_z) on the net reproductive rate, and strategic changes in habitat choice and energy allocation has limited effects in countering the negative effects from reduced prey abundance. This supports the idea that zooplankton biomass is an important factor for the distribution and abundance of mesopelagic fish. Zooplankton biomass also shows large inter-annual variations (GISKE et al. 1991), which may also potentially influence the year to year production of the fish.

The model predictions may indicate that the life history selected for in the basic run (ROSLAND & GISKE 1997) is optimal (sustainable) only at a high food input rate (i.e. in an advective regime).

Temperature (u_z) also has a noticeable effect on the net reproductive rate (Table 3), with a relatively high sensitivity index (Table 4). Inter-annual variations in water temperature, however, do not show the same variations as e.g. prey abundance, and are therefore probably not as important as a regulating factor on populations. Temporary physiological adaptations or acclimatisation (SCHMIDT-NIELSEN 1983) may also dampen the effects from shifting temperatures over the seasons. The model is unable to account for acclimatisation, since the temperature dependent functions are run with constant parameter settings. The model may, therefore, overestimate the effects from temperature fluctuations in the environment (MCKEE & EBERT 1996).

The larval stage is an important part of the life cycle of the fish, especially when considering the recruitment of pre-juveniles to the population. The larval period was, however, omitted from the model, because this stage is not well studied and the sub-models for processes would probably have to be modified for the model to be applicable to larvae.

Strategies in different environments

Through the choice of depth (habitat) the fish can balance growth (fecundity) and survival in a way that maximises net reproductive rate. The optimal strategy when the ratio between visual predation risk and feeding (μ/f) is high, is to trade growth (weight and fecundity) for survival (Table 3), and to allocate more energy to reproduction early in life (Fig. 2D).

The current model for visual mortality implies that predation risk increases with fish size, i.e. larger prey objects are more likely to be detected (EGGERS 1977;
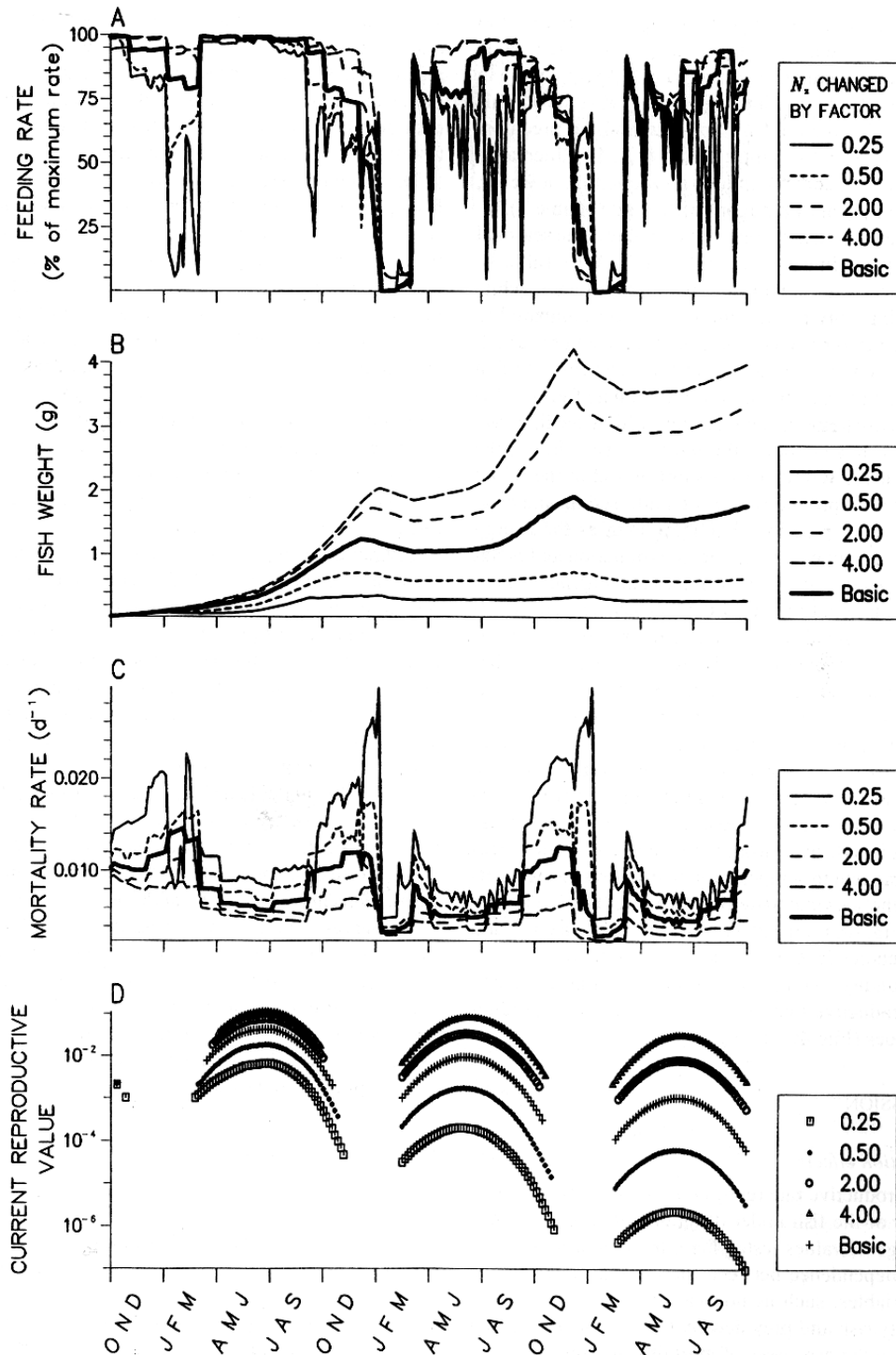
Figure 3. Average seasonal values in: A: feeding rate as percentage of maximum potential food consumption rate ($100*c_x/C_z$ in Table 1) B: fish weight (g), C: mortality rate (d^{-1}) and D: current reproductive value, for basic run and for variations in the non-visual mortality rate (changed with the factor given in the figure legend)

AKSNES & GISKE 1993). Visual capability is also assumed to increase with fish size (BRECK & GITTER 1983; AKSNES & GISKE 1993). Small fish therefore experience less visual mortality risk than larger fish at the same light intensity, but small fish also have to stay in more illuminated water to achieve the same prey encounter rate as a larger fish. Thus, considering visual processes only, the positive effects from reduced visual mortality risk at small size is countered by reduced visual capability. Large fish, however, still need more energy than small fish, and therefore, have to expose themselves more to visual predation in order to sustain metabolic requirements.

The model predicts reduced adult fish weight when the ratio between mortality and growth (μ/g) increases, and this relies on several factors. Because growth is more costly in terms of visual predation, the trade-off between growth and survival trends towards survival. Since the increased visual predation risk reduces the future prospects of survival and reproduction, the reproductive efforts are invested into current rather than into future reproductions (i.e. somatic growth). Also, because large size implies a higher visual predation risk, there is a disadvantage in being large and therefore, a selection towards smaller fish. An alternative strategy could be to grow out of the predator regime, although this option is not included in this model, and would probably require sizes that are far out of range for *M. muelleri*.

Longevity also seems to vary between different locations (GJØSÆTER 1981; IKEDA 1994), and may be a result of different prey-predator regimes. Depending on how the mortality affects the different age/size groups of the fish, the optimal timing of reproduction and allocation of energy may differ. Future survival and thus longevity may be influenced by the energy allocation patterns chosen by the fish, i.e. by altering the energy investment among future (somatic allocation) and current reproduction (WILLIAMS 1966). The model predicts different energy allocation between current reproduction and somatic growth under changing ratios of prey abundance and visual mortality risk (Fig. 2D; Table 3).

Differences in somatic condition and reproductive energy allocation was also observed between fish from fjords (Herdlefjorden and Masfjorden, western Norway) with different predator abundance (BJELLAND 1995). The population with the highest density of predators allocated more energy to reproduction early in life.

Seasonality

Considering the relatively large seasonal fluctuations in prey biomass, light conditions and surface temperatures in Norwegian fjords, it seems reasonable to assume that the life history of *M. muelleri* is adapted to these seasonal patterns in the environment.

The predicted responses when the seasonality in prey biomass and larval survival was excluded from the model support this view, but it seems that both factors have to be present in order to maintain the seasonal patterns in feeding and reproduction.

Homogeneous larval survival increases the value of oocytes, and makes oocyte production a profitable energy investment during all seasons. The seasonality in feeding is still present, although the fish feeds sporadically during the winter to support energy for oocyte production. Continuous reproduction was observed in the Benguela ecosystem off Southern Africa by PROSCH (1991) although there was a seasonal distribution in reproductive intensity (i.e. observed abundance of eggs).

Making prey biomass homogeneous throughout the season diminishes the differences between summer and winter abundance of prey. Due to higher prey abundance in the winter, feeding becomes less costly in terms of predation risk. It is therefore profitable to keep feeding rates high enough to ensure positive growth during the winter. The drop in feeding and mortality at the start of the reproductive season is a method of maximising survival to reproduction. The response may also be triggered by the lacking spring bloom in prey biomass (homogenous), which makes feeding more costly compared with the basic run. The fish therefore respire and reproduce on energy reserves until these are depleted and the fish are forced to start feeding to avoid starvation.

A seasonal distribution in temperature seems to have little influence on the patterns of feeding and reproduction. It does, however, increase fish weight as a result of temperature dependent metabolic changes. The low response to changed temperature profiles may seem strange, considering the strong effects from changes in the overall temperature (Tables 3; 4). The reason is that the seasonal changes in temperature occur primarily in the upper (30-50 m) water masses, and remain relatively stable below. Therefore, on average the temperature from the surface to about 300 m depth in Norwegian fjords does not change much over the season.

Physiology

Except for food consumption capacity (α), the physiological parameters tested seem to have little influence on the predicted strategies (Table 3). They do, however, have effect on fish weight and net reproductive rate, and if accurate predictions of biomass production and population abundance are important, one should be aware of these parameters and obtain better estimates of them.
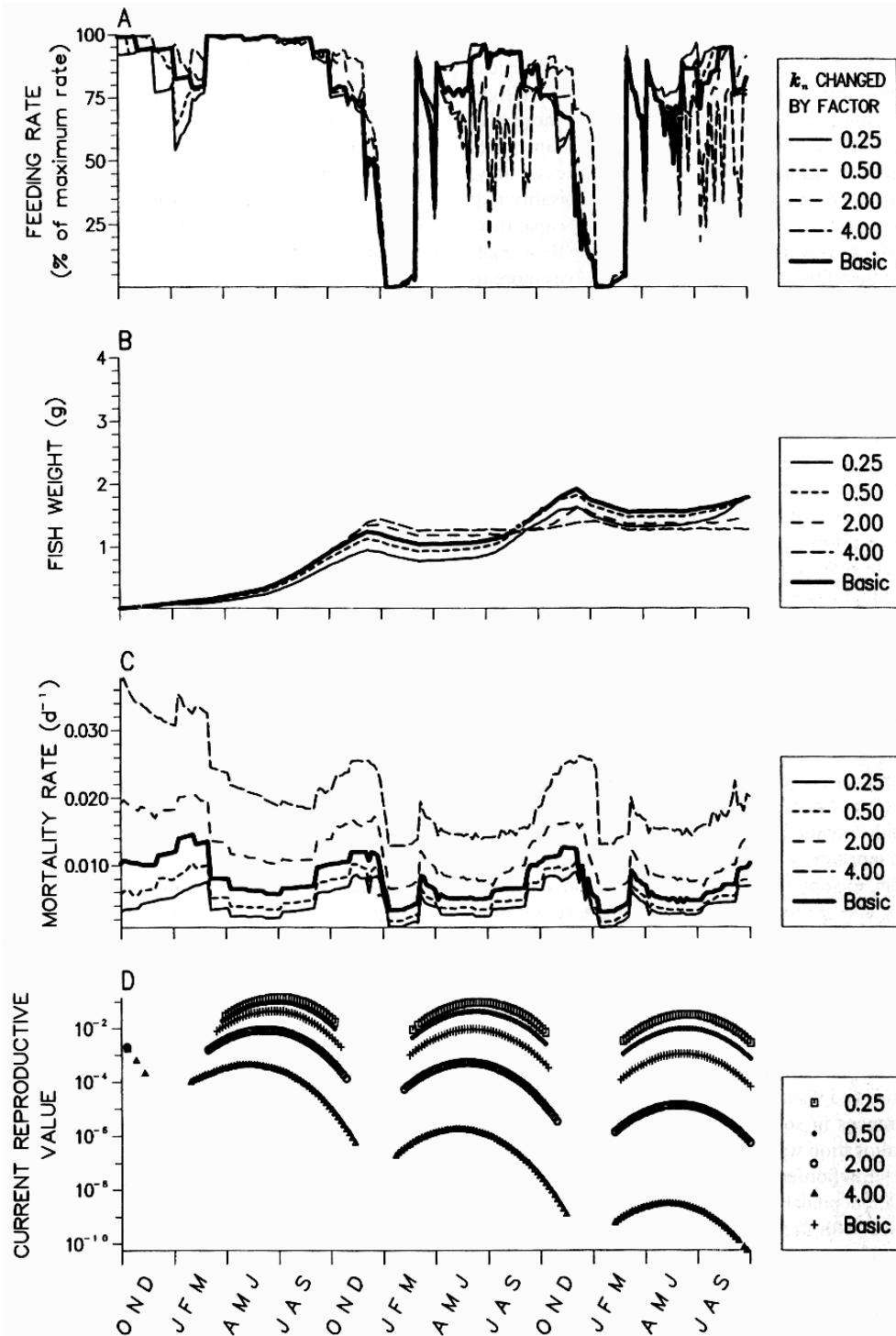
Figure 4. Average seasonal values in: A: feeding rate as percentage of maximum potential food consumption rate ($100*c_x/C_z$ in Table 1) B: fish weight (g), C: mortality rate (d^{-1}) and D: current reproductive value, for basic run and for changes in the seasonal profiles of larval survival, prey biomass and water temperature with figure legends L, P and T, respectively.

The food consumption parameter (α) is somehow unique amongst the physiological parameters because it affects both the internal energy budget of the fish (growth potential) and the ability to utilise different habitats (consumption potential). A different growth potential opens for different growth and developmental patterns, and potentially allows for a different life history strategy to take place (i.e. seasonal growth, reproductive timing and weight at maturity). Food consumption capacity also affects the ability to utilise different habitats, for example increased consumption capacity enables the fish to enter habitats with higher prey encounter rate. Alternations of the food consumption capacity therefore have the potential to change life history strategy of the fish through new patterns of development and habitat preferences. The ecological interpretation of this may be that relatively small changes in physiology or morphology can be sufficient to change a life history.

Life history – size dependent variations

In previous works focus has been on the differences between juvenile and adult habitat profitability (GISKE et al. 1990; GISKE & AKSNES 1992; ROSLAND & GISKE 1994; GOODSON et al. 1995), and the need to shorten generation time as motivational factor in the juvenile strategy (AKSNES & GISKE 1990; GISKE & AKSNES 1992; ROSLAND & GISKE 1994).

The present model includes no threshold weight for maturity to force juvenile growth. Therefore there are no juvenile fish in the model, only different size groups of fish. However, the differences in strategies between small and large fish persist. Size dependent processes in prey encounter and mortality may, therefore, be sufficient to explain the observed differences in depth preference between small and large fish.

The size dependent processes in prey encounter, growth and visual predation risk will cause large fish to experience relatively higher visual predation risk when feeding than small fish. Because large fish need more energy to satisfy metabolic requirements they have to expose themselves to relatively higher light intensity, and thus higher visual predation risk. The weight specific respiration also decreases with fish weight, and large fish therefore potentially have better ability to withstand periods with a low energy intake than small fish. The combined effects from size dependent respiration, predation and feeding make it profitable for large fish to minimise predation risk in winter rather than maximising growth and fecundity. For small fish, however, the reproductive gains from increased weight and fecundity will be higher than the predation costs fol-

lowing this strategy, and high growth in winter is the best strategy. Due to a relatively higher respiration rate, small fish also face a higher risk of starvation by reduced food intake during the winter. The 'high winter growth' strategy is clearly dependent on the ratio between visual predation risk and feeding rate (μ/f), and even small fish cease feeding in winter at high μ/f ratios (e.g. low prey density in Fig. 2).

This result is not in conflict with the assumption that juveniles benefit from growth when this may shorten generation time (AKSNES & GISKE 1990; GISKE & AKSNES 1992; ROSLAND & GISKE 1994). It only shows that other mechanisms may be participating in shaping the observed life history patterns of *M. muelleri*.

The maturity threshold was omitted here because the literature indicates that the weight at maturity is a plastic trait for *M. muelleri* (GJØSÆTER 1981; PROSCH 1991; RASMUSSEN & GISKE 1994; BJELLAND 1995; GOODSON et al. 1995). Plasticity in size and age at maturity (STEARNS & CRANDALL 1984; STEARNS 1992) is a way of maximising reproductive output under varying conditions, like in some of the runs here, where the model predicts early maturation at small sizes (Figs 1D; 2D; 3D). Whether *M. muelleri* is capable of reproducing at the weights and ages predicted here is, however, unlikely, and the interpretation of the results may rather be that a smaller and short-lived organism like an Euphausiid or a jellyfish would do better under certain conditions.

The strong impact from visual predation risk on, for example fish weight, also indicates the importance of top-down control in the formation of life histories. It is, however, important to remember that the model only considers visual predation risk as a function of visual processes, and does not account for size selection.

The results presented and discussed above indicate that there are many potential factors that participate in shaping the life history of *M. muelleri*. Both seasonal and non-seasonal factors in the environment as well as physiological variables seem to influence the predicted patterns in habitat choice, energy allocation and reproduction. Large efforts should be put into the study of biological processes, both physiological and environmental, in order to improve our understanding of the dynamics of fish populations and factors influencing their individual behaviour.

REFERENCES

Aksnes, D.L., J. Aure, S. Kaartvedt, T. Magnesen, & J. Richards 1989. Significance of advection for the carrying capacities of fjord populations. – *Marine Ecological Progress Series* 50:263-274.

Aksnes, D.L. & J. Giske 1993. A theoretical model of aquatic visual feeding – *Ecological Modelling* 67:233-250.

Anonymous 1977. Laksesild. – *Fiskets Gang* 2/77. 51-52.

Bjelland, O. 1995. *Life-history tactics of two fjord populations of Maurolicus muelleri*. – Cand.scient. thesis, University of Bergen, Department of Fisheries and Marine Biology. 42 pp.

Breck, J.E. & M.J. Gitter 1983. Effects of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. – *Canadian Journal of Fisheries and Aquatic Sciences* 40:162-167.

Clarke, T.A. 1982. Distribution, growth and reproduction of the lightfish *Maurolicus muelleri* (Sternoptychidae) off South-East Australia. – *CSIRO Marine Laboratories* Report 145. 10 pp.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. – *Ecology* 58:46-59.

Giske, J. & D.L. Aksnes 1992. Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*. – *Sarsia* 77:253-261.

Giske, J., D.L. Aksnes, B.M. Baliño, S. Kaartvedt, U. Lie, J. T. Nordeide, A.G.V. Salvanes, S.M. Wakili, & A. Aadnesen 1990. Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. – *Sarsia* 75:65-81.

Giske, J., D.L. Aksnes, U. Lie, & S.M. Wakili 1991. Computer simulation of pelagic production in Masfjorden, Western Norway, and its consequences for production of released 0-group cod. – *ICES Marine Sciences Symposium* 192:161-175.

Gjøsæter, J. 1981. Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in Norwegian waters. – *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 17:109-131.

Goodson, M., J. Giske & R. Rosland 1995. Growth and ovarian development of *Maurolicus muelleri* during spring. – *Marine Biology* 124:185-195.

Hewett, S.W., & B.J. Johnson 1992. *An upgrade of a generalized bioenergetics model of fish growth for microcomputers*. – University of Wisconsin, Wisconsin Sea Grant College Program, Sea Grant Technical Report, WIS-SG-92-250, Madison.

Houston, A., C. Clark, J.M. McNamara & M. Mangel 1988. Dynamic models in behavioural and evolutionary ecology. – *Nature (London)* 332:29-34.

Ikeda, T. 1994. Growth and life cycle of the mesopelagic fish *Maurolicus muelleri* (sternoptychidae) in Toyoma Bay, Southern Japan Sea. – *Bulletin of Plankton Society of Japan* 40:127-138.

— 1996. Metabolism, body composition, and energy budget of the mesopelagic fish *Maurolicus muelleri* in the Sea of Japan. – *Fishery Bulletin* 94:49-58.

Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. – *Journal of Fish Biology* 19:245-257.

Jørgensen, S.E. 1988. *Fundamentals of ecological modelling*. – Elsevier, Amsterdam.

Lopez, P.D.C. 1979. Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. – *Sarsia* 64:199-210.

Mangel, M. & C. Clark 1986. Towards a unified foraging theory. – *Ecology* 67:1127-1138.

— 1988. *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, NJ. 308 pp.

McGurk, M.D. 1986. Natural mortality of marine fish eggs and larvae: role of spatial patchiness. – *Marine Ecology Progress Series* 34:227-242.

McKee, D & D. Ebert 1996. The interactive effects of temperature, food level and maternal phenotype on offspring size in *Daphnia magna*. – *Oecologia* 107:189-196.

Melo, Y.C. & M.J. Armstrong 1991. Batch spawning behaviour in lightfish *Maurolicus muelleri*. – *South African Journal of Marine Science* 10:125-130.

Prosch, R.M. 1991. Reproductive biology and spawning of the myctophid *Lampanyctes hectoris* and the sternoptychid *Maurolicus muelleri* in the southern Benguela system. – *South African Journal of Marine Science*. 10:241-252.

Rasmussen, O.I. & J. Giske 1994. Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. – *Marine Biology* 120:649-664.

Rosland, R. & J. Giske 1994. A dynamic optimization model for the diel vertical distribution of a pelagic planktivorous fish. – *Progress in Oceanography* 34:1-43.

— 1997. A dynamic model for the life history of a pelagic planktivore. – *Fisheries Oceanography* 6:19-34.

Rudstam, L.G. 1989. Exploring the dynamics of herring consumption in the Baltic: applications of an energetics model of fish growth. – *Kieler Meeresforschungen. Sonderheft* 6:312-322.

Salvanes, A.G.V., D. Aksnes, J.H. Fosså, & J. Giske 1995. Simulated carrying capacities of fish in Norwegian fjords. – *Fisheries Oceanography* 4:17-32.

Salvanes, A.G.V. & B.M. Stockley 1996. Spatial variation of growth and gonadal developments of *Maurolicus muelleri* in the Norwegian Sea and in a Norwegian fjord. – *Marine Biology* 126:321-332.

Schmidt-Nielsen, K. 1983. *Animal physiology: adaptation and environment, 3rd. edn* – Cambridge University Press, Cambridge. 619 pp.

Schultz, E.T. 1993. The effect of birth date on fitness of female dwarf pearch, *Micrometrus minimus*. – *Evolution* 47:520-539.

Skartveit, A. & Olseth, J. A. (1988). *Varighetstabeller for timevis belysning mot 5 flater pa 16 norske stasjoner*. – Meteorological Report Series 7, Universitetet i Bergen. 136 pp.

Stearns, S.C. 1992. *The evolution of life histories.* – Oxford University Press. Oxford. 249 pp.

Stearns, S.C. & R.E. Crandall 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. – Pp. 13-33 in: Potts, G.W. & R.J. Wootton (eds). *Fish reproduction, strategies and tactics.* Academic Press Inc., London.

Vijverberg, J. & T.H. Frank 1976. The chemical composition and energy contents of copepods and cladocerans in relation to their size. – *Freshwater Biology* 6:333-345.

Weiss, G., G. Hubold & A. C. Bonecker 1988. Eggs and larvae of *Maurolicus muelleri* (Gmelin, 1789) (Teleostei, Sternoptychidae) in the southwest Atlantic. – *Meeresforschung* 32:53-60.

Werner, E.E. & J.F. Gilliam 1984. The ontogenetic niche and species interactions in size-structured populations. – *Annual Revue of Ecology and Systematics* 15:393-425.

Williams, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. – *American Naturalist* 100:687-690.

Young, J.W. & S.J.M. Blaber 1986. Feeding ecology of three species of midwater fishes associated to the continental slope of eastern Tasmania, Australia. – *Marine Biology* 93:147-156.

Young, J.W., S.J.M. Blaber & R. Rose 1987. Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. – *Marine Biology* 95:323-332.