

Vertical distribution and population dynamics of copepods by dynamic optimization

Øyvind Fiksen and Jarl Giske

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Vertical distribution and population dynamics of copepods are viewed as a consequence of individual maximization of reproductive value (RV). RV for all individuals of all size classes (stages) and conditions (physiological states) is found by dynamic programming, and specifies a trajectory of optimal habitats in time and space. The optimal habitat is found by balancing the risk of predation and growth. Predation risk from visually searching planktivores is included as a mechanistic submodel, and growth is a function of individual size, food concentration, temperature, and energetic costs of migratory behaviour. The optimal policy followed by single individuals eventually gives rise to the population dynamics, based on individual mortality and reproduction rates. The model focuses on the role of temperature, predators, and food resources on dynamics and distribution, and shows that food can affect predation risk through both physiological and physical mechanisms. In fact, increased food concentration may influence dynamics more through reduced predation than through increased growth, because the planktivores' searching efficiency is very sensitive to increased turbidity. This effect is suggested as a potentially important factor in the survival of planktonic organisms susceptible to visually searching predators, and may be most beneficial to macrozooplankton and fish larvae. The optimal copepod response (vertical migration) to increased density of planktivores is to seek less risky habitats, and therefore the predation risk of copepods is a non-linear function of planktivore density. The model suggests that optimal diel migration intensity is changed with food density from no migration at low food levels, reaches a maximum at intermediate levels, but is reduced again at high algal concentrations.

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Key words: copepods, diel vertical migration, dynamic optimization, modelling, population dynamics, predation, zooplankton behaviour.

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Introduction

The scope of the present work is to build a dynamic optimization model for the vertical distribution of a general copepod. The model is an attempt to extend those of Clark and Levy (1988), Mangel and Clark (1988), and Rosland and Giske (1994) by (a) taking the whole life cycle and a range of body sizes into consideration, (b) increasing the resolution of predation risk to include also non-visually searching predators, and (c) using reproductive value as the optimization criterion and thus relating fitness directly to the number of eggs laid in the simulated time period. Specifically, the question of how food, temperature, and predation influence the distribution and dynamics of a copepod population are discussed. Further, the current interest in

the population consequences of individual behaviour and habitat selection (e.g. Rosenzweig, 1991; Werner, 1992) calls for models capable of incorporating both behaviour and dynamics. Much work has been done on the dynamics of structured populations (e.g. DeAngelis and Gross, 1992; De Roos *et al.*, 1992), but not with behaviour derived from maximization of fitness.

The pelagic habitat is generally characterized by pronounced vertical gradients of light, predators, food, and temperature, and thus also of growth and mortality risk. Population dynamics depend on where in the water column the individuals live, or, rather, on the integrated effects of the environment on the vertical path each individual has followed through life. Pelagic ecosystem models and simulations of population dynamics should therefore account for the vertical behaviour of the

population. However, behaviour is seldom included in these models, and, if it is, only at a very simplistic level, decoupled from maximization of fitness.

Dynamic programming has lately been widely used in behavioural ecology (e.g. Mangel and Clark, 1986, 1988; McNamara and Houston, 1986; Houston *et al.*, 1988, 1993; Clark and Levy, 1988; Sargent, 1990; Burrows and Hughes, 1991; Bouskila and Blumstein, 1992; Rosland and Giske, 1994). This approach makes it possible to predict optimal habitats over several time scales for animals trading off predation risk and growth, to include important life history characteristics and to account for short-term behaviour like avoiding starvation. Thus, vertical distribution (or other behavioural actions) in dynamic optimization models not only depends on physical or biological properties of the environment, but also on the life-history pattern of the species and the age and internal state of the animal.

Optimality models of life cycles and spatial distributions require two kinds of theories: functional models to relate life-history variables to fitness, and mechanistic models to describe spatial patterns in variables influencing life-history traits. During the last decade, life-history theory (LHT) has evolved from a descriptive study of population dynamic variables to a predictive tool for individual behaviour. LHTs can provide direct relationships between traits like generation time, fecundity, and survivorship and fitness, and models of the evolutionary basis of animal motivation have been developed (Stearns, 1992; Roff, 1992). The required mechanistic models of fecundity and generation time as functions of environmental variables have been experimentally developed for several species, but the relation between the environment and zooplankton mortality (starvation and predation risk) has received little attention from marine ecologists (Miller and Tande, 1993).

Vertical distribution of zooplankton has earlier been described as habitat selection resulting from trade-offs, e.g. temperature-dependent physiological effects on body size (fecundity) and generation time (McLaren, 1963) or feeding versus predation risk (Johnsen and Jakobsen, 1987; Clark and Levy, 1988; Aksnes and Giske, 1990). Some preceding models, like those of McLaren (1963) and Aksnes and Giske (1990), are based on fitness maximization from life-history equations. As this concept yields the same optimum for all animals in an age group or animals in a certain developmental stage, it is called static optimization. Static optimizations do not incorporate the dynamic dependency of optimal policy on animal state and the environment, and ignore short-term motivation. Neither do static optimization techniques account for the flexible behaviour expected from natural selection acting to maximize lifetime reproductive rate (fitness), i.e. such techniques may not result in the true optimal policy followed by an animal with full information (e.g. genetic) of all factors

relevant to its fitness (but see Leonardson, 1991). Thus, the application of life-history-derived rules is in danger of producing wrong predictions due to ignorance of short-term motivation, which is likely to influence behaviour (Metcalfe and Furness, 1984; Milinski, 1985; Jakobsen *et al.*, 1988; Giske and Aksnes, 1992).

Model

A stage- and size-structured model of optimal habitat selection in a continuum of habitats is presented. The resulting population dynamics of copepods obey the unified foraging theory (Mangel and Clark, 1986) in an environment changing only with respect to irradiance. The model is based on processes at the individual level, and some processes also depend on the general condition of each individual. Most important, the chosen habitat is a function of individual fitness maximization, founded on the trade-off between somatic growth, reproduction, generation time, and predation risk. Growth, reproduction, and mortality are all size- and state-dependent processes.

The environment

The model is run in an artificial environment resembling a situation with a well-mixed surface layer (above 12 m) with a homogeneous temperature distribution and a chlorophyll maximum at the thermocline (at 12 m). Below the mixed layer, temperature converges towards 4°C with increasing depth (Fig. 1). Although this particular situation seldom occurs in the temperate oceans, the use of relatively smooth gradients makes it easier to interpret the resulting distributions in terms of the mortality risk-growth trade-off.

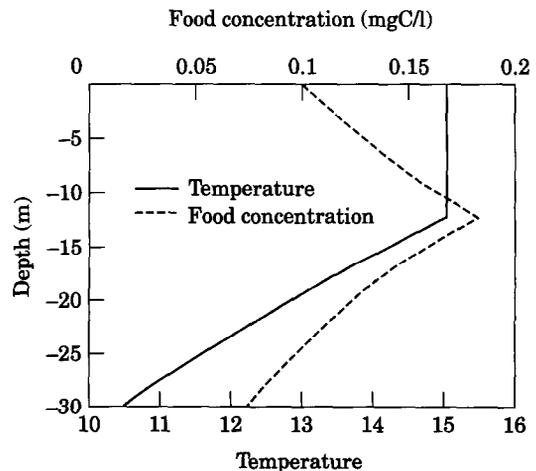


Figure 1. The vertical profiles of food (algae) and temperature used in the base run of the model. The situation is a very general one, with a well-mixed layer above a thermocline and a chlorophyll maxima at the thermocline.

Table 1. Parameters related to the calculations of light extinction in depth.

Symbol	Description	Value	Unit	Equation or reference
c_z	Local beam attenuation coefficient		m^{-1}	Kirk (1980); see text
k_0	Extinction from non-chlorophyll	0.14	m^{-1}	Aksnes and Lie (1990)
K_z	Local diffuse attenuation coefficient		m^{-1}	Eq. (1)
Ψ_z	Chlorophyll concentration in depth z		$mg\ m^{-3}$	See text
z	Depth		m	

Inclusion of dynamic plant–herbivore interactions is difficult (if not impossible) in dynamic optimization models, so we must assume that the modelled animal imposes no important top-down control on its food resource. The model is run with a non-fluctuating environment (food and temperature), only surface irradiance is changing in a diel manner (see Fiksen, 1993 for details), but the model could easily be run in a realistic, seasonal environment.

Light is an important factor in the formulation of predation risk from planktivores. Riley (1956) found the local diffuse attenuation coefficient K_z to depend on local chlorophyll concentration Ψ_z and extinction due to non-chlorophyll particles k_0 according to the equation

$$K_z = k_0 + 0.054(\Psi_z)^{0.667} + 0.0088\Psi_z \quad (1)$$

All conversions of food concentration to $mgC\ l^{-1}$ are made by assuming an $mgC:Chl\ a$ ratio of 30. Beam attenuation coefficient (Table 1) at depth z , c_z , is generally found to be 2–4 times K_z in low turbid waters (Kirk, 1980); and we assume $c_z = 3K_z$.

Model animal

In order to construct a general model, we have been parsimonious with species-specific parameterization and processes. The animal simulated should be regarded as an iteroparous female copepod, with physiological processes and animal structure represented such that the model can be adapted to several zooplankton groups. Further, the copepod is viewed as spherical and with approximately neutral buoyancy ($1\ g\ copepod = 1\ cm^3$). Then, the copepod cross-sectional area A_{cp} is found from individual wet mass, using a wet mass:C ratio of 14 (Parsons *et al.*, 1977).

State variables and the "growth within stage" concept

The first state variable is the developmental stage i (egg, 6 naupliar, 5 copepodite, and adult); the second may be termed "general internal state", i.e. condition or hunger. Both are likely to be relevant to copepod vertical behaviour (Huntley and Brooks, 1982). The general internal-state variable x brings together several aspects of individual copepod condition, such as gut and stomach contents and fats or lipids stored in blood,

liver, and muscles. The internal-state variable is reversible. It changes according to habitat quality and affects starvation, somatic mass changes and development. If x drops below a lower level x_c the copepod suffers a high risk of starvation. Developmental stage, on the other hand, is governed by the general internal state and cannot be reversed. This "growth within stage" concept (Carlotti *et al.*, 1993) is described in more detail below.

Developmental stage

Let the total copepod mass at the beginning of each developmental stage i be fixed, and denote this mass W_i . Just after moulting to the next instar mass W_i is then fixed, and the range of body mass in one instar does not overlap the range in the next or the previous instar. This is consistent with the findings of several authors (Paffenhöfer, 1971; Burkill and Kendall, 1982; Hamburger and Boëtius, 1987; Carlotti *et al.*, 1993), and the same assumption is made by Harris (1983), Carlotti and Sciandra (1989), and Carlotti and Nival (1992). Body mass of successive stages is a constant proportion of the following stage, and this proportion is equal for all stages except for eggs and adults (Table 2).

The internal state

Within each developmental stage there are 12 internal-state levels (Fig. 2), and the maximum range of the internal states increases with stage (Table 2). By feeding, the copepod may grow to a new internal state. This growth represents structural and storage mass, which in turn affects individual mass, moulting, and growth. Since growth is negative at harsh environmental conditions, body mass decreases as the internal state is reduced, while the copepod is using stored reserves to maintain metabolic needs. Total individual body mass $W_{i,x}$ is the sum of the minimum mass at stage W_i and internal state W_x (Table 3):

$$W_{i,x} = W_i + W_x \quad (2)$$

Moulting and hatching

Carlotti and Sciandra (1989) and Carlotti and Nival (1992) made the moulting rate increase with body mass and the cumulative mass-specific growth rate during the

Table 2. The copepod body mass at the start of each developmental stage, W_i , in μgC . The selected body mass for the base run is about the size of *Acartia clausi*. Values correspond to minimum body mass within stage, and for adults the maximum attainable body mass is included.

Stage	Eggs and N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5	Adult (min.)	Adult (max.)
Body mass	0.035	0.049	0.069	0.098	0.138	0.195	0.275	0.388	0.548	0.773	1.091	1.540	2.200

Table 3. Parameters used in the description of the model animal.

Symbol	Description	Value	Unit	Equation or reference
A_{zp}	Zooplankton cross-sectional area	—	m^2	See text
i	Developmental stage	—	dim.less	—
W_i	First body mass at stage i (newly moulted)	—	μgC	Table 2
$W_{i,x}$	Mass of animal in stage i and state x	—	mgC	Eq. (2)
W_x	Mass of internal state x	—	mgC	—
x	Internal state	—	dim.less	—

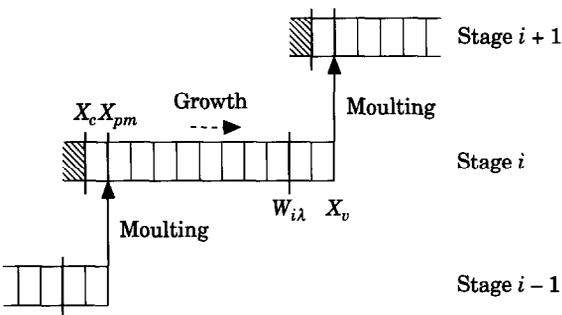


Figure 2. Illustration of the growth-within-stage concept. Post-moult internal state is x_{pm} , and increase if growth is positive and decrease if growth is negative. The copepod may die from starvation if internal state falls to x_c or below (shaded area). When $W_{i,x} > W_{i,\lambda}$, growth is inhibited, mass-specific growth rate drops and partially slows down the moulting rate (function f_2). The moulting rate function f_1 (Eq. (4)) equals 0 below $W_{i,\lambda}$ and has a turning point (“half saturation coefficient”) at x_v .

preceding 24 h. Their modelled abundance curves resemble observations nicely, and support the functional relationships assumed. We follow their approach, but make moulting rate $MR_{i,x}$ dependent on internal state x (instead of body mass) and specific growth rate $SG_{i,x}$:

$$MR_{i,x} = f_1 f_2 \tag{3}$$

where

$$f_1 = \frac{x^{k_1}}{x^{k_1} + x_v^{k_1}} \tag{4}$$

and

$$f_2 = k_2 SG_{i,x} \tag{5}$$

The variable x_v is the turning point of the f_1 function, k_1 gives the curvature of the function and k_2 is a proportionality coefficient which was stage-specific in Carlotti and Nival (1992), but constant here (Table 4). The value of the coefficient k_1 is taken from the Carlotti models, and k_2 is chosen to get development times within the range reported in Landry (1978) (see Results and Discussion). $SG_{i,x}$ is the growth rate divided by body mass $W_{i,x}$. Further, the dynamic optimization framework is not suited to accounting for the cumulative effects on moulting rate (because of the backward iteration procedure), so contrary to the Carlotti models we must assume moulting to be affected only by the specific growth rate over one hour. After moulting, the internal state is set to a low post-moult value x_{pm} , corresponding to the new growth range available in the new exoskeleton and to the hunger state generated by the non-feeding period assumed to occur in advance of, and during, moulting (Lasker, 1966; Eq. (11)).

Hatching rate H is a function of temperature T only, and is found by making the egg development time D of *Paracalanus* sp. reported in Uye (1991) the time when half the population has hatched:

$$H = \frac{\ln(0.5)}{D} \tag{6}$$

where $D = 3360(T_z + 2.2)^{-1.85}$.

The growth submodel

Huntley and Boyd (1984) developed a set of equations for growth in herbivorous zooplankton from body size,

Table 4. Parameters related to the moulting and hatching processes.

Symbol	Description	Value	Unit	Equation or reference
D	Hatching time		h	Uye (1991)
f_1	State-influence on moulting rate		dim.less	Eq. (4)
f_2	Growth-influence on moulting rate		$g\ g^{-1}\ h^{-1}$	Eq. (5)
H	Daily hatching rate		h^{-1}	Eq. (6)
k_1	Constant giving the shape of f_1	30	dim.less	Carlotti and Nival (1992)
k_2	Proportionality constant	200	dim.less	—
$MR_{i,x}$	Moulting rate		h^{-1}	Eq. (3)
$SG_{i,x}$	Specific growth rate at stage/state i, x		$g\ g^{-1}\ h^{-1}$	—
T_z	Temperature		$^{\circ}C$	Fig. 1
x_{pm}	Internal state after moulting	2	dim.less	—
x_v	Internal state at which $f_1 = 0.5$	12	dim.less	—

food availability, and temperature. This growth formulation has been shown to underestimate *in situ* growth (Kimmerer and McKinnon, 1987), but is chosen here mainly for its generality.

Food-limited growth

When food availability is below a specific satiation concentration F_c , growth is the difference between assimilation rate and metabolic costs:

$$G'_{i,x,z} = aF_z h W_d^n - kW_d^m \quad (7)$$

Here, G' is food-limited growth rate, W_d is dry body mass, hW_d^n and kW_d^m are the allometric relationships acting on filtering rate and respiration, respectively, F is food concentration in units from Huntley and Boyd (1984), and a is assimilation efficiency (Table 5).

Temperature-limited growth

At the satiation food concentration F_c , food limitation ceases and growth attains a maximum rate, limited only

by temperature. Huntley and Boyd (1984) found the maximum specific growth rate G_{max} to fit the equation:

$$G_{max} = 0.903 \exp(0.11T_z) \quad (8)$$

for a wide range of zooplankton groups. In this case growth is:

$$G_{i,x,z} = G_{max}(W_d)_{i,x} \quad (9)$$

The limiting food concentration

Now, to apply the right growth equation at each individual size, food concentration, and temperature, the satiation food concentration F_c must be reached before applying Equation (7) or (9). This is done by rearranging Equation (20) in Huntley and Boyd (1984) for F_c :

$$F_c = \frac{G_{max}W_d + kW_d^m}{ah} \quad (10)$$

where G_{max} , W_d , a , h , k , and m are as above (Table 4). F_c is the food concentration required to balance

Table 5. Parameters and variables corresponding to the growth processes.

Symbol	Description	Value	Unit	Equation or reference
a	Assimilation efficiency	0.7	dim.less	Conover (1978)
F_z	Food concentration		$mgC\ ml^{-1}$	Fig. 1
F_c	Satiation food concentration		$mgC\ ml^{-1}$	Eq. (10)
$G_{i,x,z}$	Temperature limited growth		$mgC\ ind^{-1}\ h^{-1}$	Eq. (9)
G_{lim}	Growth limitation factor		dim.less	Eq. (11)
G_{max}	Max. mass-specific growth rate as in Huntley and Boyd (1984)		$\mu gC\ mg\ dry\ mass^{-1}\ h^{-1}$	Eq. (8)
$G'_{i,x,z}$	Food limited growth		$mgC\ ind^{-1}\ h^{-1}$	Eq. (7)
h	Clearance coefficient		$mL\ mg\ dry\ mass^{-1}\ h^{-1}$	Huntley and Boyd (1984)
k	Respiration coefficient		$\mu gC\ mg\ dry\ mass^{-1}\ h^{-1}$	Huntley and Boyd (1984)
k_3	Factor preventing zero values	1.05	dim.less	—
m	Mass exponent (respiration)		dim.less	Huntley and Boyd (1984)
n	Mass exponent (filtering)		dim.less	Huntley and Boyd (1984)
W_d	Individual dry mass		$mg\ dry\ mass$	—
$W_{i,\lambda}$	Critical mass (growth limitation)		mgC	—

Equations (7) and (9), i.e. the threshold when food no longer limits growth.

Growth limitation by exoskeleton

Ingestion is known to cease before and during the moulting period for several crustacean taxa (Harpaz *et al.*, 1987; Anger *et al.*, 1989). There have also been indications of this phenomenon in copepods (Paffenhöfer, 1971; Harris and Paffenhöfer, 1976), although no clear demonstration is performed, perhaps because of experimental difficulties (Carlotti and Nival, 1992). Therefore, growth is probably limited by the exoskeleton at some point in the intermoult phase (Carlotti and Sciandra, 1989; Carlotti and Nival, 1992). We assume increasing growth limitation G_{lim} to occur beyond a stage-specific lower level $W_{i,\lambda}$ ($= 0.833(W_{i+1} - W_i)$) so that

$$G_{lim} = \left\{ \begin{array}{ll} 1 - \left[\frac{(W_{i,x} - W_{i,\lambda})^2}{(k_3 W_{i+1} - W_{i,\lambda})^2} \right] & \text{if } W_{i,x} \geq W_{i,\lambda} \\ 1 & \text{if } W_{i,x} < W_{i,\lambda} \end{array} \right\} \quad (11)$$

inducing diminution of growth as $W_{i,x}$ approaches W_{i+1} (and G_{lim} declines). Equation (11) is functionally similar to function f_4 in Carlotti and Sciandra (1989) and Carlotti and Nival (1992). Equations (7) and (9) are multiplied by G_{lim} before entering the state dynamics.

Swimming cost

The energy requirements for active movements C_m also affect growth. However, this metabolic cost is often ignored (McLaren, 1963, 1974; Enright, 1977; Slagstad, 1981; Mangel and Clark, 1988), since such energy consumption is difficult to quantify and also because several studies based on the theory of fluid dynamics (Lasker, 1966; Vlymen, 1970) or experiments (Dawidowicz and Loose, 1992) have found swimming costs to be negligible. In contrast, Torres and Childress (1983), in a study using the oxygen consumption rate of *Euphausia pacifica*, found locomotory requirements to be substantial. Also, Morris *et al.* (1985) added energy loss due to recovery strokes (pereiopod movements) and found swimming costs based on intermittent, non-steady motion to be more than three times standard metabolism at maximum speed.

Since no consensus seems to exist in the literature and because of a severe lack of data in this field (Morris *et al.*, 1985), we use a simple approach to the question of energy consumption in migration, based on resistance from drag forces. If the copepod is neutrally buoyant, then the two opposing forces are the viscous drag, which is directly dependent on the surface area and most prominent on small objects (low Reynolds number), and the dead drag, arising when water is pushed out of the way of the moving object (Mann and Lazier, 1991,

p. 25). The latter force will usually outweigh the first in copepods by several orders of magnitude, and viscous forces are therefore commonly ignored (Morris *et al.*, 1985). The total drag force F_D may be expressed using Newton's quadratic resistance law (Vogel, 1981) as:

$$F_D = 0.5C_D\sigma u^2 A_{zp} \quad (12)$$

where σ is density of salt water, u the swimming speed of the copepod, and A_{zp} the cross-sectional area perpendicular to the direction of motion (Table 6). The drag coefficient C_D is a function of Reynolds number (a function of zooplankton length, swimming speed, and viscosity, see Mann and Lazier, p. 14) specific to each object. For a sphere, it has been found to be:

$$C_D = \beta(\text{Re})^{-\varpi} \quad (13)$$

when $2 \leq (\text{Re}) \leq 500$. β and ϖ are constants, $\beta = 18.5$ and $\varpi = 0.6$ for a sphere and 85.2 and 0.8, respectively, estimated for the copepod *Labidocera trispinosa* (Vlymen, 1970). We use the parameters relating to *Labidocera trispinosa*, although the animal is represented as a sphere, and note that the copepod shape increases sensitivity to changes in Reynolds number compared with the spherical shape.

From Equation (12) we obtain force, in Newtons, which is converted to energy (Joule) by multiplying force and distance travelled Δm , i.e. $|z_t - z_{t+1}|$. These energy requirements are met by muscular work, and therefore some muscular efficiency E_m must be included. Morris *et al.* (1985) also included the energy loss from recovery strokes of pereiopods in their model, and found the mechanical efficiency E_{mech} to be about 0.35. The overall swimming efficiency E_{swim} is then $E_m E_{mech}$, and energy requirements (in joules) of swimming Δm in unit time are:

$$C_m(\text{Joule}) = \frac{F_D \Delta m}{E_{swim}} \quad (14)$$

C_m is converted to mgC, assuming (from Valiela, 1984) $1 \text{ cal} = 4.19 \text{ J}$, an oxycaloric value of $5 \text{ cal mL O}_2^{-1}$ and $1 \text{ mgC} = (12.0/22.4) \text{ RQ mL O}_2$. RQ is set to 0.8 (Morris *et al.*, 1985). Now, migratory requirements C_m (Fig. 3) can be subtracted from the growth equations.

Reproduction

Adults are allowed to spawn continuously. All growth is assumed to be allocated to gonad tissue and egg production when adult body mass exceeds some lower threshold $W_{a,\delta}$ ($= 0.25(W_{a(\max)} - W_{a(\min)})$); see Tables 2 and 6). Below this threshold no eggs are produced, and growth is allocated to somatic tissue. Matter available for reproduction m_r is:

$$m_r = W_{a,x} - W_{a,\delta} \quad (15)$$

Table 6. Parameters and variables used in the swimming cost and reproduction submodels.

Symbol	Description	Value	Unit	Equation or reference
α	Gonad-egg conversion efficiency	0.7	dim.less	—
W_e	Egg mass	3.5E-5	mgC	Table 2
b	Clutch size		Eggs	Eq. (16)
β	Constant	85.2	dim.less	Vlymen (1970)
C_D	Drag coefficient		dim.less	Eq. (13)
C_m	Metabolic cost of migration		mgC h ⁻¹	Eq. (14)
E_m	Muscular efficiency	0.25	dim.less	Hill (1950)
E_{mech}	Mechanical efficiency	0.35	dim.less	Morris <i>et al.</i> (1985)
E_{swim}	Overall swimming efficiency	0.0875	dim.less	See text
F_D	Drag force		N [kg m s ⁻²]	Eq. (12)
m_r	Matter allocated to reproduction		mgC	Eq. (15)
σ	Density of salt water	1026	kg m ⁻³	Mann and Lazier (1991)
\underline{u}	Swimming speed (average)		m s ⁻¹	—
ω	Exponent	0.8	dim.less	Vlymen (1970)
$W_{a,\delta}$	Threshold for allocation to eggs		mgC	See text
Δm	Distance travelled in unit time		m	—
Δz_{max}	Maximum distance swum per hour	20	m	See text

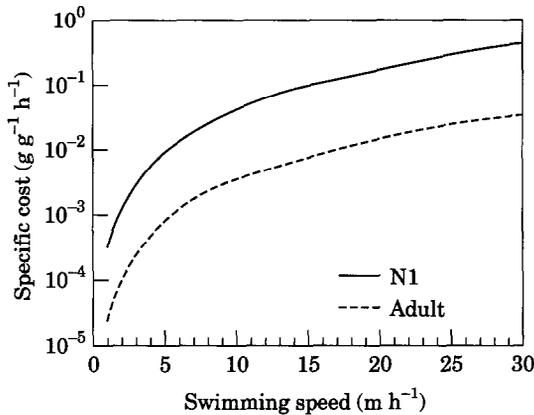


Figure 3. Mass-specific cost of swimming at various velocities for two stages (first naupliar and adult). The basic set of parameters was used in the generation of the curves.

Clutch size b is influenced by matter allocated for reproduction m_r , the gonad-egg conversion efficiency α and egg mass W_e (Tables 2 and 6):

$$b = \frac{\alpha m_r}{W_e} \quad (16)$$

When eggs are laid, all available matter (m_r) is assumed to be invested in egg production, implying that this matter is lost from the animal and all spawning individuals will take the same post-spawning mass, $W_{a,\delta}$ (Table 6).

Mortality

In zooplankton, the contribution to mortality from predation may be divided into a visual and a tactile fraction. The visual part is mainly constituted of fish, and the tactile of invertebrate carnivores and omnivores

like medusae, chaetognaths and predatory copepods, i.e. non-visually searching predators. Tactile predation depends on the spatial overlap between predators and prey, the functional response of the predator, predator evasion, and density of predators and prey, while visual predation in addition also relies heavily on the light conditions (Aksnes and Giske, 1993).

Visual predation

At a uniform prey density Z , handling time η , visual field angle Θ and a steady planktivore cruising velocity v , the feeding rate of each planktivore f is described by the Holling type II equation (Aksnes and Giske, 1993):

$$f = \frac{Z\eta^{-1}}{1 + \frac{[\eta v \pi (R \sin \theta)^2]}{Z}} \quad (17)$$

Aksnes and Giske (1993) developed a set of equations deriving the visual range R (Fig. 4) of a planktivore from the prevailing light conditions influenced by irradiance at surface I_s , fraction reflected in air-water interface ρ , turbidity (diffuse attenuation K and beam attenuation c_z), depth z , prey characteristics (cross-sectional area A_{zp} , copepod inherent contrast C_0), and planktivore eye sensitivity threshold for prey recognition ΔS_e (Table 7):

$$R^2 \exp(zK + c_z R) = \rho I_s |C_0| A_{zp} \Delta S_e^{-1} \quad (18)$$

This non-linear equation can be solved numerically for R by means of Newton-Raphson iteration (Fig. 4).

The spatial distribution of planktivores cannot be static in a dynamic model, since the copepods would then locate in areas of low or no predation risk. In nature, this would probably lead to an instantaneous relocation of the planktivores. We must therefore

assume that the planktivores may hunt everywhere, but their potential impact on zooplankton survival depends on their effectiveness. By assigning the typical planktivore density P , the total number of prey ingested is fP , and then the instantaneous zooplankton mortality rate caused by cruising visually searching predators M_v (Table 7, Fig. 4) is:

$$M_v = \frac{fP}{Z} \quad (19)$$

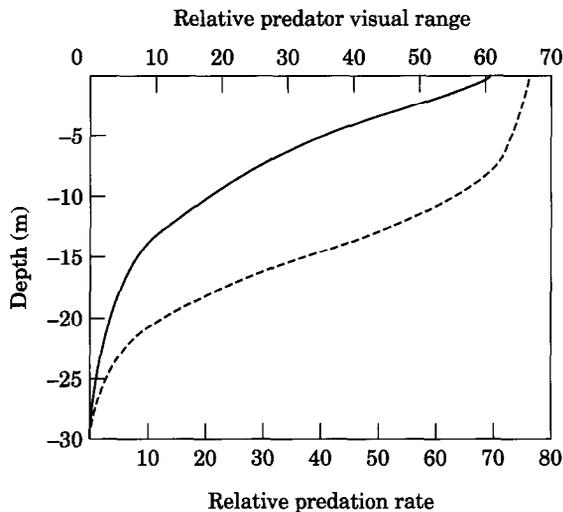


Figure 4. Values of planktivore visual range R (relating to adult copepods) and adult mortality rate M_v imposed by planktivores relative to values at 30 m. The environment was the same as in Figure 1, and parameters are the basic set. Solid line = visual range (R , Eq. 18); dashed line = visual predation rate (M_v , Eq. 19).

Tactile predation

Both encounter rate between prey and their tactile predators (ambush and cruising) and prey escape abilities are likely to increase with size (and motility). The integrated effect is likely to be a decline in tactile predation pressure with size and stage (Ohman, 1988), although this may not apply generally. In addition, size-dependent cannibalism is probably an important source of mortality in zooplankton (Kremer and Nixon, 1978). The general importance of size in assessing mortality rates is also noted by Roff (1992, pp. 117–122), with declining mortality rates with increasing size as the general rule, and by Dodson (1970), suggesting a decline in electivity by invertebrate predators above a given prey size. The opposite may apply to planktivores, which are positively size-selective for prey sizes below the size where the planktivores become gape-limited (compare Figs. 1 and 17 in Zaret, 1980). Peterson and Wroblewski (1984) developed a model for size-dependent mortality rate of fishes (or fish-sized particles), and McGurk (1986) showed this expression also to be valid for pelagic invertebrates:

$$M_e = E(W_g)^{-y} \quad (20)$$

where M_e is the mortality rate, W_g is individual dry mass, and E and y are constants of proportionality (Table 7). McGurk (1986) found that the model provided an excellent fit to reported mortality rates of pelagic organisms ranging over 16 orders of magnitude. Equation (20) is a measure of total mortality, assuming that mortality is primarily due to predation and that mortality does not depend on the spatial distribution and densities of predators and prey. We use Equation (20) as a spatially-independent source of mortality due to (tactile) predation in addition to the visual source,

Table 7. Parameters and variables used in the description of various sources of mortality.

Symbol	Description	Value	Unit	Equation or reference
C_0	Copepod inherent contrast	0.5	dim.less	Aksnes and Giske (1993)
E	Tactile predation constant	2.19E-4	h^{-1}	Peterson and Wroblewski (1984)
f	Feeding rate of planktivore		$prey\ pred^{-1}\ h^{-1}$	Eq. (17)
η	Handling time	2	$s\ prey^{-1}$	Eggers (1976)
I_s	Irradiance at surface		$\mu mol\ m^{-2}\ s^{-1}$	See Fiksen (1993)
M_e	Tactile predation rate		$prey\ prey^{-1}\ h^{-1}$	Eq. (20)
M_v	Visual predation rate		$prey\ prey^{-1}\ h^{-1}$	Eq. (19)
P	Predator density	0.01	$predators\ m^{-3}$	—
Θ	Planktivore visual field angle	30	degrees	Luecke and O'Brien (1981)
R	Visual range of planktivore		m	Eq. (18)
ρ	Light-fraction lost at surface	0.5	dim.less	Aksnes and Giske (1993)
v	Planktivore swimming speed	1.4	$cm\ s^{-1}$	—
W_g	Individual dry mass		g dry mass	—
y	Tactile predation exponent	0.25	dim.less	Peterson and Wroblewski (1984)
Z	Zooplankton density	1000	$prey\ m^{-3}$	—
ΔS_e	Planktivore eye sensitivity	3.0E-6	$\mu mol\ m^{-2}\ s^{-1}$	Rosland and Giske (1994)

and E is therefore (rather arbitrarily) divided by two to account only for the non-visual fraction.

The dynamic optimization framework

The dynamic programming procedure may be described as a three-step process (see Mangel and Clark, 1988; Giske *et al.*, 1992). First, all possible fitness values are calculated (one value for each state, stage, habitat, and time), starting with some life-history-related end condition at final modelling time or use per period fitness accretion only. Fitness values of all available habitats are found for all possible states and times by using an objective function (optimization criterion), i.e. a relationship between fitness and variables acting on fitness, like survival, growth, and fecundity. The optimal habitat is where the fitness value reaches its maximum, and the modelled animal is assumed to maximize fitness and adopt this habitat, depicting an optimal trajectory (optimal policy) through the modelled period. Second, time proceeds forwards, an initial population is assumed (here: a newborn cohort), and the development of the state and dynamics of this population (or cohort) are followed through time, as each individual follows its optimal policy regarding depth. The final step is to trace the fractions of the initial population adopting a particular behaviour to find the overall spatial distribution of the population and the resulting growth, survival, and egg production.

The optimization criterion must be related to the Darwinian concept of maximization of fitness, established through the action of natural selection (Dawkins, 1989). This criterion justifies the assumption of optimal behaviour and that the animals have a near ideal response to all known elements relevant to the trade-off decision. The objective of an individual, then, should be to maximize its contribution of descendants in the future or, in the context of an allele, to maximize its fraction in future gene pools, by optimizing survival and reproduction. For discrete time (age) intervals with one as the first age class (time interval), the expected reproductive value between present time t and some future time horizon Ω (RV_t) is defined as (the detailed

outline of these equations is given in Stearns, 1992; pp. 26–28):

$$RV_t = \sum_{j=t}^{j=\Omega} e^{-r(j-t)} \frac{S_j}{S_t} b_j \quad (21)$$

This equation can be separated into present reproduction and expected future reproduction by isolating age class t (again, see Stearns, 1992):

$$RV_t = \frac{e^{rt}}{S_t} e^{-rt} S_t b_t + \frac{e^{rt}}{S_t} \sum_{j=t+1}^{j=\Omega} e^{-rj} S_t b_t \quad (22)$$

By assuming a stable population ($r = 0$, $RV = R_0$), cancellation, and letting $(1 - M_t)$ be the total probability of surviving both visual and tactile predation and starvation between t and $t+1$ (i.e. S_{t+1}/S_t), then Equation (22) simplifies to (Table 8):

$$RV_t = b_t + (1 - M_t)RV_{t+1} \quad (23)$$

which can be solved by stepwise backward iteration starting from RV_Ω (Ω is final time) and finding $\max(RV_t)$ of successive time intervals (for a detailed description of how to do this, consult Mangel and Clark, 1988). Following this, the animal should maximize RV_t from now on at any time, by choosing the habitat which gives the optimal trade-off between growth and predation risk at its current stage i , state x , and vertical position z .

Results and discussion

Basic run in a “laboratory situation”

The dynamics of individuals entering and leaving each developmental stage is depicted as relative abundance curves (Fig. 5). The age structure stabilizes after some generations (Fig. 4), as in the model by Carlotti and Nival (1992). This indicates that the model is stable and that the rate of biological processes becomes constant at each stage, but may oscillate slightly more than in the model by Carlotti and Nival (1992). The parameter values are always those listed in tables in the model description, unless otherwise specified.

Table 8. Parameters and variables used in defining fitness.

Symbol	Description	Value	Unit	Equation
M_t	Probability (total) of mortality in time t		dim.less	—
r	Population growth rate	0	h^{-1}	—
RV_t	Reproductive value at time t		descendants	Eq. (21–23)
S_t	Probability of survival to time t		dim.less	—
b_t	Clutch size at time t		Eggs	—
Ω	Final time in modelled period	28*24	h	—

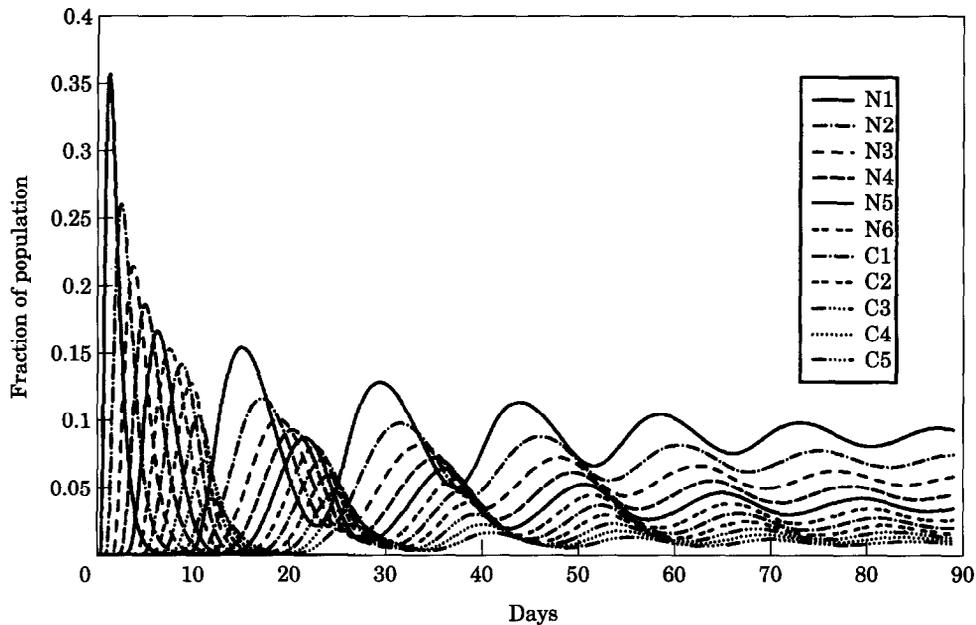


Figure 5. Age structure of the cohort (except eggs and adults) in a “laboratory” situation with no depth resolution or predation, warm water (20°C), or unlimited food concentration.

Developmental time

Under the same conditions (stable environment, no depth resolution) the developmental times of each instar can be found. Development time is not a well-defined concept, but we use it as the time taken from the origin of the cohort to the time where the stage of interest reaches its maximum relative abundance. The model was run with several food and temperature conditions, and the development times of the sixth naupliar and adult stage were recorded (Figs 6, 7). All stages have about the same duration at each temperature (Fig. 8), and the model copepod has the same proportional mass increment at all temperatures and thus performs isochronal development (Miller *et al.*, 1977).

Information about developmental time in natural environments is difficult to obtain, and few studies provide such data. Landry (1978) estimated minimum development times for *Acartia clausii* from both laboratory cultures and natural conditions. We used his data to find a reasonable parameter value to k_2 in Equation (5). Figure 8 compares the predictions from the model with the developmental estimates from laboratory cultures (with excess food and a temperature range of 5–20°C) given for *Acartia clausii* in table 1 of Landry (1978). The model seems best to fit the data from Landry (1978) at intermediate temperatures. At high temperatures, it appears to overestimate development rates. Landry (1978) presents minimum development times (not well defined) and the model gives the time to maximum relative abundance of each stage, so comparison should be done with some caution.

Basic run with vertical resolution

The basic run uses parameter values presented in tables in the model description and the environment in Figure 1. The entire cohort is initiated at the surface as eggs, and the eggs adjust to an optimal depth (do not migrate). As the age of the cohort increases and time proceeds, the individuals grow and the amplitude of their vertical migrations increases to a maximum range after about 10 d (Fig. 9A). The cohort stays at a depth of 12 m during the night (maximum temperature and food) and descends to a range of depths during the day, but the vertical migration declines towards the final time of the model. This is an effect of the reduced benefit of survival as the final model time is approached, i.e. the animals “know” that they will die at the end of day 28 and therefore accept higher mortality risk than that with a longer time horizon. This could be seen as an adaptation to regular seasonality, but also as an artefact of the method which supplies the decision-making copepod with so much information about future conditions. To bypass this artefact, one could run the model with uncertain final time (see Mangel and Clark, 1988, p. 71), but this would interfere with the sensitivity analysis.

A more detailed figure, focusing on the distribution of the cohort during one day (day 20), is given in Figure 9B. Clearly, the range of habitats occupied increases during daytime, and migration seems to be a continuous process during the crepuscular periods.

Older stages descend deeper than younger stages do, and they leave the night-time habitat earlier and ascend

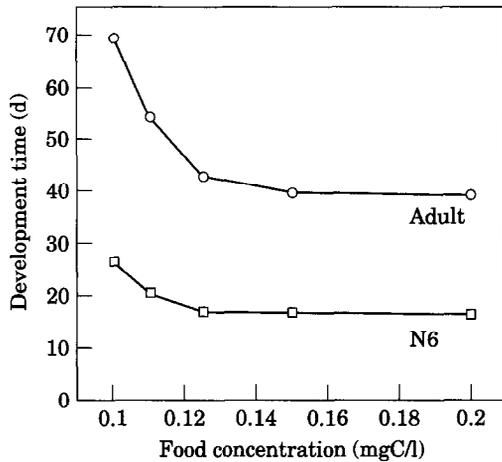


Figure 6. Development times at various food concentrations at 10°C.

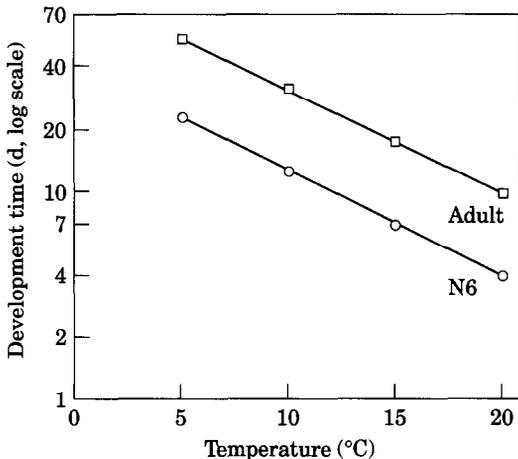


Figure 7. Development time from egg to N6 and adult stages at various temperatures (unlimited food conditions).

back later in the day. The distribution profiles are almost symmetrical around mid-day, and the daytime depths appear to increase with developmental stage of the copepod (Fig. 10).

Fitness

The reproductive value curve for an average individual (Fig. 11) takes a similar shape to that reported in Stearns (1992, p. 27), i.e. a continuously increasing curve towards maturity due to the increasing probability of reproduction taking place, declining after the first reproductive event as the expected number of descendants decreases towards the time horizon.

The model allows us to take "snapshots" of the vertical fitness profiles at any time and of all stages and internal states (Fig. 12). These plots describe the

adaptive situations offered to stages N1 and C5 at day 14 (mid-day), and the relative profitabilities of inhabiting each habitat measured as fitness. Profiles of three levels of internal states of copepodite stage 5 reveal differences in the importance of visiting the optimal habitat (Fig. 12, right panel) for each internal state, i.e. the relative canonical cost (McNamara and Houston, 1986) of not choosing suboptimal habitats. The low internal state has shallower optimal depth, and a much steeper profile of relative depth profitability compared with the higher states. Thus, the internal state affects depth distribution through relative profitabilities though the final choice may not differ much. For early instars, internal state matters less at this time (Fig. 12, left panel). The profile is sharper to all states, because of an increased importance of growth rate as they are running out of time (they must hurry to mature within the time constraint).

Sensitivity analyses

The properties of the model are investigated by sensitivity analyses (cf. Gladstein *et al.*, 1991; Houston *et al.*, 1992; Carlin and Gladstein, 1992). This is done according to Jørgensen (1986), i.e. by finding the ratio between the change in model prediction and change in parameter value. Thus, the sensitivity of a model output variable X to altering a parameter from the basic run value B to a new value p is given by:

$$S_x = \frac{(X_B - X_p)/X_B}{(B - p)/B} \quad (24)$$

where X_B is the basic run output of X and X_p is the new output from the parameter p . This expression allows a direct comparison between parameters, i.e. a larger absolute value of S_x indicates a more sensitive parameter. Average values of depth position, growth rate, predation rate, and M/g ratio from the whole cohort during the entire period are chosen as response variables. To address the question of how enhanced primary production, temperature, and planktivore density may influence distribution, growth, predation, and abundance of copepods, we ran the model at series of possible levels of these variables. The following section presents the sensitivity analyses and the results of model changes in more detail. First, the results from the sensitivity analyses are summarized (Table 9).

Temperature

In sum, the response variables are most sensitive to changes in environmental temperature. Raising the temperature leads to more rapid development, a deeper average depth location, and higher survival, growth, and egg production (Figs 13B, 14). Egg production and growth are most sensitive to an increase in temperature, while average depth and predation are more influenced

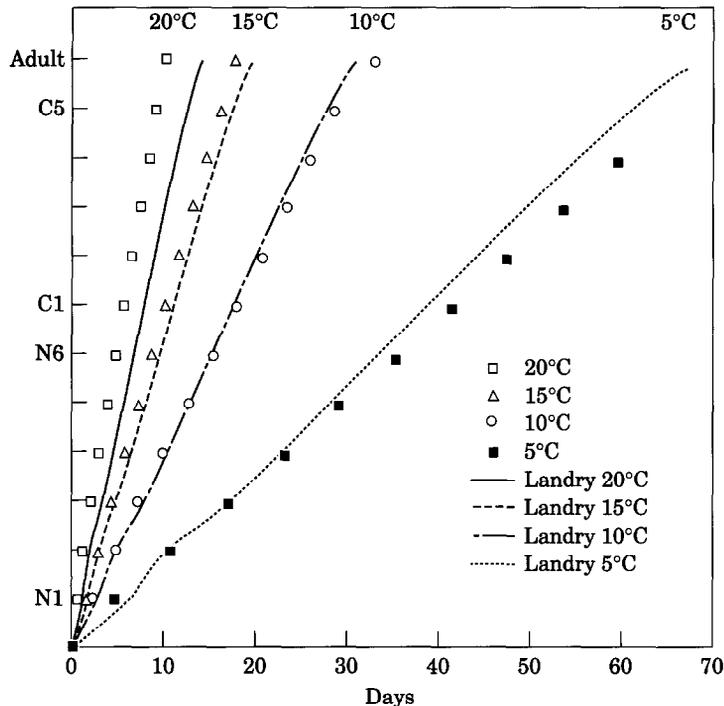


Figure 8. Development times predicted by the model at various temperatures compared to those reported by Landry (1978).

by the temperature decrease (Table 9). When the temperature is lowered, the vertical migration ceases, due to the longer time needed to reach maturation. The copepods must then take high risks to reach adulthood within the model horizon. The loss of the diel vertical migrations has severe effects on the mortality rate, while an increase in migration relative to basic run gives less reduction in predation, indicating diminishing survival returns of increasing migration.

Food resources

Shifting the profile of food resources up (unchanged profile) also changes the response variables substantially, but not as much as temperature. Increased resources affect predation rates as well as growth rates of the copepod. It could be anticipated that increased resources lead to risk-averse behaviour and deeper location (Huntley and Brooks, 1982; Dagg, 1985; Johnsen and Jakobsen, 1987). However, increased algal biomass also affects the top-down control from visual carnivores. This is due to the increased turbidity caused by increasing algal concentration, which in turn reduces the visual range and feeding rate of the predator (Giske *et al.*, 1994). The average depth of the cohort actually decreased compared with the basic run, demonstrating this point (Fig. 13C). The reduced visual predation created a shallower distribution pattern and allowed the copepods to exploit the warmer water in the mixed layer and thereby to further shorten their generation time.

Given the strong impact of temperature and planktivore efficiency (water clarity; see below) on the model output, these indirect effects are stronger than the direct growth effect of increased food.

At the lowest food concentrations (< ca. 0.06 mgC l⁻¹ at the surface) the copepods starved, no eggs could be produced within the time constraint, and the model gave no meaningful fitness values or options on distribution (Fig. 14). When the resource level was raised slightly beyond this, the only option was to maximize growth, regardless of the predation risk, resulting in a shallow depth location of individuals adopting a high risk-fast growth strategy. A further resource increase allows the copepods to relax their concern to the time constraint, and to sacrifice some growth to obtain a lower mortality rate by choosing deeper habitats (Fig. 14). Beyond this resource level (> ca. 0.1 mgC l⁻¹) the turbidity of the water allows copepods to distribute nearer the surface and still lower their mortality rates compared with runs with deeper distributions. Eventually, the mortality rate converges towards the average tactile predation rate. The increased survival has strong consequences at the population level (Fig. 14, panel showing R_0). Growth rate increases only slightly with increased resources, whereas mortality rate declines considerably, first because of increased investment in anti-predator behaviour and then because of turbidity (note that small changes in hourly rates cause large effects on the population level). The average R_0 (total egg number/

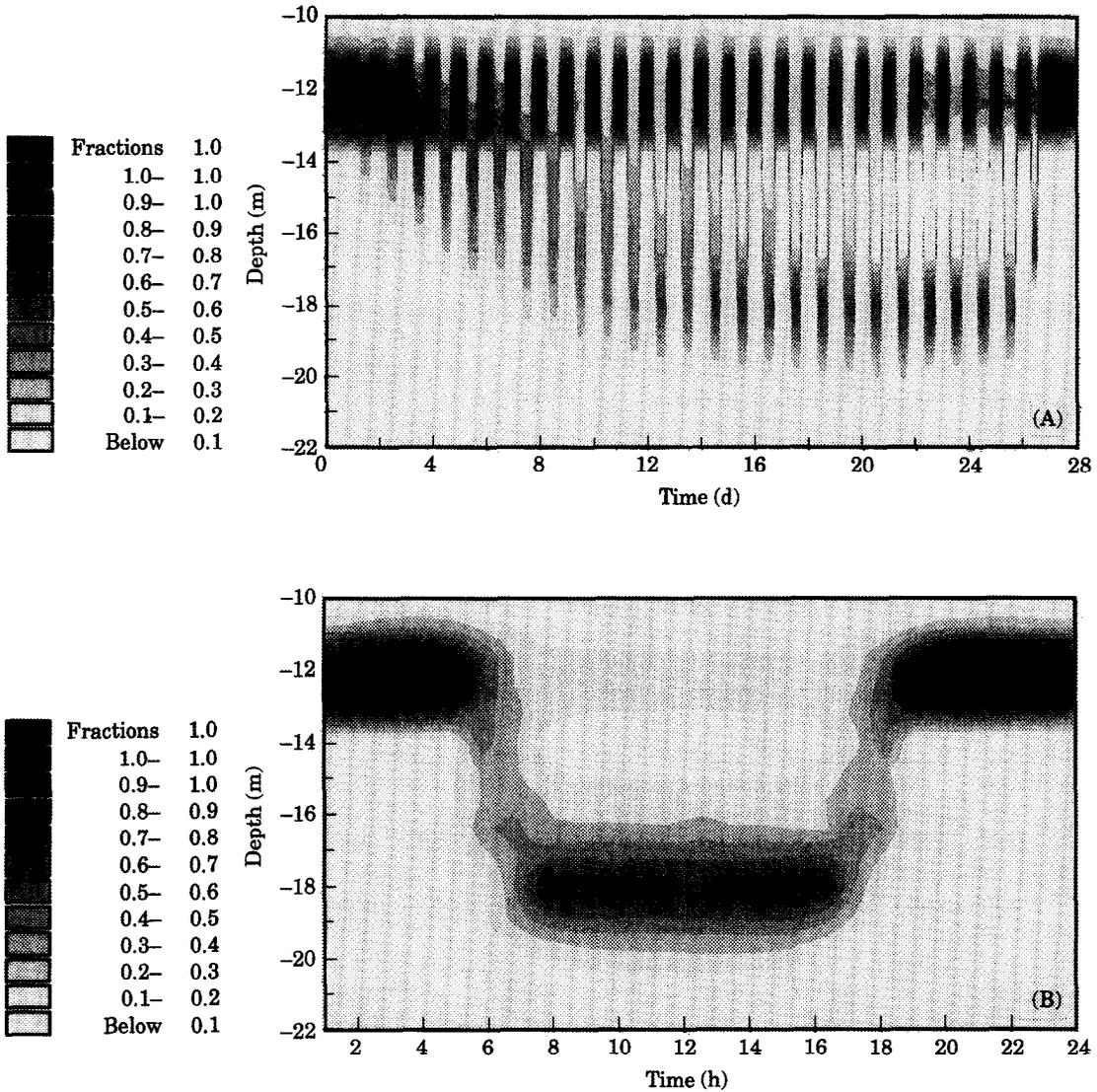


Figure 9. A. Vertical distribution of the whole cohort (fraction in each habitat) during total simulated period (upper panel) using basic parameters and environment. B. Diel distribution of the whole population (fraction in each habitat) at day 20 (lower panel).

female) shows a fairly linear relation to increased food resources (Fig. 14), but the main cause is higher survival, not enhanced growth. Thus, the most classically viewed bottom-up factor (food resources) could potentially have stronger influence on the dynamics of herbivores through top-down control in a pelagic environment.

Density of predators

The direct effect on prey numbers may be expected to be proportional to predator density (Eq. (19)). But predation risk is more sensitive to a reduction than to an increase in planktivore density, indicating a non-linear relationship due to the change in copepod anti-predator behaviour (vertical migration). Increased predator density induces progressively deeper average distribu-

tion and lower growth rate (Fig. 14). Reduced growth exposes the copepods to heavier tactile predation pressure (smaller copepods are more vulnerable) and more visual predators also tend to increase mortality rates. Mortality rate increases, but at a falling rate (Fig. 14), reflecting the prey response (vertical excursions during daytime). The combined effect is expressed as an exponential decline in the net reproductive ratio (R_0 , lower right panel) with increasing predator density.

The underlying mechanism is similar to the increased food situation; higher visual predation rate prevents the copepods from exploiting the warm mixed layer, so one cost of anti-predator behaviour is that growth rate also drops. But the decline in growth rate does not make the extended vertical migration unprofitable, since such

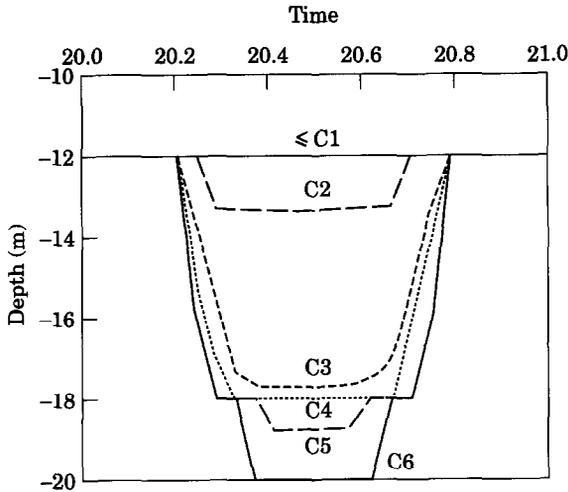


Figure 10. Average depth distribution of the different stages during day 20, basic run.

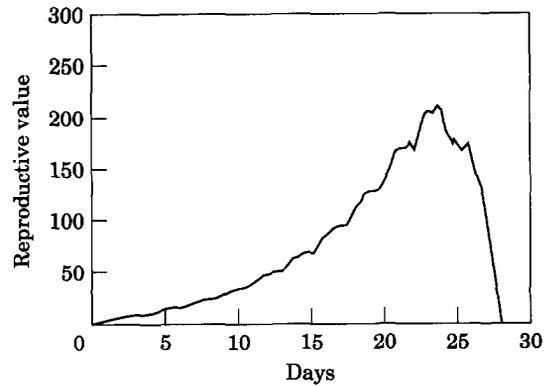


Figure 11. RV of an average individual (medium state, average stage, and depth). Fitness increases until maturation and reproduction starts, but then drops off as residual reproductive value diminishes.

behaviour efficiently counteracts the increased predation pressure. Altering planktivore eye sensitivity, copepod inherent contrast, or the density of alternative prey all act through similar mechanisms, but the model is less sensitive to changes in these parameters.

The heaviest source of mortality in the basic run is tactile predation. It is therefore clear that mortality and egg-laying are sensitive to changes in the tactile predation rate (Table 8). Less obvious, however, although the tactile predators are uniformly distributed vertically, the copepods respond to alterations in tactile predation by changing their spatial distribution. When the overall tactile predation pressure is increased (E is increased or y is decreased in Eq. (20)), the copepods respond by choosing slightly shallower depths, and vice versa when it is decreased. The reason for this change in

optimal policy is that a shorter generation time becomes more profitable as the mortality rate increases, such that the slightly higher visual predation risk is worth facing to obtain this. Particularly, it pays to follow a shallow path in the early stages, due to lower visual risk (small cross-sectional area) and the strong size dependency of tactile predation. This is most evident when the size dependency (y) is manipulated (Fig. 13D). Then, the smallest stages take the higher visual risk to grow through the “high-tactile-risk” stages as quickly as possible and compensate by investing more in avoiding visual predation later. In terms of fitness, this strategy pays off (Fig. 13D, M/g panel). Though the copepods stay in the mixed layer facing an increasing visual risk as they grow, the M/g ratio declines steadily. This panel also demonstrates that when tactile predation is low, the copepod cohort

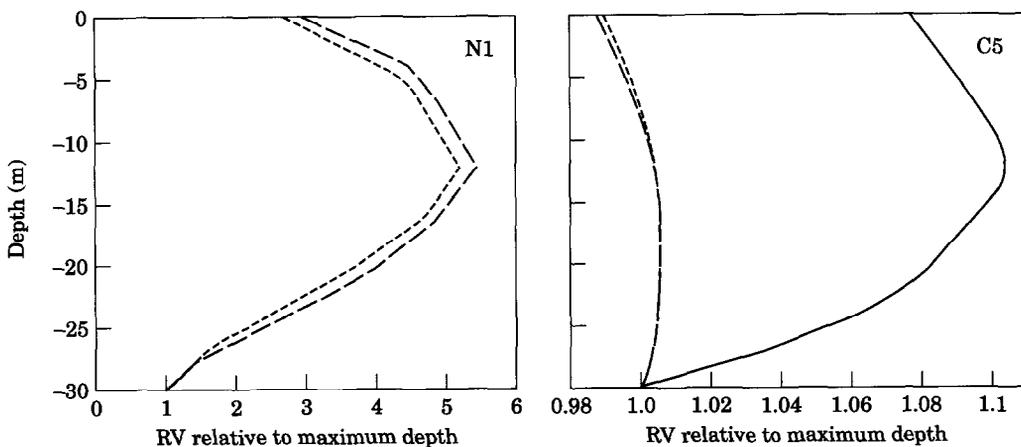


Figure 12. Vertical fitness profiles of three internal states of stage N1 (left panel) and C5 (right panel) at day 14 (mid-day). The low state of N1 is not shown because it obtains no fitness value at this time in the model. Thus, within each stage, if condition is relatively poor, remain near the chlorophyll maxima to improve condition; if condition is reasonably good, reduce mortality (stay deeper) at the expense of growth. — = low state; - - - = medium state; . . . = high state.

Table 9. Summary of the sensitivity analyses. Calculations are based on Equation (24) and values averaged over the whole model period. The most influential factors during 28 days on egg production, average depth, predation and growth rate and M/g ratio are ranked from 1 to 4. Below the fourth rank, there were only small deviations from basic run values (small S_x). Changed food concentration and temperature relates to shifting the curves in Figure 1 up or down, planktivore density is P in Equation (19), y is the exponent in the size-dependent mortality rate (Eq. (20)) and E is the tactile mortality constant (Eq. (20), Table 7).

Rank	Egg production	Depth	Predation	Growth	M/g ratio
1	Increased temperature	Reduced food concentration	Increased y	Reduced food concentration	Reduced food concentration
2	Decreased y	Decreased temperature	Reduced food concentration	Increased temperature	Increased y
3	Decreased E	Increased temperature	Decreased temperature	Decreased temperature	Decreased temperature
4	Decreased temperature	Reduced planktivore density	Decreased y	Reduced planktivore density	Increased temperature

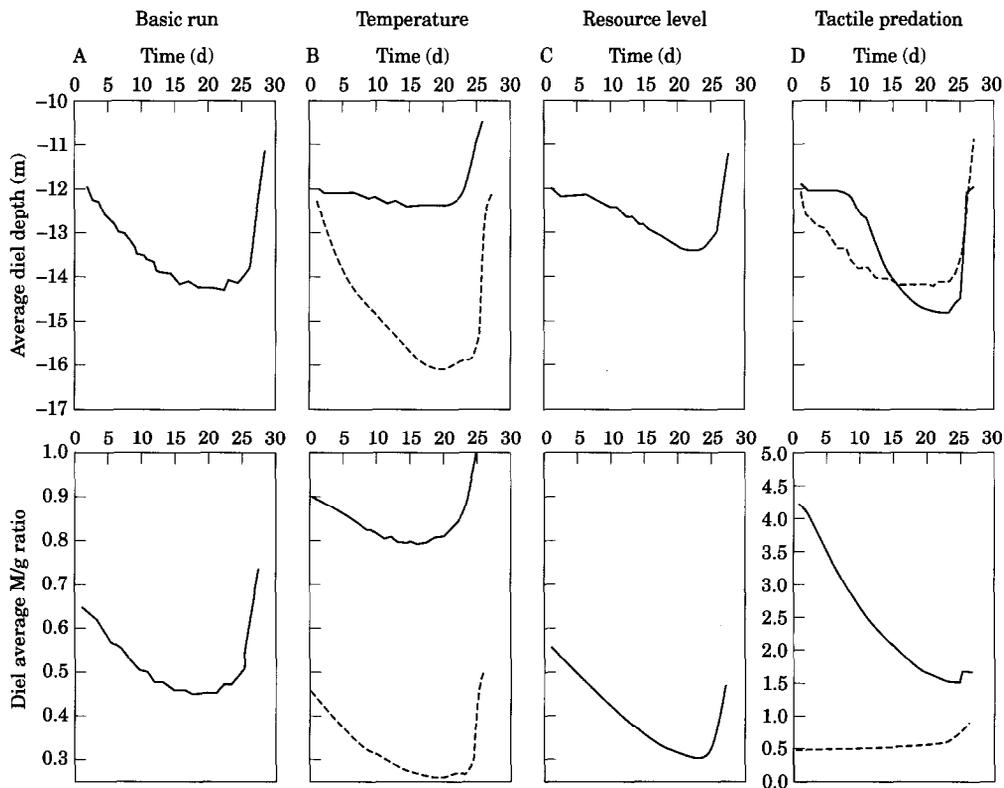


Figure 13. Depth position (upper) and M/g ratio (lower) averaged over each diel cycle during modelled time (28 days = 28 points on the graphs). A. Results from basic run serve as a reference to the altered versions. B. Shifting the profile in Figure 1 up by 3°C increases the range of vertical migration (broken lines) and vice versa when the temperature is lowered by 3°C (solid lines). C. Increased food concentration (doubled through whole column from basic run, Fig. 1) increases turbidity and allows copepods to stay shallower and exploit the warmer surface waters without risk of increased mortality. D. Changed size-dependent tactile predation ($y \pm 50\%$; Eq. (20)) influences vertical strategies through life. If copepods are more vulnerable when small, take a fast growth-high risk strategy as young, and compensate when older (solid lines). If size is less important, take a more even trajectory through life (broken lines). Note the different scale on the panel showing M/g ratio.

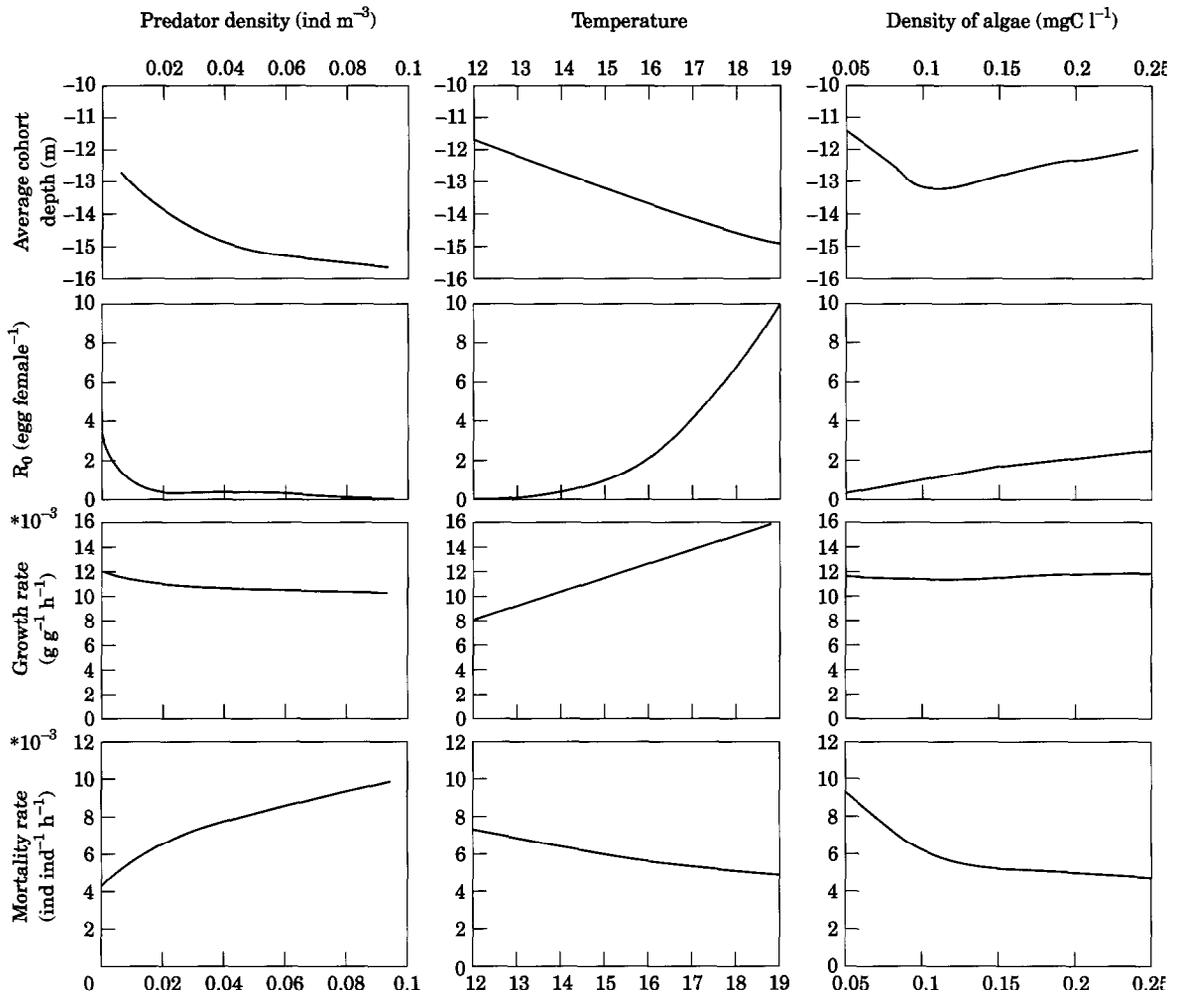


Figure 14. Influence of planktivore density (left), temperature (middle), and density of algae (right) on average cohort depth distribution (top) and life history variables (R_0 , growth rate and mortality rate). Each panel presents the results of several model runs with increasing levels of predator density, temperature, and food resources. Each point on all graphs is the average value during the whole simulation (i.e., each point in graphs of the average depth location will be the overall average of graphs like the upper panels in Fig. 13).

chooses an increasing M/g ratio with age, and vertical migration does not fully compensate for the increased vulnerability to planktivores as they grow older.

No mortality is registered from starvation. At lower food concentrations the optimal policy seems to involve a preference for more dangerous and food-rich habitats in the presence of risk of starvation (McNamara and Houston, 1987). Thus, although the animals die from predation, the ultimate cause may be lack of food, as summarized in the "better dead than unfed" statement from Huntley and Brooks (1982).

General discussion

The model is first discussed in relation to its internal elements, and then in terms of its ecological implications and relevance to the predictions.

The model

General distribution pattern

The general vertical migration pattern of copepods is to descend at dawn and ascend towards the surface at dusk (Bayly, 1986), and to increase migration range during the course of ontogenetic development (McLaren, 1963; Zaret and Suffern, 1976; Johnsen and Jakobsen, 1987). The model captures these general trends, but predicts that all size fractions undertake diel excursions to some extent.

Regular vertical movement by invertebrate predators is suggested as the reason why smaller copepods may not migrate or display inverse migratory behaviour (Ohman *et al.*, 1983). Because of the high impact of invertebrate predation on mortality rates in the model, no migration, or even reversed migration, would probably occur with

only a slightly regular diel migration of tactile predators (Ohman *et al.*, 1983; Ohman, 1990), particularly for the smallest individuals.

Indeed, caution must be taken when comparing observations in nature with distributions generated by this model. But the purpose of constructing the model was mainly as a theoretical tool, and it is not yet a predictive model (calculation tool; Loehle, 1983). Hence, the model should be evaluated by its ability to increase understanding of clarifying mechanisms and causation, and to generate ideas and guide observation. As our quantitative knowledge increases, the model may serve as a predictive tool of the dynamics of pelagic animals in applied situations.

The fitness criterion

Most decision rules used by ecologists for modelling habitat selection are ideal in the sense that they assume that the animals have total knowledge of their environment and are free to respond to this insight. However, ideal decision-making fails when information is inaccessible or too expensive to obtain. The present model first assumes that the copepods have full information about the future, including the environment, time constraints, predation risk, etc. Naturally, most of this information is not accessible to the copepods, at least not with certainty. Second, it is assumed that the marginal value of acquiring additional knowledge may not be worth the price. In particular, the cost of sampling the environment in order to test the predation pressure may be death, at least to animals with a small probability of surviving an encounter with a predator (Sih, 1987). In such situations fixed behavioural patterns may be optimal, though the pressure from predators is highly variable and avoidance may be stressful. The flexibility of behaviours may also be asymmetrical, with rapid adjustment when predation increases and slow adjustment when predation declines (Sih, 1987). However, several studies have shown that animals (most vertebrates) do forage optimally (see review by Krebs and Kacelnik, 1991), though few workers have investigated invertebrates. A large number of studies have recently examined the question of the phenotype flexibility of migratory behaviour of zooplankton. The evidence from field observations (Williamson and Magnien, 1982; Bollens and Frost, 1989a; Levy, 1990; Ohman, 1990; Stirling *et al.*, 1990; Frost and Bollens, 1992) and from experimental manipulations of predators (Bollens and Frost, 1989b, 1991; Dawidowicz *et al.*, 1990; Leibold, 1990; Neill, 1990; Tjossem, 1990; Ringelberg, 1991) indicates that a wide range of zooplankters exhibit phenotypic plasticity in vertical migration patterns. Some studies even suggest that copepods are able to respond instantaneously to the exposure of a planktivore, and to shift from no

migration to nocturnal diel vertical migration from one day to the next (Bollens and Frost, 1991), or from inverse migration to nocturnal migration in a few weeks (Frost and Bollens, 1992).

The assumption of optimal behaviour has been successful in generating a large body of theory about habitat selection and population interaction (reviewed by Rosenzweig, 1991), and may be compared with the central theme of rational expectations in economics (Muth, 1961). The principle of natural selection certainly favours those individuals (or alleles) reproducing at the highest rate, and this rewards optimal strategies. Therefore, the optimality approach should not be rejected, but used with caution, as our perception of optimality in the water column is limited.

Ecological implications

Turbidity and planktonic organisms

A correlational or descriptive relationship between freshwater discharge from rivers and secondary production has been discovered in several studies, but the mechanism at work is not known (Mann and Lazier, 1991, p. 152). For instance, in St Margaret's Bay, Sutcliffe (1973) found a good correlation between the discharge from the St Lawrence River and survival of lobster larvae, and on the east coast of Africa a similar observation has been made regarding the Zambezi river and the shrimp *Penaeus indicus* (da Silva, 1986). Off Iceland, zooplankton densities are known to be highest under conditions of early freshwater stratification and phytoplankton bloom (Thordadóttir, 1986), which may also affect the survival of the commercially important cod larvae.

Heavy freshwater run-off increases turbidity, because large freshwater discharges are generally more turbid than smaller and more regular discharges (they carry higher concentrations of soil, silt, and clay). Also, freshwater stabilizes the water column, carries nutrients, and enhances primary production, further increasing turbidity. This turbidity, in turn, benefits the survival of planktonic organisms susceptible to visually searching predators. The turbid layers may provide both shelter and food, and the necessity of displaying metabolically expensive diel excursions is lowered, allowing more intensive exploitation of regions with more food and higher temperatures. According to the predictions from the model (see Fig. 14), these factors have pronounced effects on the population dynamics of the planktonic organism, and may explain the observations mentioned above.

Increased turbidity is most beneficial to large zooplankton and small pelagic fishes, because the high-beam attenuation coefficient (Eq. (18)) is more influential at longer detection distances (visual ranges) (Giske *et al.*, 1994). This suggests that the benefit to

organisms of the size of fish larvae is large, although their visual ranges and feeding opportunities are reduced. This loss is likely to be minor compared with the gain in survival rate associated with the more pronounced loss in piscivore feeding rate. Smaller zooplankters benefit mainly from the lower overall light intensity, and may therefore assemble below the turbid layer to minimize mortality. Hence, during daytime a pattern may emerge where carnivorous zooplankton hide from planktivores within the turbid layer (e.g. a distinct chlorophyll maximum), while smaller zooplankters hide in the dark below the turbid layer (where their zooplankton predators are more susceptible to visual predators). Naturally, factors such as food quality or temperature gradient will be decisive to the distribution pattern around a chlorophyll maximum, but the results of Harris (1988) indicate that interesting predator-prey dynamics are associated with turbid layers. Hitherto the role of the specific light conditions in such layers has been ignored (but see Rosland and Giske, 1994; Giske *et al.*, 1994).

Vertical distribution and resource level

Studies relating diel vertical migration to the availability of food have suggested that food limitation can prevent the zooplankter from undertaking vertical migrations (Huntley and Brooks, 1982; Dagg, 1985; Johnsen and Jakobsen, 1987), and that only when food is abundant can the animals afford to migrate (Dagg, 1985). Others have failed to observe such a relationship (Bohrer, 1980; Frost, 1988; Ohman, 1990) or even found the opposite correlation (Koslow and Ota, 1981; Gliwicz, 1986). The present model indicates that the copepods should display different migratory behaviour to various levels of resources. At the lowest food concentrations, the optimal strategy is to stay in the chlorophyll maximum, and almost cease migration (Fig. 14). Increasing resources first leads to deeper distributions, but eventually the turbidity allows shallower distribution. This agrees both with the earlier emphasis on resources and the present view of predation and abundance of predators as the main forcing of vertical migration.

Indirect effects, population dynamics, and copepod anti-predator behaviour

The enormous reduction of encounters between planktivores and their zooplankton prey at increasing depths (Fig. 3) suggests that changes in vertical migration patterns are an efficient anti-predator behaviour. This method of predator evasion in pelagic environments therefore strongly affects the feeding rate, growth, and abundance of planktivores. The same argument applies during the piscivore-planktivore interaction (Giske and Aksnes, 1992; Rosland and Giske, 1994). The recent findings by Frost and Bollens (1992) of the ability of zooplankton to rapidly adjust their anti-predator behav-

our to increased densities of predators seem to indicate a flexible response and could be a reason for pelagic fish continuously seeking new habitats for foraging.

The mortality rate of herbivorous copepods is generally obtained by multiplying the density of prey and the functional response of predators (e.g. Ricklefs, 1990). Instead, the model developed here (Fig. 14) and the demonstrations of phenotypic plasticity in zooplankton behaviour indicate a non-linear response in prey (zooplankton) mortality rates to increased predator (planktivore) densities (Abrams, 1991, 1993). Clearly, the model captures a situation where indirect effects (Miller and Kerfoot, 1987; Abrams, 1987; Werner, 1991, 1992; Werner and Anholt, 1993) affect the dynamics of both predator and prey, and probably also other species (alternative prey) within the same community or food web.

Although many studies have emphasized how the nature and magnitude of adaptive behaviour specifies the interactions between species, this is still not reflected at the level of population and community theory (Werner, 1992). The model developed by Ives and Dobson (1987) is an exception, and shows how fitness-maximizing prey should vary investment in a costly anti-predator behaviour with the density of predators and the efficiency of the anti-predator behaviour. They predicted that the investment in anti-predator behaviour should increase initially, but then decrease as the behaviour becomes more efficient (their Fig. 3A). Our study obtains the same result (increased efficiency, reduced migration, higher growth through more turbidity; Fig. 14) but the mechanism is quite different and related to resource level.

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