A MODEL OF OPTIMAL LIFE HISTORY AND DIEL VERTICAL MIGRATION IN *CALANUS FINMARCHICUS*

Øyvind Fiksen & François Carlotti

A copepod in a seasonal environment continuously faces the trade-offs among allocating surplus growth to a storage compartment (lipids), to somatic growth or to reproduction. By building up lipids, it can survive periods with low food, and gain reproductive success the following season by transforming fat to eggs. Also, copepods face a trade-off between survival and growth, as surface waters generally are more risky and productive than the dark refuges at greater depths, both in the diel and annual temporal scale. Implicit in these trade-offs are the numbers of generations, population dynamics and productive potential of the copepod. The authors develop a model which is used to investigate (1) how optimal diel and ontogenetic vertical migration might vary with season, individual state (size and lipid reserves) and growth conditions; (2) whether fat is mainly used for overwintering or for fueling reproduction in early spring; and (3) the adaptive value of behavioural flexibility in migration patterns. The model suggests an explanation for observations of absence of vertical migration during spring bloom and before descent to overwintering, and it suggests 1-2 successful generations per year in its basic version. It shows that migratory strategies are not similar between stages and strongly depend on the level of accumulated reserves, that the risk of predation can affect growth, distribution and number of generations and that one should expect phenotypic plasticity in DVM patterns. The model is very sensitive to the rate of metabolism during dormancy.

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INTRODUCTION

In a recent review, Verity & Smetacek (1996) advocated the importance of morphology and life history strategies in structuring pelagic ecosystems, and suggested a more synthetic focus on how predation and resources act through behaviour, morphology, physiology and life history to direct trophic relations. In this paper, we describe a model which predicts the optimal pattern of energy allocation (to growth, reproduction and lipid reserves) and habitat selection on both diel and seasonal temporal scale of the copepod *Calanus finmarchicus* (Gunnerus). This species is very abundant, and may structure the pelagic community in North Atlantic waters.

The central frame in which we have to understand life history and behavioural phenomena, is how they are related to fitness, i.e. how they relate to the ultimate goal of any living organism: to leave as many descendants as possible in the future (Roff 1992; Stearns 1992). A major problem in earlier studies of the adaptive significance of diel vertical migration (DVM), has been how to measure the relative importance of different selective forces, like temperature, food resources, and risk of predation (Kerfoot 1985; Lampert 1989; Williamson & al. 1996). This often led to single factor hypotheses. Now, models treating DVM as a trade-off between growth and risk of mortality have gained more support (Clark & Levy 1988; Mangel & Clark 1988; Ohman 1990; Fiksen & Giske 1995), due to their ability to unify fitness components in a single currency. Also, interesting interactions between DVM and other life history traits sensitive to the predator regime, like size at maturity, have been reported (De Meester & al. 1995).

Current biogeochemical and food-web models ignore the way individuals proceed to maximise fitness, and the flexible repertoire of behaviours they possess in doing so. This is similar to assuming that animals can be treated as particles, purely controlled by their environment, though this is rarely stated. However, copepods are known to respond readily to changes in their physical and biological surroundings: diapause, DVM and seasonal vertical migrations are dynamic responses to changes in resource availability or predation pressure

(LEIBOLD 1990; OSGOOD & FROST 1994; KAARTVEDT 1996; HIRCHE 1996a). These are the most amenable responses to environmental fluctuations, as altering the phenology is generally less costly and more flexible than other alternatives (MILLER & al. 1991). The recent analyses of North Sea data from the Continuous Plankton Recorder (CPR) survey (HAYS 1995a; HAYS & al. 1996) suggest that behaviour of *C. finmarchicus* also may be quite responsive to the abundance of planktivorous fish (*Clupea harengus* L.).

Many copepods seem to prefer microzooplankton instead of phytoplankton due to their higher nutritional value. Recently, OHMAN & RUNGE (1994) showed that *C. finmarchicus* can grow and reproduce at high rates on a diet consisting of ciliates and other microzooplankton. This complicates models of zooplankton production, as a simple linear food chain is not sufficient to describe the food environment. Here, we treat food as something that is available in certain quantities at different times of the year and with a spatial distribution based on 'common sense' assumptions. Similarly, we treat mortality rates as tied to seasons and habitats, justified by assumptions on predator abundance and efficiency, and only weakly coupled to stage or size.

Table 1. Functions of growth in CIV-CVI, development of stages up to CIV and the risk of predation in space and time. Parameter values are listed in Table 2.

Ingestion and metabolism in CIV-CVI (modified from CARLOTTI & RADACH 1996)

$$f_1 = p_1(st)k_1 \begin{cases} 0, & \text{if } \phi(z,t) < p_2 \\ \dfrac{\phi(z,t)-p_2}{p_3-p_2}, & \text{if } p_3 > \phi(z,t) \ge p_2 \\ 1, & \text{if } \phi(z,t) \ge p_2 \end{cases}$$ Ingestion rate as a function of stage and food abundance $\varphi(z,t)$ (Fig. 6).

$$f_2 = p_4 \cdot (p_5)^{T(z,t)}$$ Temperature dependence of ingestion rate.

$$f_3 = W^{p6}$$ Allometric ingestion relation, W is somatic body mass in µg carbon.

$$I = f_1 \cdot f_2 \cdot f_3$$ Total ingestion [µgC ind^{-1} d^{-1}]

$$f_4 = (1-p_7) \cdot I$$ Egestion

$$f_5 = p_8 W$$ Routine metabolism

$$f_6 = p_9 I$$ Active metabolism

$$G = I - f_4 - f_5 - f_6$$ Growth, µgC assimilated ind^{-1} d^{-1}

Development rate and moulting probability of stages below CIV

$$D' = \frac{6419+691}{[T(1,t)+10.6]^{2.05}}$$ Temperature dependence in development time (days) from spawning to CI.

$$D = D' \cdot \begin{cases} \dfrac{300}{100+\phi(1,t)}, & \text{if } 200 > \phi(1,t) \\ 1, & \text{if } 200 \le \phi(1,t) \end{cases}$$ Influence of food on development time, food is not limiting above 200 µgC L^{-1}

$$D_s = \frac{D}{7}$$ The average time between each stage (including hatching), i.e. days stage^{-1}.

$$D_r = \frac{1}{D_s}$$ The moulting rate [d^{-1}] used for stages from eggs to CIV.

$$P_m(t) = 1 - \exp(-k_2 D_r dt)$$ The corresponding probability of moulting during the time interval dt, slightly tuned (k_2) to fit the points in CORKETT & al. (1986).

We seek to explain how an optimal *C. finmarchicus* balances growth and risk of mortality so that fitness is maximised, constrained by a seasonal and spatially heterogeneous environment. We treat this as a state-dependent life history problem (MᶜNᴀᴍᴀʀᴀ & Hᴏᴜsᴛᴏɴ 1986, 1996; Hᴏᴜsᴛᴏɴ & al. 1988; Mᴀɴɢᴇʟ & Cʟᴀʀᴋ 1988), where states are the structural body size and fat reserves (lipids). A major problem for copepods is to survive winter. To do this they have to build up a sufficiently large lipid storage (Hɪʀᴄʜᴇ 1996b). Also, their predators may be more abundant or more efficient in near surface waters, where food and temperature give best opportunities for growth. In addition, they must lay eggs at the best time of the year for the reproductive success of the eggs. These are essential elements copepods must trade-off to ensure as many viable descendants in the future as possible.

THE MODEL

Structure of the model organism

Stages from eggs to copepodite III (CIII) are represented by simple boxes, and transfer (development) is assumed to be a function of food and temperature only (Table 1). We deliberately chose to keep these stages at a coarse resolution, because their behaviour is not considered, and much computer time is saved by this simplification. It is often argued that these stages suffer higher mortality and thus maximise survival to reproduction by minimising development time (Wᴇʀɴᴇʀ & Gɪʟʟɪᴀᴍ 1984; Fɪᴋsᴇɴ & Gɪsᴋᴇ 1995). Their vertical and developmental strategy is therefore assumed to be fixed:

stay near the surface, grow and develop at maximal rates, i.e. follow a simple 'maximise growth' rule. This is in accordance with theory (Wᴇʀɴᴇʀ & Gɪʟʟɪᴀᴍ 1984) and observations, juvenile stages are found in surface layers, allocate all their surplus gain to somatic growth, and usually perform no or only minor DVM (e.g. Kʀᴀᴜsᴇ & Rᴀᴅᴀᴄʜ 1989).

For stages CIV and above we introduce two state variables (similar to Hᴀʀʀɪs 1983; Cᴀʀʟᴏᴛᴛɪ & al. 1993); (1) the structural body mass x, and (2) the amount of lipids y, stored in the fat sac. The maximum load in the storage compartment, $Y(x)$, increases with x for CIV and CV, while adults can not change their structural mass (Fig. 1). Cᴀʀʟᴏᴛᴛɪ & al. (1993) compiled data on the proportion of storage mass in the late copepodites of *C. finmarchicus*, and found that storage may account for as much as 50-60 % of total dry body mass in CV (e.g. Sᴀʀɢᴇɴᴛ & Fᴀʟᴋ-Pᴇᴛᴇʀsᴇɴ 1988), but less in adults. Here, we let total storage (including fat in the fat sac, cells, muscles etc.) be at most 70 % of CV (carbon), less for CIV and adults, respectively (Fig. 1). The fat/structural mass ratio is assumed to increase more rapidly in CVs than in CIVs (Fig. 1). Adults have a critical moulting and maturation weight (structural) at 110 µgC, and can then allocate assimilated matter to storage or to reproduction. Copepodite stages CIV (15-40 µgC) and CV (40-110 µgC) can allocate to growth or storage. The storage is not affected by moulting and can be carried across stages.

If growth is negative, lipids will be metabolised, while structural growth is irreversible. The copepod will starve and die at a constant rate when growth is negative and the lipids are spent ($y = 0$). Diapause is initiated if the

Table 1. Continued.

Predation (and starvation) risk in space and time

$$m_c'(z, day) = m_c(z) + m_c(z)\sin(\pi \frac{day}{361})$$

$$m_n(day) = m_n + m_n \sin(\pi \frac{day}{361})$$

Seasonal fluctuation of daily predation rate in habitat 1 (Hab1) and habitat 2 (Hab2) for all stages (predation is invariant with time in Hab3), *day* is day of year. (See also Table 2.)

$$m_c(z, t) = m_c'(z, day)\left[0.5 + k_3 \sin(\pi \frac{h}{24})\right]$$

$$m_c(z = 3, t) = m_c(z = 3)$$

Diel variation in predation rate, the parameter k_3 sets the level of fluctuation between midnight and midday and *h* is the hour of the day. (See also Table 2.)

$$\mu_c(y, z, t) = 1 - \exp\{-[m_c(z, t) + \sigma(y)]dt\},$$

$$\sigma(y) = \begin{cases} k_4, & \text{if } y \leq 0 \\ 0 & \text{else} \end{cases}$$

Mortality risk for the state-resolved stages CIV-CVI in the time interval t to $t+1 = $ dt. Risk of starvation is state dependent.

$$\mu_n(t) = 1 - \exp\{-m_n(day)dt\}$$

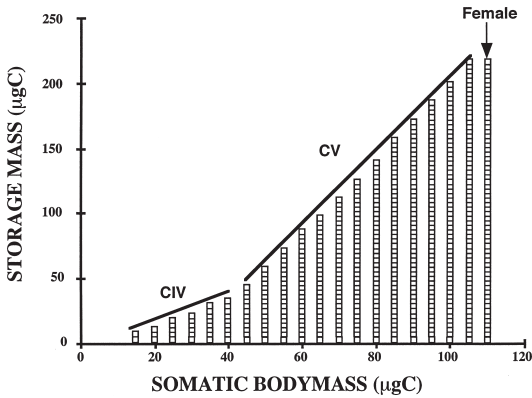Mortality risk for stages < CIV, which only fluctuate seasonally.

Fig. 1. The state space of individual CIV (15-40 µgC), CV (45-105 µgC) and females (110 µgC). Maximum load of fat increases with somatic body mass, so that it corresponds to at most 70 % of total mass on carbon basis. The fat/soma ratio shows a steeper increase in CV than in CIV (line). The figure shows the (discrete) resolution of the state space, i.e. the total number of possible combinations of somatic and storage mass a copepod can be in. Starvation is induced along the x-axis ($y = 0$, see Table 1), when the lipid compartment is exhausted. The sum of somatic mass (x-axis) and storage mass (y-axis) gives total body mass in µg carbon.
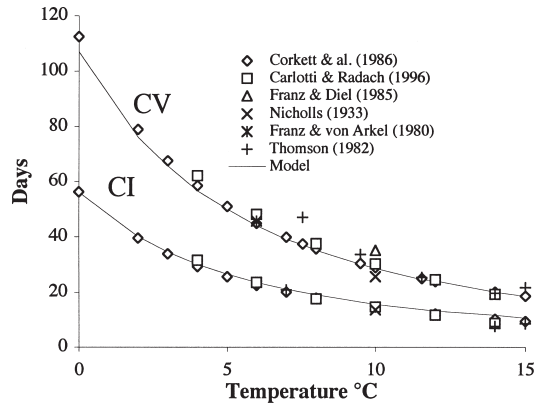

Fig. 2. The development time from hatching to stage CI and CV at superabundant food but various temperatures, from the experiments and models. Development time is based on Heinle graphs (the time when the cumulative proportion of stages below CI or CV equals 0.5, see e.g. MILLER & TANDE 1993). Time required to grow into stage CV gave best agreement when a Q_{10} of 2.5 (1 at 10 °C) was applied. Ingestion rate is reduced by 25 % to balance for the abandoned function f4 (see text) from CARLOTTI & NIVAL (1992). All parameters are listed in Table 2.

copepod enters the 'deep' habitat (Hab3) and stops migrating, and the descent to Hab3 (preparation for diapause) is assumed to cost 1 % of the copepod's total body mass.

Growth and development

The temperature dependency of development from eggs (including hatching time) to CIII (D') was found in CORKETT & al. (1986), and we applied their empirical development rate to the median stage CI for all stages (Table 1). At low food densities, the development of nauplii (D) is hampered, and from VIDAL (1980) it seems like food is not limiting above about 200 µgC L^{-1}, but strongly limiting below 50 for the development time of *Calanus pacificus* (Brodsky). Hence, we assume development time to be doubled at 50 µgC L^{-1} and non-limiting above 200 µgC L^{-1} for the feeding naupliar stages (> NIII) and a hyperbolic decline in development time between (and below) these food densities (Table 1). By simply assuming equal residence time (D_s) in each stage (isochronal development), moulting rate (D_r) and probability (P_m) in each nauplier stage are deduced. The same values are used for stages CI, CII and CIII (Table 1).

For the older stages (CIV, CV and adults), growth is a function of temperature, food and somatic body mass, similar to CARLOTTI & RADACH (1996), which is based mainly on the formulations (functions f1 to f6 in Table 1)

from CARLOTTI & NIVAL (1992), and on the concept of 'critical moulting weights'. However, some changes have been made. First, the model contains no information of individual age, only their stage, size and reserve load. This, and the backward iteration procedure (see below), implies that the cumulative influence on ingestion as the individual approaches the next critical moulting weight (function f4 in CARLOTTI & NIVAL 1992), must be abandoned. Second, transfer is not a cumulative function of weight (function f10 in CARLOTTI & NIVAL 1992), instead moulting takes place when individual weight equals the critical moulting weight. Nor does growth affect mortality *per se* (their function f9), and partitioning of matter between growth and reproduction (their f8) is here a result of the optimisation, i.e. a prediction, not a forcing of the model.

The predicted development times from hatching to CI overlap those from CORKETT & al. (1986) and other sources fairly well (Fig. 2), however, due to the simple stage-structured model which induces a diffusion of individuals through stages, it was necessary to tune rate of moulting down to obtain this fit (Table 1). A way to avoid such problems is discussed by MILLER & TANDE (1993) and CARLOTTI & NIVAL (1992), but would be too computer-demanding in the present model. The development times to CV are also comparable with other reported and modelled values (Fig. 2).
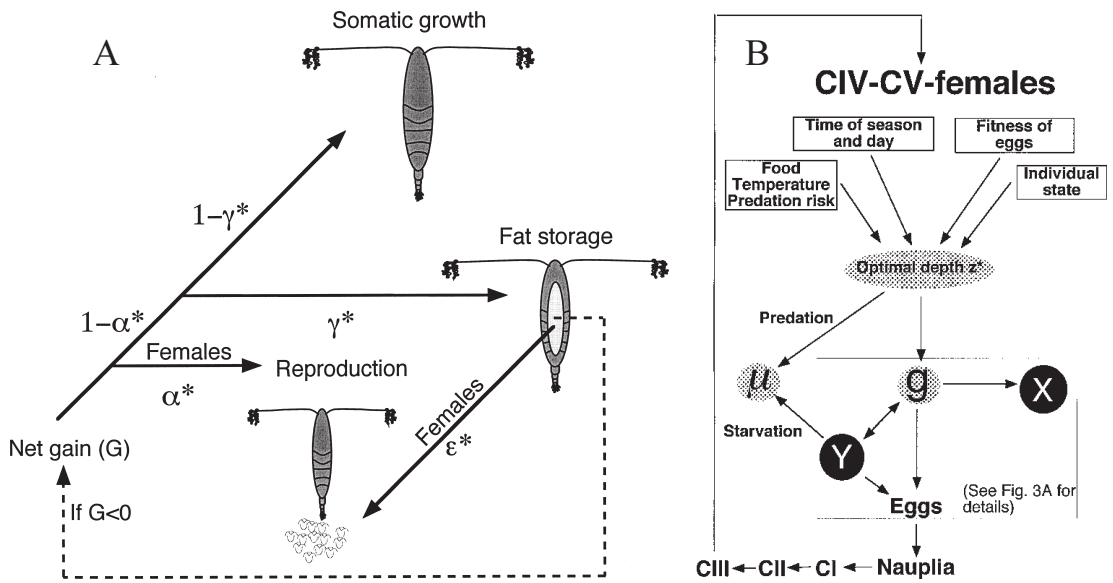
Fig. 3. An overview of important variables, rates, state variables and operators of optimality. A. A flow-diagram of the operators of optimality on the different uses of surplus gain and state variables. Net gain is the assimilated matter – basic metabolism, and if it is > 0, it may be used for reproduction (females), structural (somatic) growth or to storage (fat). If net gain is negative, energy will be supplied from the fat reserves. Fat can also be used in reproduction. B. A conceptual diagram on the connection between life cycle, environment, decision variables, vital rates and states (in stages CIV to females) in the model. The most prominent factors affecting the optimal depth, and directly and indirectly the vital rates (μ and g) are listed in boxes. The state variables x and y, and the allocation pattern (in the frame, and in Fig. 3A) are important to the number of eggs produced at different times. The life cycle is completed as eggs develop to nauplii, CIII and then to CIV again.

State dynamics and reproduction

A growing *Calanus* can allocate surplus gain to somatic tissues x, to lipids (reserves) y, or, if it is a mature female, to egg production b (Fig. 3A, B). The state dynamics are described by

$$x(t + 1) = x(t) + G(1 - \alpha)(1 - \gamma)$$

$$y(t + 1) = y(t) + G(1 - \alpha)\gamma\delta k_5 - y(t)\varepsilon \tag{1}$$

where G is the net gain between t and $t + 1$, α is the fraction of this gain allocated to reproduction, γ is the fraction allocated to reserves, δ is the reduction of basic metabolism in a hibernating copepod and k_5 is the conversion factor from assimilated matter to energy densities of lipids (and when lipids are used in respiration). The state compartments are constrained by a maximum and a minimum (zero) thresholds of fat content (Fig. 1). For negative growth, the reserves are metabolised (Fig. 3B), and if $y = 0$, they starve.

Some unanswered questions remain of how *Calanus* utilises lipids to produce eggs, e.g. in advance of the spring bloom (HIRCHE 1996b). Most likely, lipids are fueling the build-up of gonads during late winter (GATTEN & al. 1980), and thus enhancing the production of eggs. We have added this possibility by letting the copepod make eggs out of fat, so that ε in Eqs 1 and 2 (below) is the fraction of fat storage allocated to gonads. Reproduction b thus consists of the net growth not allocated to reserves or somatic growth plus the lipids used for egg (gonad) production:

$$b = \frac{G\alpha + y\varepsilon}{2\omega} \tag{2}$$

where ω is the matter required to produce one egg and other symbols as above. The number of eggs is multiplied with the sex ratio (0.5), since the model is based on females only. At most 20 % of the total lipid storage can be transformed to eggs per day.

Egg laying tends to vary greatly, depending on diets, location, etc. (HARRIS 1996; HIRCHE 1996b). From the studies presented in Fig. 4 it seems that *Calanus* fed natural mixtures of food particles can produce more eggs than if they are fed unialgal diets, and the assumption
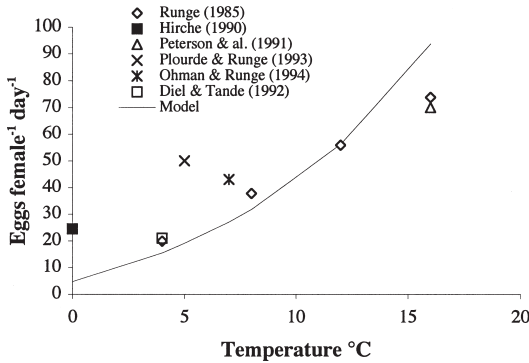
Fig. 4. The temperature-fecundity relationship under supera-bundant food conditions and fixed temperature (10 °C). All parameters are listed in Table 2.
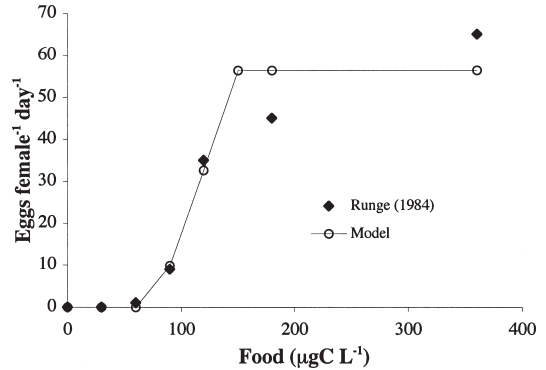

Fig. 5. The effect of food abundance on spawning, using basic run parameters (Table 2).

that spawning rate increases at higher temperatures seems justified (Fig. 4). To our knowledge, the only available study of egg laying from the laboratory, with constant temperature and varying food is RUNGE (1984), with *C. pacificus*. However, *C. pacificus* and *C. finmarchicus* produce similar numbers of eggs (RUNGE 1985) under different temperatures, so we take the correspondence between model and these data (Fig. 5) as an indication that the bioenergetics are within reasonable range.

Risk of mortality

Models of zooplankton dynamics may relate mortality rate to e.g. body size, habitat, light conditions, food supply or predator abundance, or simply use fixed constants to close the model. The major difficulties associated with measuring mortality rates have resulted in a low number of studies on zooplankton mortality, though new techniques may encourage such measurements in the future (WOOD 1994; OHMAN & WOOD 1996; NISBET & WOOD 1996). For *C. finmarchicus*, *in situ* mortality

Table 2. List of parameters.

Parameter	Description	Unit	Value
$p_1(st)$	Maximum ingestion rate in CIV, CV and CVI[1]	$\mu gC\ \mu gC^{-1}\ d^{-1}$	1.5, 1.3, 1.0
p_2	Lower limit of feeding	$\mu gC\ L^{-1}$	50
p_3	Food is unlimiting above p_3	$\mu gC\ L^{-1}$	200
p_4	Temperature coefficient, Q_{10} = 2.5, 1 at 10 °C	-	0.4
p_5	Temperature coefficient	-	1.096
p_6	Exponent in allometric relationship	-	0.7
p_7	Assimilation efficiency	-	0.7
p_8	Routine excretion rate	$\mu gC\ \mu gC^{-1}\ d^{-1}$	0.04
p_9	Active metabolism, proportionality constant	-	0.02
k_1	Correct for lack of moulting	-	0.75
k_2	Fitting development time to CORKETT & al. (1986)	-	0.9
k_3	Difference in predation between day and night	-	1.0
k_4	Starvation rate when fat is absent	ind $ind^{-1}\ d^{-1}$	0.2
k_5	Energy difference assimilated matter/fat	-	0.7
δ	Diapause metabolism	-	0.2
ω	Egg weight	μgC	0.23
$m_c(z)$	Depth (habitat z) specific mortality (see Table 1)	ind $ind^{-1}\ d^{-1}$	0.04, 0.02, 0.001[2]
m_n	Mortality in stages < CIV	ind $ind^{-1}\ d^{-1}$	0.08

[1] This parameter is set to give maximum ingestion rates (for CIV, CV and CVI, respectively) in the range from DARO (1980) and GAMBLE (1978), given the rest of the formulation on ingestion (Table 1). The values are different from those used in CARLOTTI & RADACH 1996 because they adapted their values to *C. finmarchicus* in the North Sea, which are smaller in size and contain less lipids than those in North Atlantic waters (CARLOTTI & al. 1993).

[2] For Hab1, Hab2 and Hab3, respectively. Note that the realised rates are expressed in Table 1, and vary with time of day and season.

is reported to be strongly correlated with depth by AKSNES & MAGNESEN (1983), and it is likely that the level of irradiance (and the reactive distance of planktivores) will make risk of mortality fluctuate in a diel and seasonal manner (AKSNES & GISKE 1993; GISKE & al. 1994).

In order to model the phenology of *Calanus*, the temporal and spatial variations in risk will be important forces shaping optimal life histories. As a basic point of view, we hold that for the later stages of *C. finmarchicus*, mortality can be tied to (see Table 1 and Fig. 3B): 1) habitats (m_c), with higher risk of mortality in well lit surface waters where they can be seen by visually searching predators (CLARK & LEVY 1988; AKSNES & GISKE 1990; 1993; GISKE & al. 1994; AKSNES & BLINDHEIM 1996); 2) time of the year and day (m_c'), with risk of mortality increasing towards summer, when temperature and light (and thus searching efficiency), abundance and activity of predators are at maximum; and 3) individual state $\sigma(y)$, i.e. a low state (no fat reserves) induces a risk of starvation and, indirectly, more exposure to predation by staying closer to the surface. AKSNES & MAGNESEN (1983) found that mortality decreased strongly when *C. finmarchicus* grew larger, so we use a higher basic rate of mortality (m_n, but they do not suffer from starvation) for stages < CIV (no behaviour) than for stages above (Table 2).

Seasonally, we let predation rate be a sinusoidal curve, reaching its maximum in mid-summer (Fig. 6; Table 1). Mortality fluctuates also on a diel basis (m_c), reflecting the irradiance at the surface (Table 1). From this reasoning, risk (μ_c and μ_n) varies over the year, day, and habitat (Fig. 3B). A starvation rate of 0.2 d^{-1} is added to mortality when the fat reserves are empty ($y = 0$). As dynamic models are based on risks of mortality, the rates are converted to probabilities by the exponential distribution (Table 1; MANGEL & CLARK 1988). The overall level of mortality was set to obtain a stable population.

Environment

In our basic run, we use a major spring bloom, continuously decreasing food through summer (organic matter is slowly exported) and low food levels for the rest of the year (Fig. 6). Also, food abundance and temperature are high in the surface layer (Hab1), dropping off by 50 % in the subsurface habitat (Hab2), and there is no food and low and stable temperature in Hab3 (Fig. 6). The term 'food' should be interpreted in the widest sense, including abundance and quality of the food items (phytoplankton and microzooplankton). Temperature follows a sinusoidal curve over the season and increases towards the surface (Fig. 6).

Calculation of optimal habitat and allocation through time

The result of natural selection is that individuals adopt morphologies, behaviours, and phenologies that maximise their fitness (Fig. 3A, B). For a long time, evolutionary ecologists have discussed the correct measure of fitness (STEARNS 1992). We applied the Perron Frobenius Theorem (MCNAMARA 1991; FIKSEN 1997) to calculate fitness, as it seems to provide a solution to the problem of maximising fitness that is simple and intuitive, and merges the prospects of the young (larval ecology) into the life history decisions, i.e. the value of laying an egg will depend on the expected future reproduction of the egg. That is, we let fitness be the number of descendants left far into the future, found by multiplying fitness (expected future reproductive success) of the eggs $F_n(1,t)$ with the number of eggs b produced by a female at t and add the expected future fitness $F_c(x, y, t+1)$ of the resulting new states in the dynamic programming equation (see MANGEL & CLARK 1988 for an introduction to dynamic programming):

$$F_c (x, y, H) = 1 \qquad (3)$$

$$F_c(x, y, t) =$$
$$\max_{z, \alpha, \gamma, \varepsilon} \left\{ bF_n(1, t+1) + \left[1 - \mu_c(y, z, t)\right] F_c(x', y', t+1) \right\} \qquad (4)$$

Here, the Eq. 3 gives the 'terminal fitness', i.e. the value of surviving to the 'horizon' H, the end of the model, which is set to 1 independent of state. In a sequential, backward working procedure, the maximal fitness F_c and corresponding optimal z^*, α^*, ε^* and γ^* are found for all x and y at all times. The term $\mu_c(y, z, t)$ is the probability of dying from predation and starvation between $t+1$ and t, with the state dependency and spatial and temporal variations as explained above (Tables 1 and 2). The state dynamics are incorporated in expression 4 as $x = x(t)$, $x' = x(t+1)$, $y = y(t)$, and $y' = y(t+1)$, in Eq. 1 above, and the outcome of the state dynamics are defined by the optimal combinations of z^*, α^*, ε^* and γ^* (Fig. 3A, B). Note that if $F_n(1, t+1)$ is removed from the expression, the optimisation criterion changes from maximising rate of increase (future descendants) to maximisation of lifetime reproductive output (R_0). Implicit in the above expression is the optimal solution to the allocation of fat in production of gonads and eggs (ε^*), which would reduce lipid storage y', and increase the number of eggs according to Eq. 2.

To find the fitness of an egg $F_n(1,t)$ at time t, the link to fitness in older stages must be established, even though the younger stages are assumed not to have any

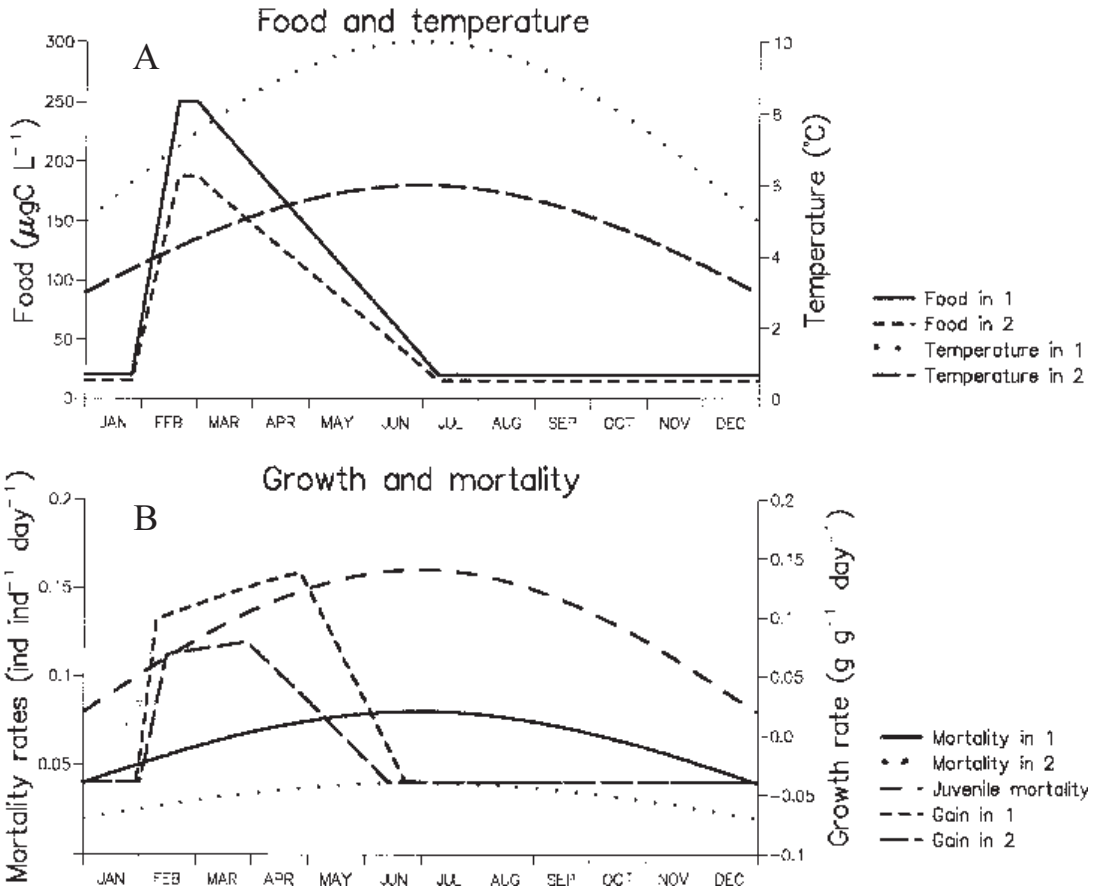## Food and temperature

Growth and mortality

Fig. 6. A. The hypothesised seasonality of the food and temperature in Hab1 (surface) and Hab2 (subsurface). In Hab3 (deep water) no food and a stable temperature (2 °C) is assumed. B. The comparable growth and mortality rate in Hab1 and Hab2 and the mortality of eggs-CIII. Mortality in Hab3 is constant ($m_3 = 0.001$ d^{-1}). Equations for the curves are listed in Table 1. The subsurface-layer is half the surface for mortality, food and temperature.

other options than to stay near the surface and grow and develop at maximum rates. The equations are

$$F_n(s, H) = 1 \tag{5}$$

$$F_n(s,t) =$$
$$[1-\mu_n(t)]\{P_m(t)F_n(s+1,t+1)+[1-P_m(t)]F_n(s,t+1)\} \tag{6}$$

with $F_n(s,t)$ the fitness of an individual in stage s (egg-CIII) at time t, and $F_n(s = 1,t)$ the expected contribution to future generations from an egg laid at time t, which enters into Eq. 4. The probability of moulting from one stage to the next $P_m(t)$ is food and temperature dependent (Table 1), and mortality is as explained in Table 1.

Population dynamics

The dynamics of egg abundance $N_e(t)$ is simple; adults ($N_{x,y,z}(t)$) produce them, they moult to nauplii and they are subject to predation (Table 1):

$$N_e(t+1) =$$
$$[1-\mu_n(t)]\left\{N_e(t)[1-P_m(t)]+\sum_{x>X_a,y=0,z=1}^{X,Y,Z}N_{xyz}(t)b_{x,y,z}\right\} \tag{7}$$

Similarly, the dynamics of NI-CIII $N_s(t)$ are simple box-transfer (moulting) across stages, and survival:

$$N_s(t+1) =$$

$$\left[1-\mu_n(t)\right]\left\{N_{s-1}(t)P_m(t) + N_s(t)\left[1-P_m(t)\right]\right\} \tag{8}$$

The dynamics of CIV and beyond are a more complex matrix projection (not stated), as they are spread into states and habitats through time. We apply the optimal values of depth (z^*) and allocation rules (α^*, γ^*, ε^*) for all combinations of states and times, to determine the development of the population. All processes are as described above. The model is initiated in mid winter (1 January), with one CV (female) of median size and reserves.

RESULTS

Basic run

The model is run for three similar years, using the environment in Fig. 6, but only results from the second year are presented in Figs 7-13. The average fat content of females (Fig. 7A) and CIV-CV (Fig. 8A) show major seasonal fluctuations, with a build-up of storage in April and May, a slow decrease until next January (diapause), and a sudden drop at the initiation of the spring bloom in February. In overwintering females, the fat left after the hibernating period is converted to eggs (Fig. 7A, C), so the fat content is reduced a few weeks earlier in females than in copepodites. The copepodites start their preparation for winter in late March, when an increasing proportion of assimilated matter is allocated to storage (Fig. 8A, B). Females show a more abrupt switch in allocation patterns, after the first week of April, they direct all surplus energy to lipids, while before this time, all was used in egg production. In the model *C. finmarchicus* produce 2 generations, or three peaks of increase in total abundance (Fig. 7C), where the first two are from the same ascending population. The overwintering females spawn ahead of the bloom, while the resting CVs must mature before they reproduce. By chance in the interpolation process (cf. MANGEL & CLARK 1988, p. 228) and as a result of the eggs which are laid at different times, the state-distribution of the population spreads out as the model runs. The average number of eggs laid per female increases in summer as temperatures rise (Fig. 7C). It is clear that only a small fraction of the eggs laid late in the season will reach a state high enough to survive winter (the high mortality rate in April, see Fig. 7C), and individuals die off in large numbers as food abundance decreases.

The average (based on biomass) migratory pattern is to stay near the surface in the bloom period (late Febru-

ary) and in April/May (Figs 9 & 10). Then a gradual descent of the population to the overwintering habitat takes place. Both the DVM and seasonal migration patterns are state dependent (Figs 9 & 10). It is obvious that individuals with a high fat/somatic mass ratio can afford a less risky vertical migration strategy, particularly by descending to overwintering depths earlier (Fig. 9). Low state individuals may have to stay in surface layer through the whole winter, because the risk of starvation exceeds the danger of being eaten by predators. This is not apparent in the basic version, but if the surface layer is given some growth potential throughout the winter, this becomes optimal for individuals in low condition (not shown). Consequently, with some growth in surface, no individuals starve in the model ('better dead than unfed'; HUNTLEY & BROOKS 1982).

DVM is most intense in March, after the bloom and while predation risk is increasing (Figs 9 & 10). This is also at a time when the fitness (i.e. expected future reproductive success) of eggs is shrinking (see below), so hurrying on to mature and reproduce may be a waste of energy. Instead, it is time to show more concern about predators, and to fill up the fat reserves to survive winter. The ascent in April is a way of filling up reserves as much as possible just before descent, so it is worthwhile to take the high risk associated with seeking surface layers at this time. When reserves are sufficiently filled up, *C. finmarchicus* start downward migration to the safer overwintering habitats. Fat-rich individuals may start the downward migration nearly 2 months before the low state individuals (Fig. 9). Also, between stages, strategies are not similar (Fig. 10). Adults show strong DVM after the spring bloom, but stop migrating quite early, and are also first to migrate down to overwinter. Copepodites IV show less extensive migrations, and stay in surface layer for a longer period of time, while CV show strong DVM through summer, and only a rather brief period of 'surface swarming' before descent.

Most *Calanus* overwinter as CV (Fig. 11), which is the stage where the highest fat/somatic body mass ratio can be reached (Fig. 1). Some overwinter as adults as well, and these have the option to spawn without further somatic growth. No moulting, maturation or gonadogenesis can be fueled from fat in the model (but may be in nature), so overwintering as adults can be advantageous to have the possibility of spawning in advance of the bloom. It is interesting to see that the three peaks of spawning seen in the relative abundance of eggs disappear in later stages, and in terms of relative abundance, it would appear from CV and females as if only one generation was produced.
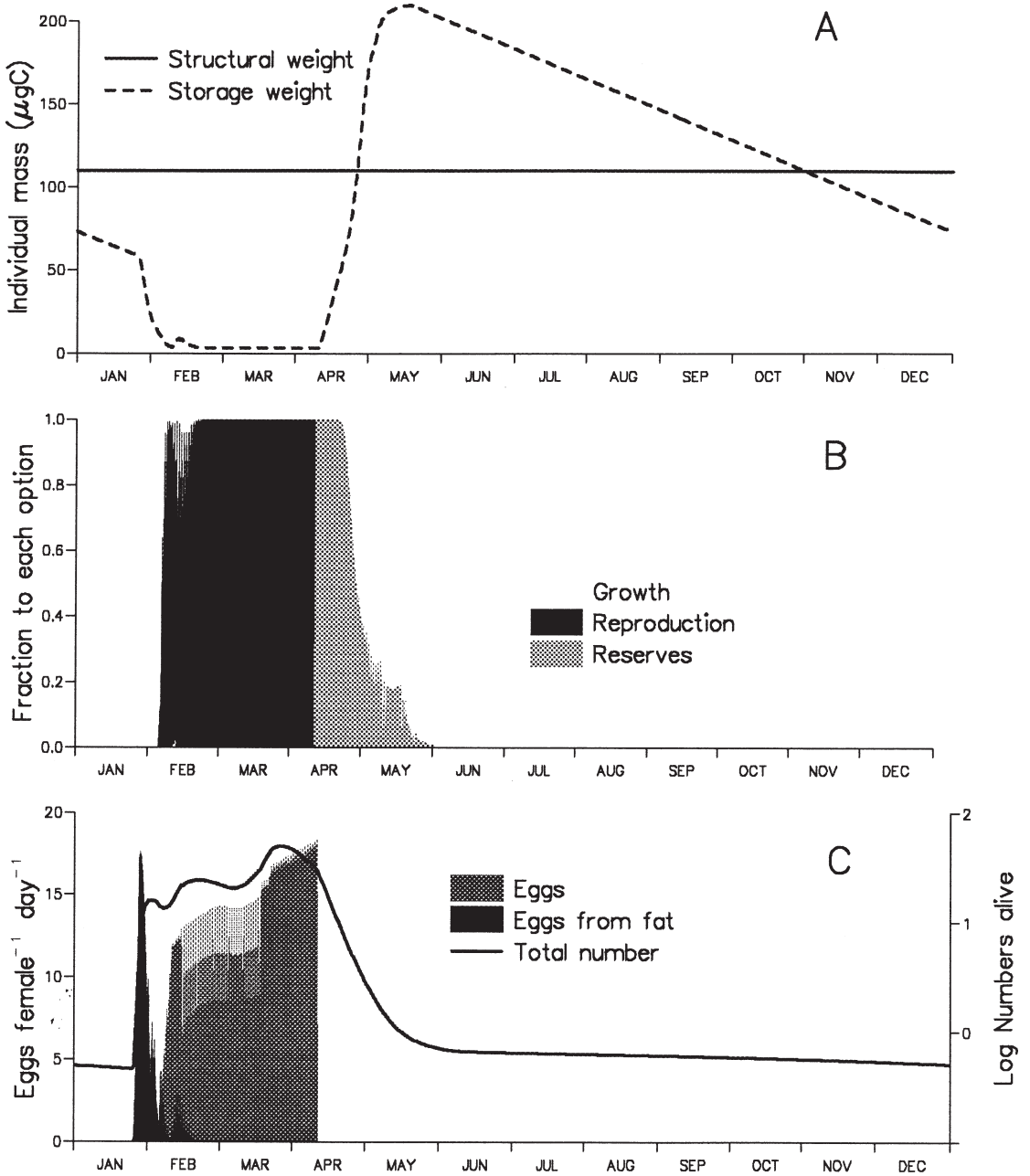
Fig. 7. Females in the basic run. A. The (averaged) development of the two state variables: structural (fixed for females) and storage compartment. B. Allocation patterns: fraction of assimilated matter used for growth (or when growth is negative: basic metabolism supported by stored reserves; white area), reproduction (black area) or storage (grey area) over time. C. The total abundance (line) and spawning per female, from allocation of surplus gain (grey) and when lipids are used for reproduction (black area).

Fitness in basic version

The fitness value (Eqs 4 & 6) reflects the expected future success of an individual, and is clearly variable with state and season (Figs 12 & 13). The value of egg production is high early in the season, and then drops off as the probability that the egg will either mature and give rise to a second generation, or reach a state which enables it to survive winter, declines. Also, the fitness
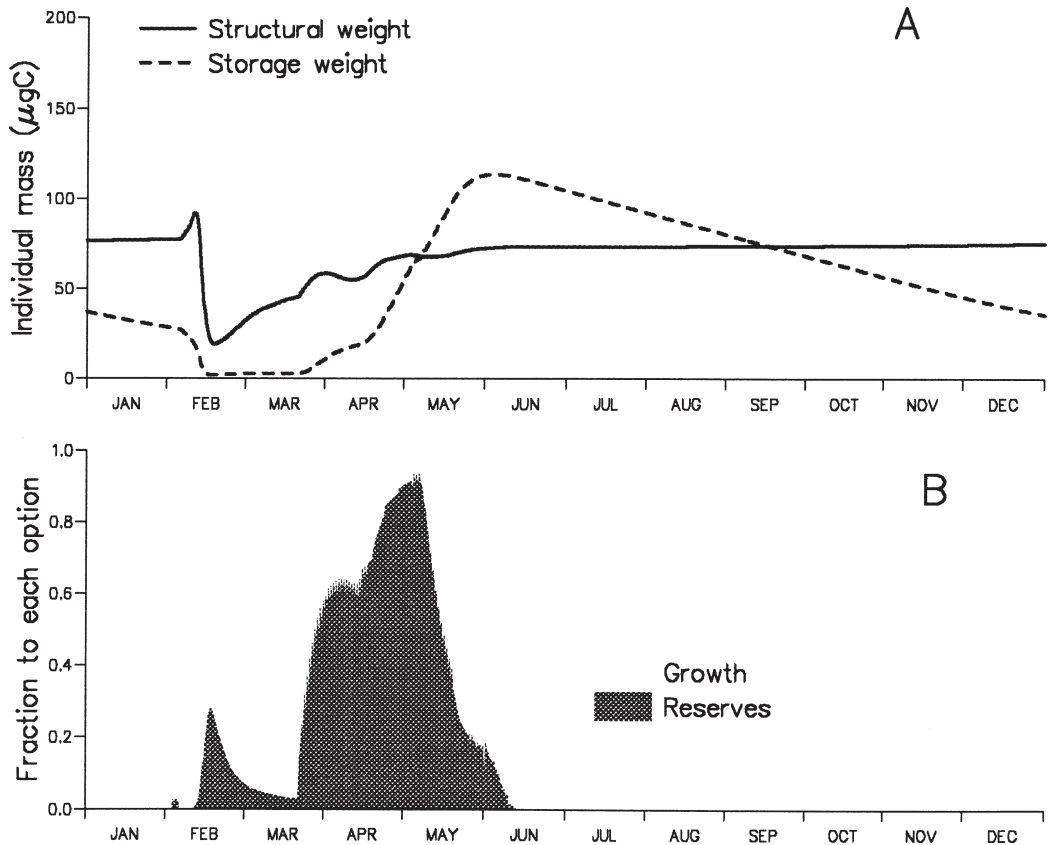
Fig. 8. CIV and CV in the basic run. A. The (averaged) development of the two state variables structural and storage compartment. B. Allocation patterns: fraction of assimilated matter used for growth (or when growth is negative: basic metabolism supported by stored reserves; white area) or storage (grey area) over time.

of all states increase towards the spring bloom, due to the increasing expectation of surviving to the next spawning event. No surprise, individuals with a large fat sac have considerably higher fitness in winter than low state individuals. Note that starving copepodites suffer a higher rate of mortality than stages CIII and below; therefore the fitness value is extremely sensitive to fat load at end of the productive season (Fig. 13). Fitness does not fluctuate much between years, indicating a stable population ($r = 0$).

The use of a fitness measure which does not take the expectation of survival and reproduction of eggs into account will give a completely erroneous solution to the life history problems of a copepod in seasonal environments. When the model is run with a fitness criterion saying 'maximise lifetime reproductive output' ($= R_0$), the population goes extinct after 2 years (not shown). This rule will predict much lower allocation to fat reserves, and much more to reproduction through-

out the season, leading to heavy starvation in winter. Obviously, copepods do not maximise lifetime reproductive output, they somehow assess the environment and concentrate spawning at the time when juveniles meet favourable conditions.

Sensitivity analysis to the effects of mortality and DVM

Mortality has a major effect on the life history of the modelled *Calanus*. If mortality is increased in Hab1 ($m_1 = 0.06$), the copepod spend more time in the safer, deep habitats, and will grow slower. As a result, the zooplankton developing in spring will have less matter to allocate, so less will be available for reproduction and only one generation emerges. Further, a smaller fraction overwinter as adults, it will now pay to use the early spring to grow and descend as soon as the appropriate state is reached. Reducing mortality in surface ($m_1 = 0.03$) causes opposite changes, the second generation becomes
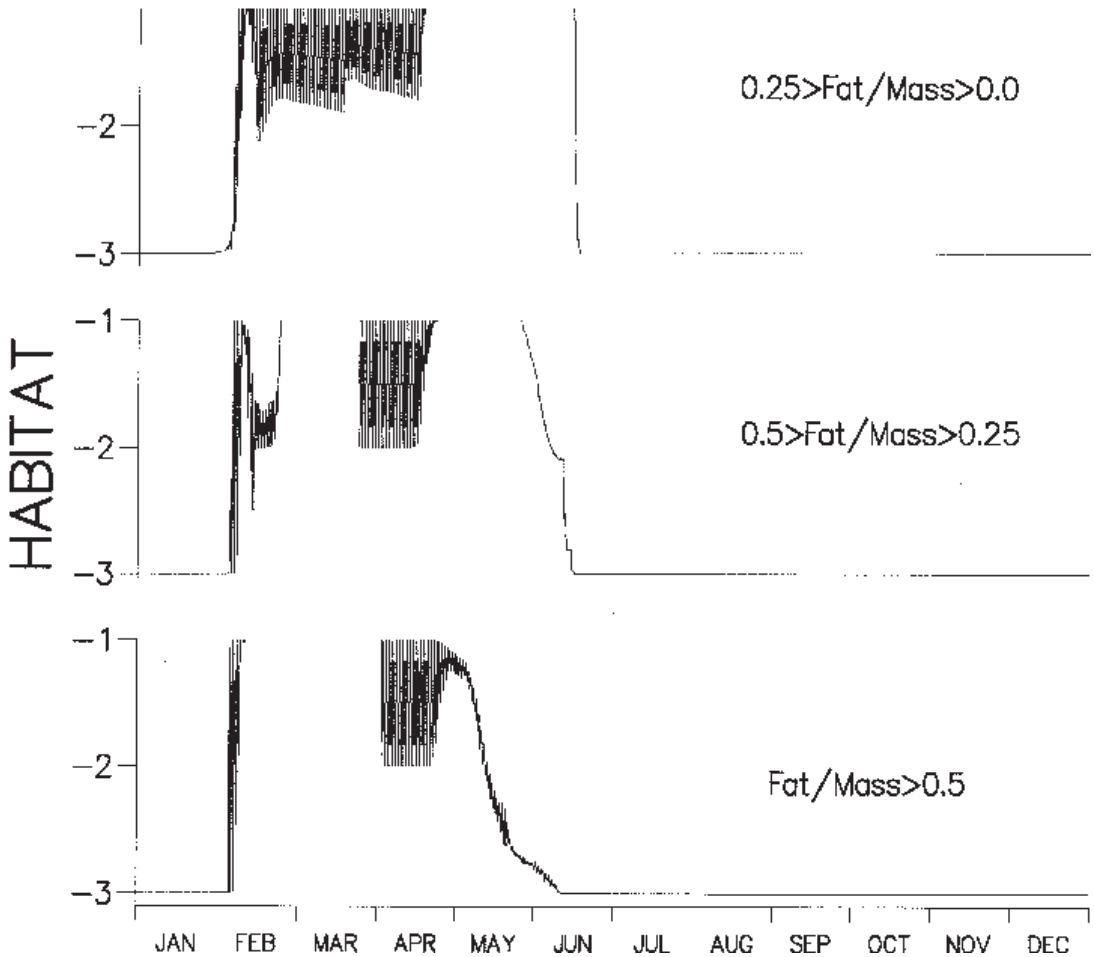
Fig. 9. The vertical distribution of 3 distinct condition groups through year 2, from an average of the whole population above CIV. Habitats 1-3 refer to the conditions specified in Fig. 1. The absence of the line means that no (or only very few) individuals are in the state-space at the time. Upper panel: low condition, fat is less than 25 % of body mass. Middle: medium condition, lipids are between 25 and 50 % of total mass. Lower panel: high condition, lipids constitute more than 50 % of body mass.

Table 3. The benefit of flexible behaviour on population dynamics as measured by total abundance after three years. The column 'Population' lists the abundance of individuals with fixed strategies divided by the abundance of individuals with flexible strategies. Note that this is not the effect from the modification *per se*, only the effect of behavioural change to the new situation (in the second year).

Description	Modification	Population
Mortality in surface	+ 0.01 [d⁻¹]	0.916
Mortality in surface	+ 0.02 [d⁻¹]	0.766
Mortality in surface	+ 0.04 [d⁻¹]	0.430
Mortality in surface	− 0.02 [d⁻¹]	0.947
Food in surface	* 2	0.424
Food in surface	* 0.75	0.118
Temperature in surface	+ 2	0.797
Temperature in surface	− 2	0.615

more prominent, and DVM ceases completely except for a period about halfway through the growth season.

The mortality rate of juveniles (m_n, Table 2) and the strength of the diel variations in mortality (k_3, Table 2) also modify the behaviour of copepodites in a similar manner. When m_n is increased to 0.1 d⁻¹ the production of a second generation becomes less profitable, consequently a more careful (more DVM) strategy comes forth. The opposite is true for a m_n value of 0.06, then it will pay the earliest juveniles to go for a spawning before winter. In these cases, modification of DVM patterns will be the operator deciding the number of generations and total production of the stock. In effect, an increase in predation pressure on either level in the life cycle should be met with more risk-averse behaviour.
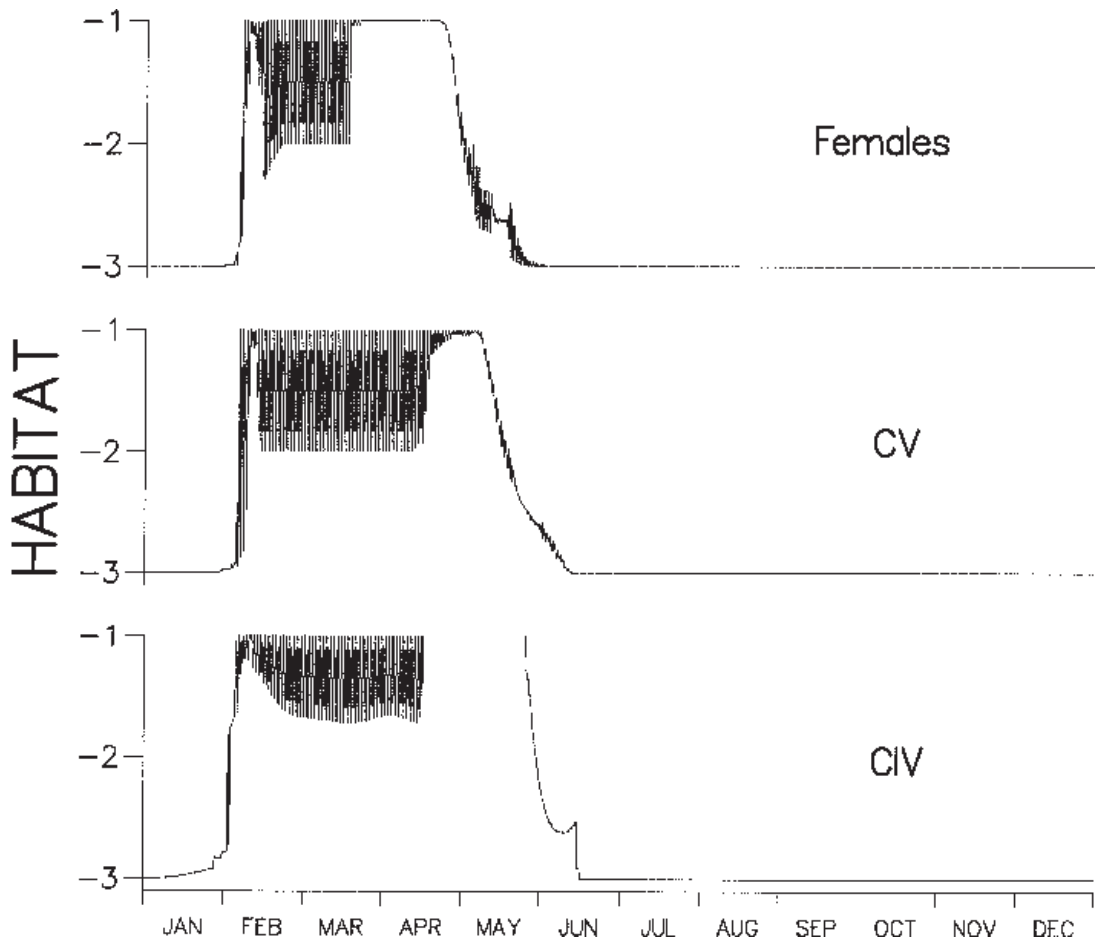
Fig. 10. Average vertical distribution of stages CIV (lower panel), CV (middle) and adults (upper) in the second year.

How important is the flexibility of behaviour?

Lately, many observations have been made on the ability of zooplankton to adjust their behaviour phenotypically to a fluctuating predator regime (e.g. OHMAN 1990; LOOSE & DAWIDOWICZ 1994; KLEIVEN 1996; KAARTVEDT 1996). What is the magnitude of the benefit associated with flexibility to *C. finmarchicus* in the present model? To test this, we ran the model successively with fixed and flexible behavioural repertoires for simulations with the second year diverging from the others. The population growth is most sensitive to fixed patterns when food levels are diminished and risk in surface increased (Table 3). Particularly, only a minor reduction in food levels (25 %) causes major starvation through winter, as the copepods then fail to supply enough storage to avoid starvation in winter. This indicates the importance of not underestimating the level of energy required to manage through the winter, and

the possibility that natural populations will ensure fat storage large enough to manage even if conditions in spring and winter turn out to be below average. For mortality, an increase is more severe than a decrease (Table 3). Likewise, we may therefore expect copepod behaviour to be more sensitive to an increase in predation risk, than to decreases. From the numbers in Table 3, there seems to be good reason to expect plasticity in DVM of *C. finmarchicus* in response to predation, food and temperature.

Is lipid storage mainly for survival or reproduction?

It has been discussed whether the lipid storage in copepods serves mainly as a resource through winter or as a way of fueling spawning in early spring (BÅMSTEDT 1986; HAGEN & SCHNACK-SCHIEL 1996). Under which conditions will the ability to store fat for egg produc-
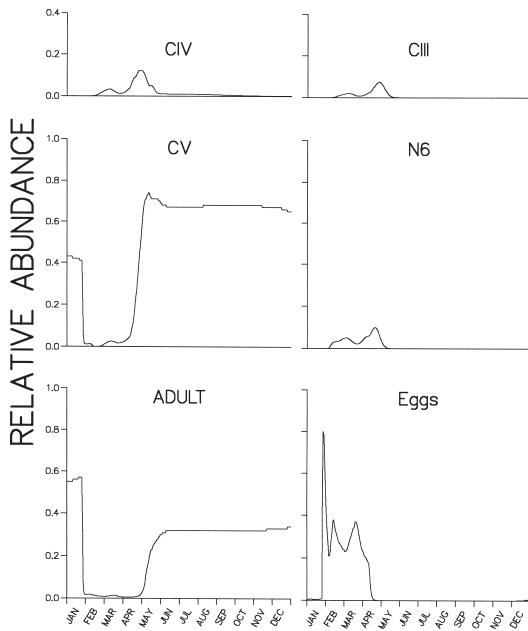
Fig. 11. Relative abundance of different stages. Note the three spawning events, where the first two are form the overwintering generation.

tion be important? First, by omitting the possibility of egg production from lipids and comparing the total abundance after 3 years (as in Table 3), the population abundance scales to 0.64 of the basic version (36 % fewer individuals), i.e. there is a strong demographic benefit in this ability. The simulation without the 'eggs-from-fat' assumption (Fig. 3A) differs from the basic version in several respects: (1) The overall fat load and structural size is reduced somewhat (average level down by about 10 %); (2) the second generation disappears almost completely; (3) the ascent early in spring and later, before descent (Figs 9 & 10), becomes less prominent. But still, the population has some extra fat left after the winter when the spring bloom starts. Obviously, even the small stochasticity implicit in the state dynamics (state interpolation) will make it necessary to carry some excess lipids to buffer the probability of storage depletion in advance of the bloom. Thus, the copepod on average ends up in spring with some extra energy, and utilising this for spawning may be a good option.

Diapause metabolism

The model is very sensitive to the diapause reduction in metabolism. In the basic version, the winter diapause was set to 0.2 (Table 2), i.e. a reduction to 20 % of normal level. If this parameter (δ) is set to 0.25, the abundance after 3 years drops by 86 %, very high loads

of lipids are gathered before descent and only one generation is produced. Contrary, setting δ to 0.15 leads to abundances 4.5 times the basic run, low fat reserves and several peaks of spawning. The model does not allow any feeding through winter, but adding this as a possibility would reduce the sensitivity to this parameter.

DISCUSSION

The model and field data on C. finmarchicus

The model suggests that diel strong vertical migration will be optimal only for parts of the season, and strongly constrained by the need to gain enough storage material to survive winter. Patterns of DVM are related to the combined effects of (1) the fitness-value of the spawned eggs, i.e. their 'match' with favourable conditions for development and growth; (2) the seasonal patterns of mortality, food and temperature; and (3) the individual state (fat reserves and body size). It turns out that absence of DVM in the period with highest risk of predation may be optimal (Figs 9 & 10), particularly for low state individuals. Even the early work on *C. finmarchicus* suggested that physiological state could influence the DVM pattern (MARSHALL & ORR 1955).

Another consistent observation on DVM in *C. finmarchicus* is its absence during spring blooms (TANDE & BÅMSTEDT 1985; EILERTSEN & al. 1989; KRAUSE & RADACH 1989; DURBIN & al. 1995a, b). This is also predicted by the model (Figs 9 & 10), and is attributed to the high fitness value of spawning at this time of the season, which gives the eggs time to develop, build up fat reserves for the winter (while avoiding predators by DVM) and possibly contributing to a second generation. Indeed, there is another potentially strong mechanism at work during blooms that could explain surface swarming (absence of DVM). During blooms, the phytoplankton itself increases the turbidity of the water (self shading), thus increasing light attenuation and dims the water column enough to constrain predation from visual predators (GISKE & al. 1994; FIKSEN & GISKE 1995; AKSNES & UTNE 1997). As the spring bloom declines, however, the profitability of DVM increases, but just before descent to the safe wintering habitat, the model predicts copepods will take the high risk and stay at the surface to fatten before winter (Figs 9 & 10). In FIKSEN & GISKE (1995) it was shown how low-medium-high food levels could switch DVM from none to intense and then gradually levelling off again at higher food concentrations. For a long time people have been puzzled by observations of *Calanus* in large numbers at surface in midday even on bright sunny days (RUSSELL
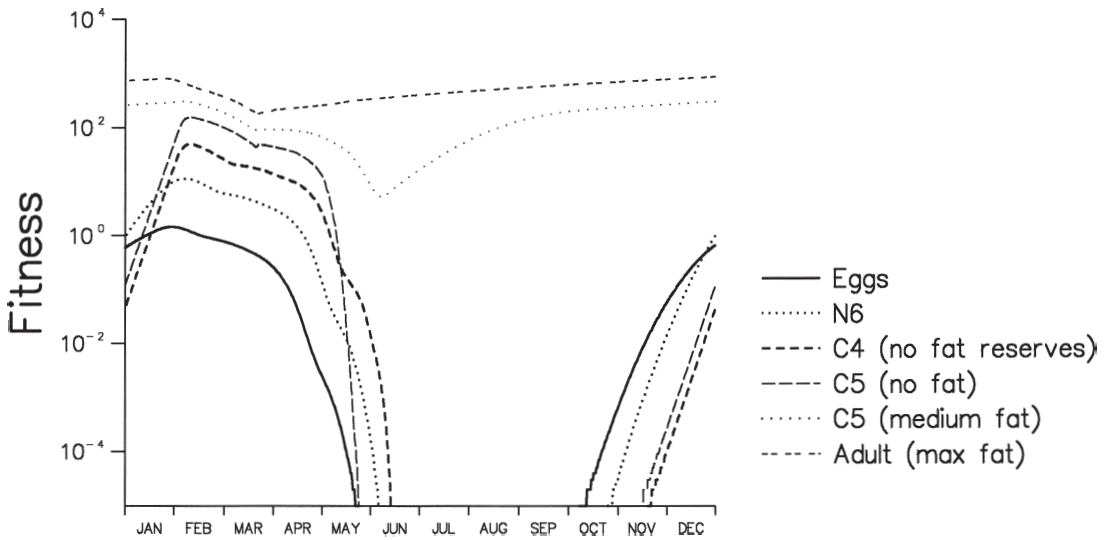
Fig. 12. Fitness values (from Eqs 3 & 4) of some stages and lipid levels. Before the winter season the stages susceptible to starvation (above CIV) and in low condition have lowest fitness.
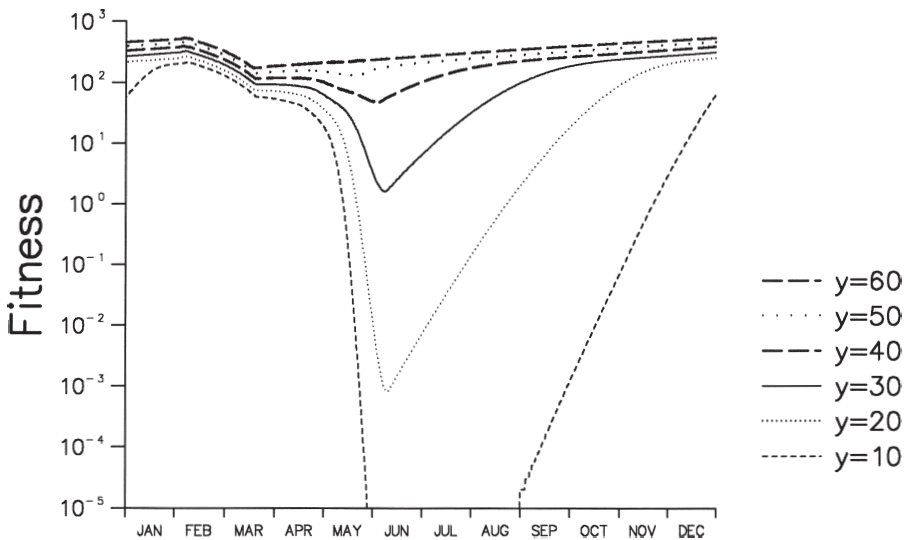

Fig. 13. Fitness of being in various conditions (lipid reserves) for a large CV. The legend shows the state resolution (see Fig. 1), with 60 as the highest load and 0 as the lowest (starving).

1928; NICHOLLS 1933). However, such behaviour can be adaptive in light of the threat of starvation in winter, even without considering variability in planktivore abundance. Including also the phenotypic flexibility in DVM patterns that seems available to these animals (FROST 1988; BOLLENS & FROST 1989a, 1989b, 1991; KAARTVEDT 1996), one should not be surprised to find large variations in migration patterns, even on short time scales. The abundance of planktivores will have a strong influence on the emerging DVM patterns in the model,

and this has been seen explicitly in the analyses of the CPR data in the North Sea by HAYS (1995a) and HAYS & al. (1996). They found a correlation between DVM of *C. finmarchicus* (and other zooplankters) and the abundance of herring (*Clupea harengus*) in the period 1958-1994. In the model the switch in DVM gave consequences in form of reduced number of generations and changes in allocation patterns. It would be interesting to see if this also occurs in nature. HAYS (1995b) discussed the difference in DVM of *Calanus* in Arctic

and temperate areas. In the Arctic *Calanus* does not seem to perform DVM (HANSEN & al. 1990), whereas in all temperate areas HAYS (1995b) found active DVM from the CPR records. He suggested that the special light conditions at high latitudes could remove the advantage of DVM. However, the visual range of planktivores is very sensitive to illumination (AKSNES & GISKE 1993; AKSNES & UTNE 1997), so minor light differences could reduce predation risk at the surface during night relative to day even at high latitudes. Another possibility, implicit in the model, is the short and intense nature of the productive season in the Arctic, so *Calanus* would run a high risk of starvation unless enough lipids are stored to survive the winter. Naturally, the comparatively small difference in diel irradiance contributes to the absence of DVM, but the model illustrates how the time constraint imposed by seasonality can modify DVM patterns considerably.

The model predicts a highly state-dependent timing of descent to diapause (Figs 9 & 10). The data in WIBORG (1954) show that from August through November the CV present in the surface were smaller than deeper dwelling copepodites. In a study from the Clyde Sea area NICHOLLS (1933) found that CIV and CV above 30 m were almost invariably smaller than individuals from deeper layers. In the Gulf of Maine, during late spring in 1989, DURBIN & al. (1995b) found the average C content of CV to be on average 66 µg C in the surface and 132 µg C near bottom, where animals seemed to be preparing for diapause. The latter study also reported highly variable DVM patterns between years and sampling stations, supporting phenotypic plasticity in this behaviour for *C. finmarchicus*.

During winter a major decrease in carbon content (72 % decrease) of CV has been observed (TANDE 1982), which is comparable to the results from the model. GATTEN & al. (1980) found that the lipid level in *Calanus* females agreed well with the total lipid level in the eggs laid, and concluded that all lipids left after overwintering and moulting into adults were spent on eggs. The results from the model also suggests that all fat should be allocated into eggs in advance of the bloom. The eggs and first nauplii will develop with no food, so pre-bloom spawners will have descendants which are larger and able to reproduce or descend earlier than late spawners. The maturation process and moulting from CV to adults are often pointed out to be based on internal supply (e.g. TANDE 1982; SARGENT & FALK-PETERSEN 1988). In the model we have let the lipids left after the winter be put directly into eggs, but in effect, this is similar.

The model suggests that the uncertainty in state dynamics would make it profitable to carry some surplus fat. Most eggs originating from lipids in early spring were made of the extra fat from individuals which spent less energy than expected through winter. One may anticipate a higher level of such 'insurance' lipids in nature where stochasticity will apply at several levels (spatial patchiness, variable timing and strength of the spring bloom, predator abundance etc.). The benefit of extra lipids in spring is of course enhanced fecundity at a beneficial time (for the eggs), but gaining fat is risky: it can only be acquired by staying longer in surface layers and at increased exposure to planktivores.

Behaviour, life history and population models

The model shows that the ability of a plastic response to environmental fluctuations will have a substantial influence on the abundance of *Calanus* (Table 3). The implication of this is that models should account for behavioural flexibility in seasonal and spatially heterogeneous environments, and that predation, resources and interactions between these forces and behaviour and life cycle strategies must be explored to understand (and maybe predict) population dynamics of copepods.

An alternative to the individual flexibility is frequency dependent selection, i.e. the existence of genetic polymorphism in life history traits and migratory behaviour (OHMAN 1990). Thus, if DVM and allocation rules are fixed for each of a suite of genotypes, a frequency of rules could stabilise in the population, based on the variability of the environment. If the timing and duration of the bloom is variable, we should expect the frequency of strategies to reflect this stochasticity. If this is the case, clones of individuals with strong DVM will multiply in years with high predation pressure, while clones with no or weak DVM will spread in years with low abundance of planktivores. Likewise, in years or areas with prolonged algal production, clones generating two or more generations will have higher reproductive success and increase their ratio next year. However, phenotypic plasticity has been demonstrated for a number of zooplankton species (e.g. BOLLENS & FROST 1991; LOOSE & DAWIDOWICZ 1994), and we may assume this to apply to *C. finmarchicus* as well (KAARTVEDT 1996; HAYS 1996).

REFERENCES

Aksnes, D.L. & J. Blindheim 1996. Circulation patters in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. – *Ophelia* 44:7-28.

Aksnes, D.L. & J. Giske 1990. Habitat profitability in pelagic environments. – *Marine Ecology Progress Series* 64:209-215.

—— 1993. A theoretical model of aquatic visual feeding – *Ecological Modelling* 67:233-250.

Aksnes, D.L. & T. Magnesen 1983. Distribution, development, and production of *Calanus finmarchicus* (Gunnerus) in Lindåspollene, Western Norway, 1979. – *Sarsia* 68:195-208.

Aksnes, D.L. & A.C.W. Utne 1997. A revised model of visual range in fish. – *Sarsia* 82:137-147.

Båmstedt, U. 1986. Chemical composition and energy content. – Pp. 1-58 in: Corner, E.D.S. & S.C.M. O'Hara (eds). *The biological chemistry of copepods*. Oxford University Press, Oxford, U. K.

Bollens, S.M. & B.W. Frost 1989a. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. – *Limnology and Oceanography* 34:1072-1083.

—— 1989b. Predator induced diel vertical migration in a marine planktonic copepod. – *Journal of Plankton Research* 11:1047-1065.

—— 1991. Diel vertical migration in marine zooplankton: rapid individual response to predators. – *Journal of Plankton Research* 13:1359-1365.

Carlotti, F., M. Krause & G. Radach 1993. Growth and development of *Calanus finmarchicus* related to the influence of temperature: experimental results and conceptual model. – *Limnology and Oceanography* 38:1125-1134.

Carlotti, F. & P. Nival 1992. Model of copepod growth and development: moulting and mortality in relation to physiological processes during an individual moult cycle. – *Marine Ecology Progress Series* 84:219-233.

Carlotti, F. & G. Radach 1996. Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled 1-D model. – *Limnology and Oceanography* 41:522-539.

Clark, C.W. & D.A. Levy. 1988. Diel vertical migrations by sockeye salmon and the antipredation window. – *The American Naturalist* 131:271-290.

Corkett, C.J., I.A. McLaren & J.-M. Sevigny 1986. The rearing of the marine calanoid *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov, and *C. hyperboreus* Kroyer with comment on the equiproportional rule. – Pp. 539-546 in: Shriever, G., H.K. Schminke & C.-T. Shih (eds). *Proceedings of the Second International Conference on Copepoda, Syllogeus* 58. National Museum of Canada, Ottawa, Canada.

Daro, M.H. 1980. Field study of the diel feeding of a population of *Calanus finmarchicus* at the end of a phytoplankton bloom. – *Meteor Forschung-Ergebnisse, Reihe A* 22:123-132.

De Meester, L., L.J. Weider & R. Tollrian. 1995. Alternative antipredator defences and genetic polymorphism in a pelagic predator-prey system. – *Nature* 378:483-485.

Diel, S. & K. Tande 1992. Does the spawning of *Calanus finmarchicus* follow a reproducible pattern? – *Marine Biology* 113:21-31.

Durbin, E.G., R.G. Campbell, S.L. Gilman & A.G. Durbin 1995a. Diel feeding behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. – *Continental Shelf Research* 15:539-570.

Durbin, E.G., S.L. Gilman, R.G. Campbell & A.G. Durbin 1995b. Abundance, biomass, vertical migration and estimated development rate of the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. – *Continental Shelf Research* 15:571-591.

Eilertsen, H.C., K.S. Tande & J.P. Taasen 1989. Vertical distribution of primary production and grazing by *Calanus glacialis* Jaschnov and *C. hyperboreus* Krøyer in arctic waters (Barents Sea). – *Polar Biology* 9:253-260.

Fiksen, Ø. 1997. Allocation patterns and diel vertical migration: modeling the optimal *Daphnia*. – *Ecology* 78:1446-1456.

Fiksen, Ø. & J. Giske 1995. Vertical distribution and population dynamics of copepods by dynamic optimization. – *ICES Journal of marine Science* 52:483-503.

Franz, H.G. & W.G. van Arkel 1980. Zooplankton activity during and after the phytoplankton spring bloom at the central station in the FLEX-box, northern North Sea, with a special reference to the calanoid copepod *Calanus finmarchicus* (Gunn.). – *Meteor Forschung-Ergebnisse, Reihe A* 22:113-121.

Franz, H.G & S. Diel 1985. Secondary production of *Calanus finmarchicus* (Copepoda: calanoidea) in a transitional system of the Fladen Ground area (northern North Sea) during the spring 1983. – Pp. 123-133 in Gibbs, E. (ed.). *Proceedings of the 19th European Marine Biology Symposium*. Cambridge University Press, Cambridge.

Frost, B.W. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. – *Bulletin of Marine Science* 43:675-694.

Gamble, J.C. 1978. Copepod grazing during a declining spring phytoplankton bloom in the northern North Sea. – *Marine Biology* 49:303-315.

Gatten, R.R., J.R. Sargent, T.E.V. Forsberg, S.C.M. O'Hara & E.D.S. Corner 1980. On the nutrition and metabolism of zooplankton. XIV. Utilization of lipid by *Calanus helgolandicus* during maturation and reproduction. – *Journal of the Marine Biological Association of the U. K.* 60:391-399.

Giske, J., D.L. Aksnes & Ø. Fiksen 1994. Visual predators, environmental variables and zooplankton mortality risk. – *Vie et Milieu* 44:1-9.

Hagen, W. & S.B. Schnack-Schiel. 1996. Seasonal lipid dynamics in dominant Antarctic copepods: energy for overwintering or reproduction? – *Deep-Sea Research* 43:139-158.

Hansen, B., U.C. Berggren, K.S. Tande & H.C. Eilertsen 1990. Post-bloom grazing by *Calanus glacialis*, *C. finmarchicus* and *C. hyperboreus* in the Polar Front, Barents Sea. – *Marine Biology* 104:5-14.

Harris, J.R. 1983. The development and growth of *Calanus* copepodites. – *Limnology and Oceanography* 28:142-147.

— 1996. Feeding ecology of *Calanus*. – *Ophelia* 44:85-109.

Hays, G.C. 1995a. Zooplankton avoidance activity. – *Nature* 376:650.

— 1995b. Diel vertical migration behaviour of *Calanus hyperboreus* at temperate latitudes. – *Marine Ecology Progress Series* 127:301-304.

Hays, G.C., A.J. Warner & D. Lefevre 1996. Long-term changes in the diel vertical migration behaviour of zooplankton. – *Marine Ecology Progress Series* 141:149-159.

Hirche, H.J. 1990. Egg production of *Calanus finmarchicus* at low temperature. – *Marine Biology* 106:53-58.

— 1996a. The reproductive biology of the marine copepod, *Calanus finmarchicus* - a review. – *Ophelia* 44:111-128.

— 1996b. Diapause in the marine copepod, *Calanus finmarchicus* - a review. – *Ophelia* 44:129-143.

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

Huntley, M. & E.R. Brooks 1982. Effects of age and food availability on diel vertical migration of *Calanus pacificus*. – *Marine Biology* 72:23-31.

Kaartvedt, S. 1996. Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. – *Ophelia* 44:144-156.

Kerfoot, W.C. 1985. Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. – *Contributions in Marine Science Suppl.* 27:91-113.

Kleiven, O. 1996. *Habitat use in Daphnia: significance of chemical substances from co-occurring organisms.* – Dr.scient. thesis, University of Bergen, Bergen.

Krause, M. & G. Radach 1989. On the relations of vertical distribution, diurnal migration and nutritional state of herbivorous zooplankton in the northern North Sea during FLEX 1976. – *Internationale Revues des gesamten Hydrobioloie* 74:371-417.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. – *Functional Ecology* 3:21-27.

Leibold, M.A. 1990. Resources and predators can affect the vertical distributions of zooplankton. – *Limnology and Oceanography* 35:938-944.

Loose, C. & P. Dawidowicz 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. – *Ecology* 78:2255-2263.

McNamara, J.M. 1991. Optimal life histories: a generalisation of the Perron-Frobenius Theorem. – *Theoretical Population Biology* 40:230-245.

McNamara, J.M. & A.I. Houston 1986. The common currency for behavioral decisions. – *The American Naturalist* 127:358-378.

— 1996. State-dependent life histories. – *Nature* 380:215-221.

Mangel, M. & C.W. Clark 1988. *Dynamic modeling in behavioral ecology.* – Princeton University Press, Princeton. 308 pp.

Marshall, S.M. & A.P. Orr 1955. *The biology of a marine copepod* Calanus finmarchicus *(Gunnerus).* – Oliver & Boyd, London. 188 pp.

Miller, C.B., T.J. Cowles, P.H. Wiebe, N.J. Copley & H. Grigg 1991. Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. – *Marine Ecology Progress Series* 72:97-91.

Miller, C.B. & K.S. Tande 1993. Stage duration estimation for *Calanus* populations, a modelling study. – *Marine Ecology Progress Series* 102:15-34.

Nicholls, A.G. 1933. On the biology of *Calanus finmarchicus*. III. Vertical distribution and diurnal migration in the Clyde Sea-area. – *Journal of the Marine Biological Association of the U. K.* 19:139-164.

Nisbet, R.M. & S.N. Wood 1996. Estimation of copepod mortality rates. – *Ophelia* 44:157-169.

Ohman, M.D. 1990. The demographic benefits of diel vertical migration by zooplankton. – *Ecological Monographs* 60:257-281.

Ohman, M.D. & J.A. Runge 1994. Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. – *Limnology and Oceanography* 39:21-36.

Ohman, M.D. & S.N. Wood 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. – *Limnology and Oceanography* 41:126-135.

Osgood, K.E. & B.W. Frost 1994. Ontogenetic diel vertical migration behaviors of the marine planktonic copepods *Calanus pacificus* and *Metridia lucens*. – *Marine Ecology Progress Series* 104:13-25.

Peterson, W.T., P. Tiselius & T. Kiørboe 1991. Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. – *Journal of Plankton Research* 13:131-154.

Plourde, S. & J.A. Runge 1993. Reproduction of the planktonic copepod *Calanus finmarchicus* in the lower St. Lawrence Estuary: relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. – *Marine Ecology Progress Series* 102:217-227.

Roff, D.A. 1992. *The evolution of life histories.* – Chapman and Hall, New York, USA. 535 pp.

Runge, J.A. 1984. Egg production of the marine, planktonic copepod, *Calanus pacificus* Brodsky: laboratory observations. – *Journal of Experimental Marine Biology and Ecology* 74:53-66.

— 1985. Egg production rate of *Calanus finmarchicus* in the sea off Nova Scotia. – *Archiv für Hydrobiologie, Beihefte Ergebnisse der Limnologie* 21:33-40.

Russell, F.S. 1928. The vertical distribution of marine macroplankton. VII. Observations on the behaviour of *Calanus finmarchicus*. – *Journal of the Marine Biological Association of the U. K.* 15:429-454.

Sargent, J.R. & S. Falk-Petersen 1988. The lipid biochemistry of calanoid copepods. – *Hydrobiologia* 167/168:101-114.

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

Tande, K.S. 1982. Ecological investigations on the zooplankton community of Balsfjorden, Northern Norway: generation cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). – *Journal of Experimental Marine Biology and Ecology* 62:129-142.

Tande, K.S. & U. Båmstedt 1985. Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in arctic waters of the Barents Sea. – *Marine Biology* 87:251-258.

Thompson, B.M. 1982. Growth and development of *Pseudocalanus elongatus* and *Calanus* sp. in the laboratory. – *Journal of the Marine Biological Association of the U. K.* 62:359-372.

Verity, P.G. & V. Smetacek 1996. Organism life cycles, predation and the structure of marine pelagic ecosystems. – *Marine Ecology Progress Series* 130:277-293.

Vidal, J. 1980. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. – *Marine Biology* 56:111-134.

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.

Wiborg, K.F. 1954. Investigation of zooplankton in coastal and offshore waters of western and north-western Norway with special reference to the copepods. – *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 11:245-252.

Williamson, C.E., R.W. Sanders, R.E. Moeller & P.L. Stutzman 1996. Utilization of subsurface food resources for zooplankton reproduction: Implications for diel vertical migration theory. – *Limnology and Oceanography* 41:224-233.

Wood, S.N. 1994. Obtaining birth and mortality patterns from structured population trajectories. – *Ecological Monograph* 64:23-44.