Ecology, 78(5), 1997, pp. 1446–1456

ALLOCATION PATTERNS AND DIEL VERTICAL MIGRATION: MODELING THE OPTIMAL *DAPHNIA*

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Abstract. I present a model which at the same time evaluates optimal diel vertical migration (DVM) and optimal allocation patterns to growth or reproduction in the cladoceran *Daphnia magna.* The combined policies that maximize the intrinsic rate of increase r are found using the Perron Frobenius Theorem and dynamic programming. The model attempts to incorporate two traditions in aquatic behavioral ecology within the same model framework: variations in vertical migrations (short time behavior) and age or size at maturity (life history models).

The predictions from the model are compared with observations from an experiment in thermally stratified flow-through tubes containing various concentrations of fish exudates. The model is able to reproduce many of the observations of both DVM and allocation, though there are some interesting deviations. I look at theoretical behavior and life history consequences of various size dependencies in mortality. Finally, I do a comparative analysis of two fitness measures, the intrinsic rate of increase r, and the net lifetime reproduction, R_0, where it turns out that the use of r makes predictions in better agreement with the observations.

Key words: Daphnia magna; *diel vertical migration; dynamic programming; fitness; intermediate allocation; life history; optimal behavior; population dynamics.*

INTRODUCTION

The diel vertical migrations (DVM) and life histories (like age or size at maturity) of many marine and freshwater organisms have been shown to depend on the density and type of predators present (e.g., Dodson 1988, Bollens and Frost 1989*a*, *b*, 1991, Dawidowicz et al. 1990, Tjossem 1990, Machácek 1991, 1993, 1995, Ringelberg 1991, Dawidowicz and Loose 1992, Stibor 1992, Larsson and Dodson 1993, Loose 1993, Weider and Pijanowska 1993, Bollens et al. 1994, Loose and Dawidowicz 1994, Reede 1995). Vertebrate predators (which prefer larger prey) often induce increased amplitude and duration of DVM, smaller size at first reproduction, and smaller neonate size (Lynch 1980, Zaret 1980), while invertebrate predators (which are less efficient on larger prey) may cause the opposite responses. These responses are regarded as adaptive features that reduce the susceptibility to predation. The ability to regulate the antipredator behavior phenotypically with the risk of predation will improve individual fitness, as defense is generally associated with a cost (Harvell 1990, Riessen 1992).

Because vertical profiles of food concentration and temperature usually are strong in aquatic environments, major reductions in growth and reproduction are associated with staying deep in the water column (Loose and Dawidowicz 1994). However, when fish are abundant, predation risk will generally show the opposite trends, with a high risk of mortality in illuminated surface waters (e.g., Aksnes and Giske, 1990, 1993, Giske et al. 1994). Therefore, vital rates will be strongly affected by individual (spatial) behavior and life history strategies. Thus, models predicting population dynamics of cladocerans should include variations in life history with predator density or predator type, and consider the demographic costs or benefits associated with vertical migration.

The demonstrated dynamic interaction between environment and plasticity in behavior emphasizes the importance of combining ecological and evolutionary theory to model population dynamics of zooplankton (Gabriel 1993). To be able to predict population dynamics through a season, we need not only an ecological model and a good description of functional and physiological relations, but also a reliable model of motivation, i.e., a model that can select among the available life history and behavioral options. For this purpose, optimality models are suitable. The well-documented ability of induced responses in zooplankton is encouraging for optimality modeling, and in particular for state variable models (Mangel and Clark 1986, 1988, Clark and Levy 1988, Houston et al. 1988, Rosland and Giske 1994, Fiksen and Giske 1995). Optimality models assume organisms to have global information about the environment (possibly modified by constraints), so the accumulating evidence of flexibility and induced responses to environmental variables (including predators) increase the realism of this approach.

Manuscript received 22 November 1995; revised 6 August 1996; accepted 16 October 1996.

DVM and life history traits are often treated separately, both in models (Clark and Levy 1988, Gabriel and Thomas 1988, Taylor and Gabriel 1992) and in experimental studies (e.g., Stibor 1992, Lampert 1994, Loose and Dawidowicz 1994). This is natural, as they describe phenomena on different time scales. Still, both are often responses to the same stimulus, and the consequences on growth and survival are similar. Here, I present a model that simultaneously calculates optimal allocation to growth or reproduction and optimal DVM as a function of time, environment (light, predators, food, temperature) and the state (body mass) of an individual *Daphnia magna.*

Model

To be able to compare the model with the experiments performed by Loose and Dawidowicz (1994; referred to here as LD94) at the Max Planck Institute for Limnology (Plön, Germany), the model is outlined in close agreement with their experimental set-up. Specifically, I consider *Daphnia magna* in 1 m deep flow-through tubes containing excess food (2.0 mg carbon/L), a strong vertical temperature gradient (Fig. 1, data from LD94) and a diel surface irradiance cycle similar to that used by LD94. The modeled individuals are initialized at the surface, at midday, and with a dry body mass of 21.5 μg.

State dynamics, growth and reproduction

In the experiments of LD94, specific growth rate in *D. magna* was a linear function of temperature. A regression of the data from the dilution experiment (their Fig. 3B) yielded the equation $g = 0.0316T - 0.1158$ ($r^2 = 0.94$, $P < 0.05$), where T is the temperature in degrees Celsius, and g is the daily specific growth rate. However, this growth equation is based on an increase in body mass only, leaving out the egg production. To find expressions for total growth rate at low- and high-food situations, I derived individual body mass M_1 at the end of each experiment from the data in LD94 (their Fig. 6B), and added the total dry mass of the eggs B produced after each treatment in the combination experiment (see LD94: Table 5). Then growth is found from:

$$g = \frac{\ln((M_1 + B)/M_0)}{t_1 - t_0}$$

where $t_1 - t_0$ is the time span of the experiment and M_0 is the initial body mass (21 μg dry mass). The equations for the lines through these points are $g = 0.037T - 0.31$ ($r^2 = 0.97$, $P < 0.05$) and $g = 0.047T - 0.31$ ($r^2 = 0.98$, $P < 0.05$), respectively, for the low-food and high-food cases (in LD94, the combination experiment), assuming an average dry egg mass of 6.0 μg (Dawidowicz and Loose 1992). Thus, growth is basically a function of depth (Fig. 1A).

The state of the modeled cladoceran is characterized by its size $X(t)$ (in micrograms of dry mass) through time. Total gain G within each time step is

$$G = X(t)(\exp(\tau g) - 1)$$

where g is defined by the regressions above and τ is the length of each time interval. The state dynamics are

$$X(t + 1) = X(t) + (1 - \alpha)G \quad (1)$$

where $1 - \alpha$ is the fraction of G allocated to increase in somatic body mass (i.e., growth). Matter allocated to reproduction $R(x, z, \alpha)$ is

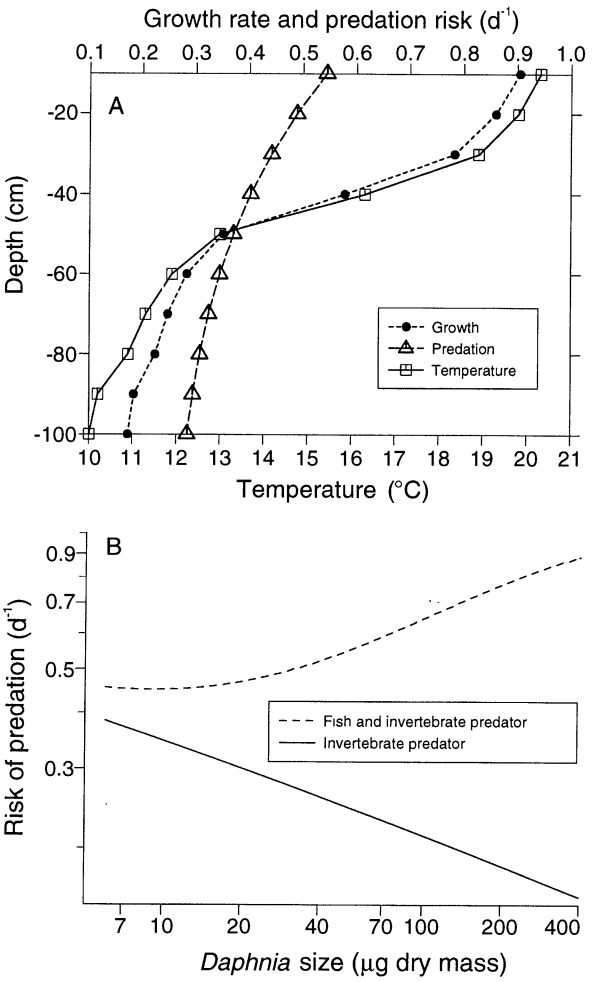

FIG. 1. (A) Vertical profiles in the tubes (temperature, growth, and predation risk), corresponding to the situation in the dilution experiment in LD94. The risk profile relates to a 200-μg *Daphnia* during daytime, a fish concentration of 0.01 fish/L, and proportionality constant $m = 0.15$ (Eq. 3). At night, risk will be approximately invariable throughout the column. (B) The risk of predation during one day, with no fish (invertebrate predators only) and 0.01 fish/L in addition to the invertebrates. The curve is taken from 10 cm depth, at midday. The rate of predation from invertebrates is $E(x) = k_2 (x \times 10^{-6})^{-y}$, where x is the body size, and k_2 (0.001 h^{-1}) and y (0.25) are constants of proportionality.

$$R(x, z, \alpha) = \alpha G. \quad (2)$$

Clutch size is found by dividing $R(x, z, \alpha)$ by the average mass of an egg. I have assumed no size dependency in specific growth rate, meaning that fecundity will be linearly related to female size, provided constant allocation and egg size. Eventually, some physiological or morphological constraints must affect growth, so I have set a maximum (dry) body mass of 400 μg. Cladocerans like *Daphnia magna* lay clutches, and molt as each clutch is released, while I let the females reproduce continuously. A detailed inclusion of molting and brood formation would complicate the model considerably (see Fiksen and Giske 1995 for an example of stage resolution), but may be important for some biological properties, like size at first reproduction.

Predation risk

I assume predation rate from planktivores $\beta(x, z, t)$ to be proportional (constant of proportionality [fitted] is m) to fish density P, the area of the image of the zooplankton $A(x)$ and light level $I(z, t)$ at depth z:

$$\beta(x, z, t) = \frac{mI(z, t)PA(x)}{A(\hat{x})} \quad (3)$$

with $A(\hat{x})$ equal to the area of an individual in the median state $\hat{x}$. The area of the prey is based on the assumption of a spherical body shape and neutral buoyancy. Light is scattered and decays exponentially with depth. During daytime (i.e., from ≈0400 to 2000), LD94 measured irradiance just below the surface to 17.9 and 1.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the bottom, with algal concentrations of 2.0 mg C/L (i.e., the attenuation constant K is 2.6 m^{-1}). As values for the low-food case were not presented in the paper, this attenuation coefficient (=1.28) was found using the equation in Riley (1956) expressing light extinction as a function of chl a:

$$K = k_0 + 0.054(\text{chl } a^{0.6667}) + 0.0088 \text{ chl } a,$$

where k_0 is the nonchlorophyll extinction (=1.13 from the values in the high-food case), and chl a is in milligram of chl a per cubic meter (assuming C/chl a ratio of 30). The general equation (Beers Law) for light extinction with depth is $I(z, t) = I_0(t)\exp(-zK)$, where $I_0(t)$ is irradiance just below the surface (night level was not specified in LD94; I used 0.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Risk of mortality from visually guided predators will therefore display an exponential decrease in depth, but will increase with size (Fig. 1).

Though I focus on the effect of fish, there will usually also be a considerable predation pressure from invertebrates on daphnids, particularly for a species like *D. magna,* which only occasionally coexists with fish. In general, the risk of being killed by such predators declines with body size (Zaret 1980). Here, I make the simplifying assumption that the shape and level of this source of mortality are described by an equation given by McGurk (1986), where daily mortality rate $E(x)$ drops linearly with size in a log–log plot (Fig. 1B).

These rates are converted to the risk of being eaten within each time step from the exponential probability function:

$$\mu(x, z, t) = 1 - \exp[-\tau(\beta(x, z, t) + E(x))]. \quad (4)$$

Fitness

Several alternative ways of measuring the fitness consequences of various behaviors or life histories exist (Stearns 1992). The fitness currency which includes both timing of reproduction and number (or quality) of descendants, the instantaneous rate of increase r of an individual (or an allele), is often considered superior to measures like R_0, which only count the numbers of offspring (Sibly and Calow 1986, Sibly 1989, Giske et al. 1993). In any state, at any time, animals should maximize their expected rate of increase.

McNamara (1991) showed how the life history that maximizes the individual's rate of increase r can be calculated using the Perron Frobenius Theorem and dynamic programming (see Mangel and Clark 1988, for a readable introduction to dynamic programming in behavioral ecology). The optimal strategy is found from a "terminal condition," i.e., the fitness value at the end of the final time interval (called the "horizon," H). Then the procedure works backwards in an iterative, stepwise manner, adding the number of eggs $R(x, z, \alpha)$ times the fitness value of the egg at the time of birth $F(1, t + 1)$, and adding the residual fitness of our focus individual $F(x, t + 1)$. For growing populations, the fitness value of the egg increases as we move backwards in time, because the number of descendants that the egg will be likely to have during its lifetime increases. Thus, the organism should strive to have as many offspring as possible as early as possible in a productive environment. McNamara (1991) demonstrated that this procedure eventually (if $H - t$ is sufficiently large) will converge to a stationary strategy, the same strategy that maximizes the life history parameter r, in that particular environment.

Thus, fitness $F(x, t)$ is defined as the total number of expected descendants at the final time (as McNamara 1991), including daughters produced by daughters, and so on for a parthenogenetic *Daphnia.* In mathematical terms, using the processes defined earlier (Eqs. 1–4), the specific terminal condition and the general dynamic programming equation can be expressed as

$$F(x, H) = \max_{1 \le z \le 10} [1 - \mu(x, z, H)] \quad (5)$$

$$F(x, t) = \max_{1 \le z \le 10, 0 \le \alpha \le 1} [(1 - \mu(1, z, t))R(x, z, \alpha)F(1, t + 1) + (1 - \mu(x, z, t))F(x', t + 1)] \quad (6)$$

where $F(x, t)$ is the maximum attainable fitness value of an animal in state x at time t, with the optimality

operators z and α. The portion of growth allocated to reproduction influences the future state of the individual; therefore $x' = x + (1 - \alpha)G$, as defined in Eq. 1. Note that this way of maximizing r using dynamic programming is less computer-intensive and easier to implement than the method suggested by Roff (1992:84).

Within a dynamic optimization procedure, the strategy that maximizes lifetime reproductive success R_0 is found from the basic dynamic programming equations:

$$F(x, H) = \max_{1\le z\le 10, 0\le\alpha\le 1} [(1 - \mu(x, z, H))R(x, z, \alpha)] \quad (7)$$

$$F(x, t) = \max_{1\le z\le 10, 0\le\alpha\le 1} [1 - \mu(x, z, t)] \times [R(x, z, \alpha) + F(x', t + 1)] \quad (8)$$

with all symbols as defined earlier.

The model is run with a time horizon of >40 d (1000 h). This should account for a realistic lifetime expectancy in *Daphnia.* I use a maximum (400 μg) and a minimum dry body mass (6 μg; eggs), which is divided into exponentially increasing intervals. I am interested in tracking a single individual through life, so I cannot separate the intervals into two new states (Mangel and Clark 1988: 228). Instead, I interpolate to the nearest integer value, and check that the state space and time intervals are scaled such that several state intervals are crossed even at low growth rates. The resolution is 1 h timestep, 500 states, 10 habitats, and 6 different allocation options (0, 0.2, 0.4, 0.6, 0.8, 1) within each time interval. The model is computer intensive (it takes about 20 min to run on a SPARC 10 computer), even after the running time is greatly reduced by allowing the animals to move only 20 cm up or down in one hour.

Results

I present the simulations first in relation to the results of LD94, and then some predictions from a more theoretical perspective, investigating optimal strategies of behavior and growth as the mortality changes. First I turn to the data, and run the model for (1) the different concentrations of fish kairomones (the dilution experiment), and (2) four different combinations of foods and predators (the combination experiment).

Vertical migration: the dilution experiment

LD94 showed how the increased density of planktivores (i.e., the concentration of some fish kairomone) increased the intensity of DVM. They were able to quantify the costs in terms of a reduced growth rate associated with this antipredator response. However, it turned out that the response was not homogeneously distributed across fish densities. Over a wide range of fish densities, no response was observed, while major changes were seen at intermediate concentrations. This is also reflected in the model (Fig. 2), where three groups of migration responses can be recognized. First, when there are no fish present (the control experiment), animals should stay in the warmest habitat. Second, no significant migration appears for the next four levels of dilution, where daphnids are predicted to stay above the thermocline and migrate only 20 cm up during the night. Third, the threshold for proper diel vertical migration is ≈0.02 fish/L. At this concentration DVM is switched on as the individual reaches a certain body size, but for the two highest concentrations, DVM is independent of size (Fig. 2). Naturally, the levels of these thresholds will rely on the proportionality constant m in Eq. 3, while the rather abrupt switch in migration strategy is caused by the vertical shape of the temperature profile: predation risk must exceed a threshold before it becomes advantageous to enter the cold bottom water. When daphnids first have to migrate, they might as well go very deep, as the marginal reduction in growth is low beyond 50 cm depth, while mortality risk drops exponentially throughout the water column (Fig. 1A).

The model does not explain the complete absence of DVM at the highest fish density (Fig. 2), nor the DVM pattern observed at intermediate densities. The first discrepancy could perhaps be explained by constraints in the perceptive ability of *Daphnia,* i.e., they may not have perfect information about the environment. This could also be a strategy: the cost of gaining such information may be too high for an animal unlikely to survive an encounter with a predator (Sih 1987), or if risk is temporally variable, some extra caution could be taken while fish are present to ensure survival to the less risky periods.

Vertical migration: the combination experiment

The vertical behavior of *D. magna* in four combinations of food (high and low) and predator densities (absent, and 0.1 fish/L) is compared with the results of LD94 in Fig. 3 and Table 1. The temperature profile is slightly different from the dilution experiment, and the results presented in Table 5 in LD94 have been utilized to find relations between temperature and specific growth rate at the two concentrations of algae (see Model description). Clearly, the simulations without fish always predict the daphnids to be in the warmest habitat (Fig. 3). For the simulations with fish, intense DVM is predicted, which may be attributed to the factors mentioned above.

The combination experiment by LD94 provided information about the average body mass, egg production, and depth of the individuals at the end of the experiment (117 h after incubation). The model comes quite close to the observed values for most of these combinations (Table 1). The values most difficult to predict correspond to the case with abundant food and no fish, where some sort of size dependency in mortality (like reduced risk at larger body size) or possibly fecundity (increased efficiency in egg production) is

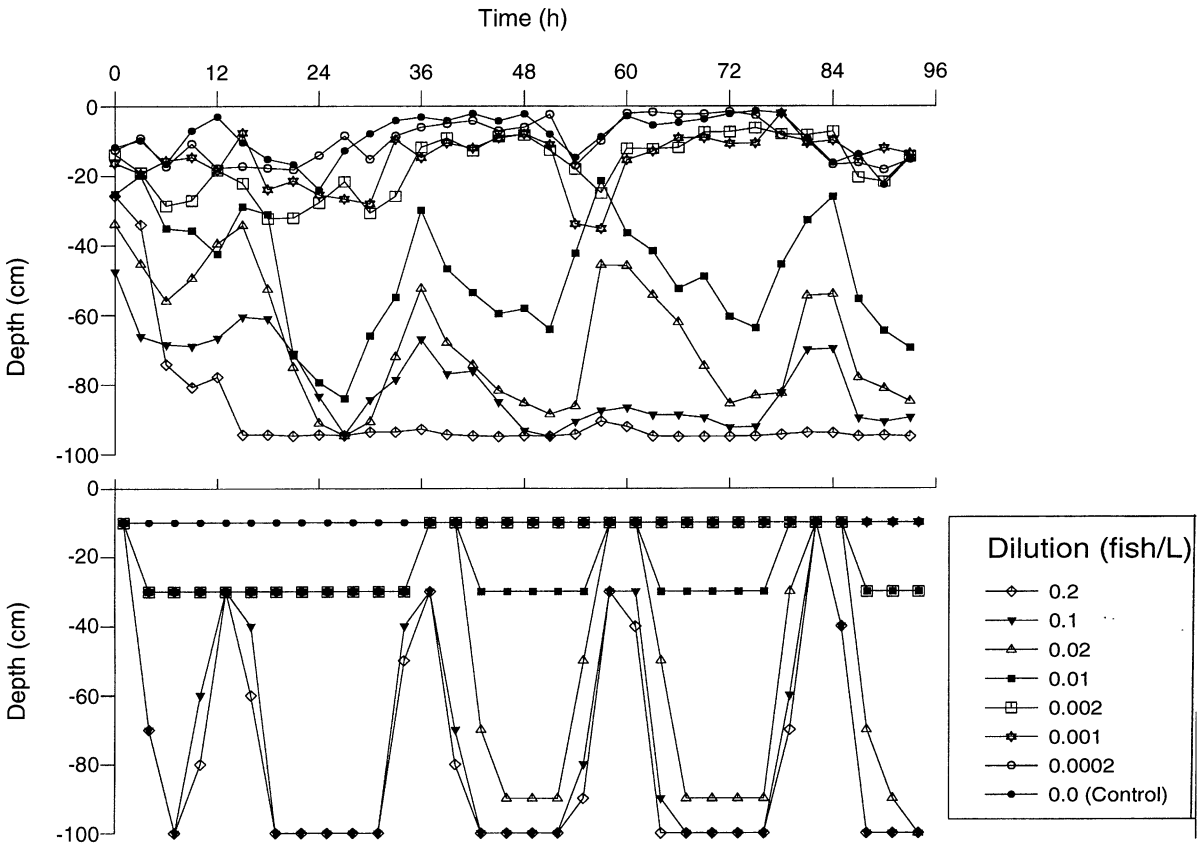

FIG. 2. Comparing model and experiment: the dilution experiment. The upper panel shows the mean depth recorded by LD94 for increasing density of fish kairomones. The experiment (and model) was initiated at midday, such that every 24th hour is midday. The lower panel shows modeled results for the baseline version of the model. Optimal habitat is displayed for every 3rd hour.

necessary to explain the large body size observed at the end of the experiments.

Life history patterns

To see how the optimal pattern of allocation and life history traits are affected by increasing risk of predation from planktivores, I ran two versions of the model, one with full spatial resolution and another where the animals were forced to stay in the upper, most light-intense habitat (Fig. 4). Each version was run for eight different predator densities. These simulations allowed me to study the interactions between life history variables and DVM, which also have been done in experiments recently (De Meester et al. 1995, Reede and Ringelberg 1995). The optimal age and size at maturity resulting from these simulations are quite similar, despite the large differences in mortality and growth patterns (r decreases considerably as P increases, Fig. 4D). Still, there are major deviations at high predator densities, when intense DVM is advantageous. While the nonmigrating animals allocate as much as they can to reproduction, the migrating animals pay the cost of a slower growth rate, but can allocate more to somatic mass increase, as they are less vulnerable in the deeper habitats (Fig. 4). Despite the similarities in age and size at maturity, there are large differences in growth (i.e., allocation to growth) after maturation (Fig. 5), even at intermediate predator densities.

DVM and growth patterns may interact in complex ways. The opportunity of selecting a safer, but colder habitat, can make it profitable to postpone development and maturity to gain survival. In this case, major allocation to growth will endure for a longer period. The migrating individuals will, however, always do equally well or better than the nonmigrating, and at high planktivore densities the demographic cost of not migrating will be immense (Fig. 4D). Decreasing fish density incurs lowered predation risk, particularly to larger individuals, and maturing later and larger becomes profitable (Fig. 4B and C). However, in growing populations maturing late and large involves demographic costs, unless there are some specific benefits in a larger size (Stearns 1992, Taylor and Gabriel 1992). The benefits in this case are reduced mortality from invertebrates and increased fecundity, and this causes size and age at maturity to increase considerably as fish densities diminish. If the invertebrate source of mortality is left out (while the animals are denied DVM), the life

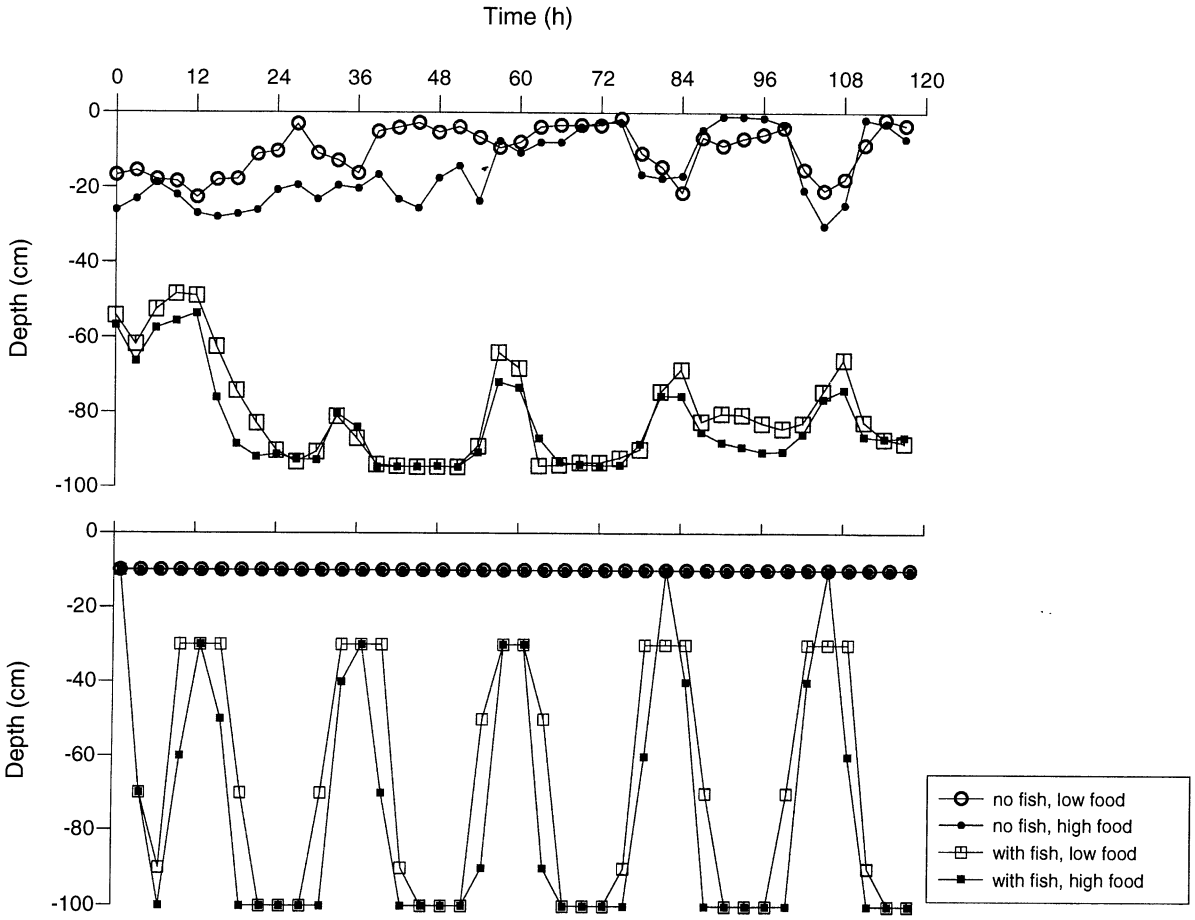

FIG. 3. Habitat selection for *Daphnia magna* in four combinations of food (0.1 mg/L or 2.0 mg/L) and predators (absent or 0.1 fish/L). The combination experiment from LD94 (upper panel) and the corresponding predictions from the model (lower panel) are depicted.

TABLE 1. A comparison of life history parameters from the model and the combination experiment in LD94.

	Low food (0.1 mg/L)				High food (2.0 mg/L)			
	LD94	r	r-inv	R_0	LD94	r	r-inv	R_0
Without fish								
Dry mass (μg)	121.9	144.5	144.5	144.5	326.1	285.7	98.9	349.6
Egg number	8.4	3.2	3.2	3.2	15.6	16.1	19.6	6.9
Depth (cm)	15.3	10.0	10.0	10.0	9.9	10.0	10.0	10.0
With fish (0.1 fish/L)								
Dry mass (μg)	33.6	45.6	50.0	50.0	57.5	50.0	50.0	50.0
Egg number	0.0	0.0	4.6	7.8	0.0	3.5	3.7	4.9
Depth (cm)	80.3	66.3	42.0	26.9	83.5	75.6	74.8	67.8

Notes: The model is run for 1000 h, but values of body size, eggs and average depth are presented after 117 h to be consistent with the data (and to eliminate terminal effects). Depth is averaged over the first 117 h (both model and experiment). The model versions (r and R_0; see Eqs. 5–8) include invertebrate predation risk in addition to fish, (i.e., mortality drops with increasing body mass when no or few fish are present). The second version (r-inv) has predation from fish only and uses r as a measure of fitness. The final version of the model maximizes R_0 (net lifetime reproduction). "Low food" and "high food" refer to situations described in LD94.

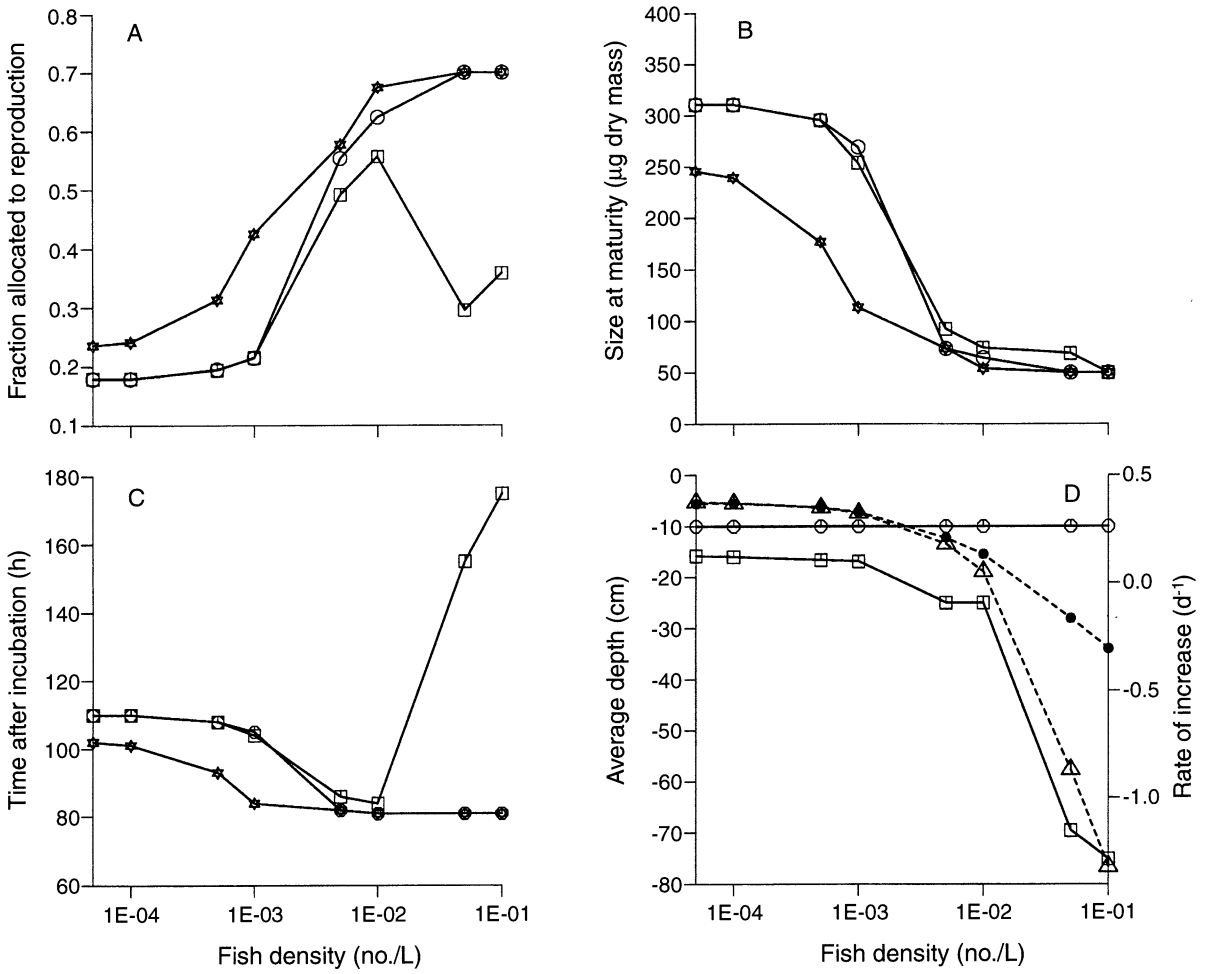

FIG. 4. Overall averages of life history parameters and behaviors from simulations with increasing densities of fish. Open squares: free to perform DVM. Open circles: fixed at 10 cm depth (no DVM). The lines with stars as markers refer to a case with no DVM and no invertebrate predation. (A) Fraction of growth allocated to reproduction within the first 117 h after incubation. (B) Size in μg dry mass at maturity (i.e, when 10 eggs are produced). (C) Age in hours after incubation at first clutch (10 eggs). (D) Overall average location in depth (solid lines) and rate of increase after 1000 h (dashed lines). Filled circles are individuals free to perform DVM; triangles are those fixed at 10 cm depth.

history changes (Fig. 4). The benefit of large size is lowered, and age and size at maturity will be reduced across all levels of fish predation (Fig. 4A–C). The advantage of improved fecundity will still be present, so optimal daphnids should grow also after maturity, but much less than if invertebrate predators are a threat (Fig. 5).

The model predicts intermediate allocation to growth after maturity for all predator regimes but the highest (Fig. 5). Resource partitioning is most pronounced for intermediate densities of fish (i.e., 0.01 fish/L), when growth continues throughout the modeled period (Fig. 5). There is a "terminal effect" (Mangel and Clark 1988) in the pattern of allocation, caused by the fact that as the model approaches the final time, the eggs will have less time to mature and reproduce within the model horizon. After this point (≈300 h in the 0.01 fish/L simulation), eggs produced late will increase their value relative to eggs laid early because they have a greater probability of surviving until the horizon, and reproduction will be maximized, regardless of timing (i.e., the strategy is more similar to the "maximize R_0" strategy). This may involve growing large, to be able to lay more eggs closer to the horizon, if the benefit is not offset by high risk of predation with larger size (as in the 0.1 fish/L case in Fig. 5).

The ecological situation analogous to the model horizon effect could be seasonality, like winter or other predictable events with fatal consequences. The terminal effect of this (predicted by the model) would be to grow larger before winter (cease neonate production, because they would die without reproducing), and then lay many resting eggs (ephippia) just before winter. If the onset of winter is less predictable, this strategy becomes less important, but is still present.

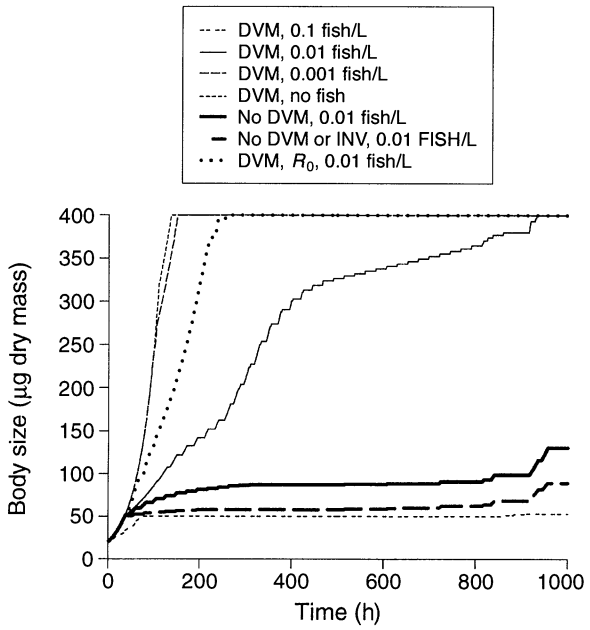

FIG. 5. Growth patterns at selected fish concentrations.

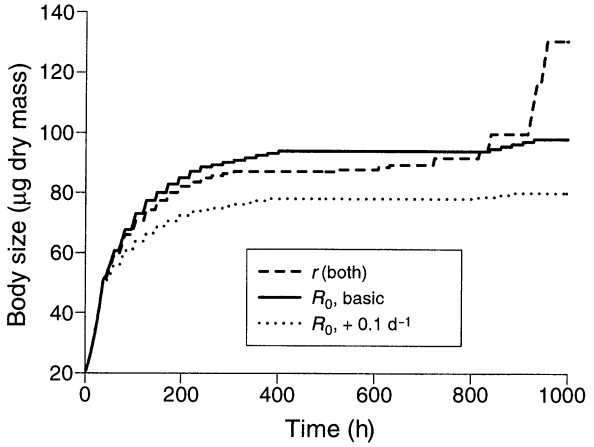

FIG. 6. The patterns of growth depend on whether r or R_0 are used as fitness currency. For r, the line covers two simulations, one baseline and one with a uniformly increased mortality (0.1 d^{-1}). There is no response to the increase in mortality. For R_0, there is a shift to less reproductive effort relative to the baseline version. For all simulations, the daphnids are fixed in the upper layer, with fish densities at 0.01 fish/L.

R_0 *or* r *as fitness measure?*

The different properties of the fitness currencies, r and R_0 are implied by comparing the emerging life histories and DVM patterns in Tables 1 and 2, and in Figs. 5 and 6. When the combination experiment is simulated using R_0 as optimization criterion, the resemblance between predicted and observed values is reduced for most cases. Only the body size after 117 h for the high food + fish situation is closer to the observed average value when R_0 is defined as fitness. Otherwise, rate of increase is superior in all situations, though the choice of fitness measure may not be critical for many scenarios. The baseline model was run with r and R_0 as optimization criteria for a range of predator densities (Table 2). I traced the emerging populations consisting of individuals adopting the alternative policies, to see how two theoretical clones with different units of fitness would compete. Clearly, the r policy is always superior to the R_0 in terms of descendants alive after 40 d, independent of the predation pressure. Generally, the r policy is to take higher risk (stay higher up in the water column) and mature earlier and smaller in relation to the R_0 policy. This is true for all fish densities but the 0.1 fish/L case (Table 2). At this high predator density, the r-maximizing strategy shifts from early maturation, high growth, and spending much time above the thermocline, to deeper habitat selection and reduced growth. This is caused by the negative expectation of r, which makes survival relatively more important, and removes the advantage of laying eggs early. Even though the two fitness measures predict similar age and size at maturity at some levels of predation risk, they may still give rise to very different growth patterns after maturity (Fig. 5). The R_0 strategy predicts more matter allocated to growth after maturity than the

TABLE 2. A comparison of allocation to reproduction (1 indicates that all surplus growth is allocated to reproduction), vertical position, size at maturity (SAM, µg dry mass), age at maturity (AM), and rate of increase predicted by use of R_0 and r through decreasing densities of fish.

Fish (no./L)	Allocation		Depth		SAM		AM (h)		r (d^{-1})	
	r	R_0	r	R_0	r	R_0	r	R_0	r	R_0
0.1	0.36	0.47	75.1	68.6	50.0	50.0	175	154	−0.306	−0.350
0.01	0.56	0.24	25.0	43.7	74.3	172.4	84	127	0.131	0.104
0.001	0.22	0.10	16.9	25.0	253.9	329.6	104	115	0.327	0.315
0.0001	0.18	0.15	16.0	16.0	310.7	318.7	110	111	0.369	0.368
0.0	0.18	0.15	10.0	10.0	310.7	318.7	110	111	0.376	0.374

Notes: Rates of intrinsic increase r are found from a submodel that calculates the number of descendants originating from one female. In this population-dynamics model, the female and all her descendants (all females) follow an optimal policy through time and space. Allocation and depth are averages after 117 h, while SAM and AM are the size and time when she can release a clutch containing 10 eggs, i.e., total matter allocated to reproduction yields 10 eggs.

r strategy, so measuring animal size at a later stage than 117 h would be better to distinguish between the fitness measures.

If the size-dependent mortality is shifted uniformly up or down across size, there is no effect on life history variables, as long as DVM is fixed and r is the criterion to be maximized (Fig. 6). This was also found by Taylor and Gabriel (1992) from maximizing r in the Euler–Lotka equation. However, this is not the case for R_0 simulations, which will be affected by a uniform shift in the mortality rate (Fig. 6). From Eqs. 6 and 8 it can be seen that a constant k added to μ will turn out differently for the two cases. In the r case, a constant will influence current ($[1 - \mu(1, z, t) - k]\ R[x, z, \alpha]\ F([1, t]$) and future fitness ($[1 - \mu(x, z, t) - k]\ F[x, t]$) equally (both $F[1, t]$ and $F[x, t]$ will be multiplied by $\Pi_{H-t}\ k$), so patterns of allocation will not be affected. For R_0, current reproduction will become more profitable, because current reproduction will only decrease its value by k, while future fitness will be reduced by $\Pi_{H-t}\ k$. Thus, the optimal life history response of, e.g., a disease striking equally animals of different sizes or ages will be reduced allocation to growth if we use R_0, and no change if we use r.

Discussion

I have shown how optimal habitat selection and the trade-off between current and future reproduction can be modeled within the same framework. I found that the optimal reaction norm to increasing predation from fish is to mature earlier and at a smaller size (Machácek 1991, Reede 1995), to allocate more to reproduction after maturity, and to perform DVM when the predation risk is sufficiently high (Fig. 4). The model predicts DVM to display a major change from 0.01 to 0.05 fish/L. This shift occurs after size and age at maturity have reached their minimum values (Fig. 4), and can be related to the stratified water column (Loose 1993). Altering allocation patterns thus seems to have primacy to DVM at the lower range of fish concentrations. The model also confirms recent experimental results (Figs. 4 and 5): (1) some life history traits of daphnids with no DVM should be more sensitive to fish kairomones than those with DVM (Reede 1995, Reede and Ringelberg 1995); and (2) the relaxation of predation from fish or intensified predation from invertebrate predators will induce a shift in allocation patterns leading to larger adult body size (Weider and Pijanowska 1993, Tollrian 1995).

Simulations of the experiments conducted by LD94 yielded a reasonable fit to the observed vertical migration and allocation patterns (Figs. 2–4, Table 1). However, it is clear that the model cannot explain the size at maturity without the assumption of some gain in survival with size. If this is the cause of the large size at maturity at low fish densities, it suggests that *D. magna* could be adapted to encounter invertebrate predators at some time in their lifetime, though the experimental individuals never have been exposed to them (Weider and Pijanowska 1993). Thus, they may invest more in growth than predicted by an optimality model ignoring this possibility. It is, however, possible that the continuous reproduction pattern assumed in the model could be responsible for the early (and small) maturation when invertebrate predation was removed (Table 1, Fig. 4). In nature, clutch release is coupled to the molting process. The choice of how much to allocate to reproduction will be constrained by this, as the number of eggs may be limited by space in the brood chamber or the size-dependent ability to nourish neonates. It may be that this factor could reduce the necessity of an invertebrate risk of predation to improve fit with the data from LD94 (Table 1).

The model does not consider the possible influence of maternal effects and the trade-off between offspring size, viability, and number of offspring in different predation regimes (Glazier 1992, Ebert 1993, Lampert 1993, 1994, Boersma 1995, Tollrian 1995). It is only concerned with the adaptive strategies (within constraints like minimum and maximum body size) under various situations. In principle, the trade-off between size, viability, and number can be included in the model, though it requires a stage-structured framework and complicates the model further. Also, the model is applicable to situations where clones have evolved different combinations of allocation pattern and DVM in response to predation regimes (intrapopulational genetic polymorphism). In some recent experiments, De Meester (1993) and De Meester et al. (1995) showed that clones with larger size at maturation (fixed) exhibited deeper daytime distributions, but had similar fitness. My model allowed the size at maturity to be flexible, but a simulation with minimum size at maturity at 150 μg and 0.01 fish/L gave an average depth of 37.5 cm (below the thermocline during the day after reaching maturation) for the first 117 h; while depth for the basic 50-μg maturity threshold was 25 cm (Table 2). The fitness (r = 0.131 d^{-1} vs. 0.085 d^{-1}) was higher for the 50-μg threshold, but then the model does not account for the increased fitness of larger neonates. Similarly, clones with different genetically fixed DVM patterns may balance fitness through altering allocation patterns (SAM) in changing predation situations.

Taylor and Gabriel (1992) predicted intermediate allocation of resources to reproduction for most scenarios of predation, particularly when mortality decreased with size. This is also true for the present model. Contrary to their model, my model predicts resource partitioning throughout the whole life-span of an optimal *Daphnia* for a range of fish densities around 0.01 fish/L (Fig. 5). Intermediate allocation is the general observation from laboratory data (Taylor and Gabriel 1992). To some extent, the continuous resource partitioning in the model is related to the DVM of the animal, which reduces susceptibility to predation but limits growth, and therefore elongates the period when resource par-

titioning is profitable. But the main reason (as prolonged intermediate allocation is also evident when the daphnids are not allowed to migrate [Fig. 5]), is that such allocation represents the optimal trade-off between the higher fitness value of an early egg, the risk of being killed with low reproductive output, and investment to increased size and future reproduction.

More studies on how changing fitness definitions influence predictions about life history evolution have been called for (Stearns 1992:33). Also, Roff (1992: 398) advised modelers to try several measures of fitness, and demonstrated how conclusions on optimal life histories may deviate between different currencies. The present model applies the most common density-independent measure, the instantaneous rate of increase r and the expected lifetime fecundity R_0. It was shown that maximizing r always resulted in more descendants alive after several generations (Table 2), and that r compared better with the data in this case (Table 1). The two measures of fitness give fundamentally different conclusions on the optimal response to a perturbation like altered size-independent mortality (Fig. 6) or changed predation regimes (Fig. 5).

The large body of evidence suggesting flexible responses of zooplankton to environmental and predator cues favors the use of optimality models to understand and predict behavior and life history. Optimality models either assume that optimal behaviors or life histories can be expected in a typical environment, or that animals have evolved reaction norms to cope with environments varying on small spatial or temporal scales (Roff 1992, Stearns 1992). The major disadvantage with optimization models is their inability to incorporate density dependence or feedback mechanisms between predators and prey, or plants and herbivores. This may be critical when *Daphnia* have a strong impact on their resources, i.e., at high zooplankton densities. For such situations, other modeling approaches (e.g., Ideal Free Distribution; see Giske et al. 1997) are more appropriate. The framework applied in the present study includes not only flexible responses of behavior and several life history variables, but also allows many elaborations of constraints, physiological states, ecological processes, and environmental detailing. The models of others (Gurney et al. 1990, Hallam et al. 1990, McCauley et al. 1990), emphasizing the physiology of individuals and how aspects of physiology and environment can affect population dynamics may be able to describe the dynamics of cultured populations. But when predation, behavior, and life history are important (which is generally the case for natural populations) these models will not be sufficient to model population dynamics. The combination of a structured and detailed model of physiology, and an optimization model that allows the daphnids to trade off growth and mortality (or current vs. future reproduction) such that fitness is maximized, may provide a way of integrating the advantages of both approaches.

Acknowledgments

I am most grateful to Carsten Loose for providing the data, and to C. W. Clark and an anonymous referee for improving the manuscript. I thank Jarl Giske, Dag L. Aksnes, Rune Rosland and Ole Kleiven for discussions and comments, and the Norwegian Research Council for financial support.

Literature Cited

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

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

Boersma, M. 1995. The allocation of resources to reproduction in *Daphnia galeata:* against the odds? Ecology **76**: 1251–1261.

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

Bollens, S. M., and B. W. Frost. 1989*b*. Predator induced diel vertical migration in a marine planktonic copepod. Journal of Plankton Research **11**:1047–1065.

Bollens, S. M., and B. W. Frost. 1991. Diel vertical migration in marine zooplankton: rapid individual response to predators. Journal of Plankton Research **13**:1359–1365.

Bollens, S. M., B. W. Frost, and J. R. Cordell. 1994. Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. Journal of Plankton Research **16**:555–564.

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

Dawidowicz, P., and C. J. Loose. 1992. Cost of swimming by *Daphnia* during diel vertical migration. Limnology and Oceanography **37**:665–669.

Dawidowicz, P., J. Pijanowska, and K. Ciechomski. 1990. Vertical migration of *Chaoborus* larvae is induced by the presence of fish. Limnology and Oceanography **35**:1631–1636.

De Meester, L. 1993. Genotype, fish-mediated chemicals, and phototactic behavior in *Daphnia magna*. Ecology **74**: 1467–1474.

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

Dodson, S. 1988. The ecological role of chemical stimuli for the zooplankton: predator-avoidance behavior in *Daphnia*. Limnology and Oceanography **33**:1431–1439.

Ebert, D. 1993. The trade-off between offspring size and number in *Daphnia magna:* the influence of genetic, environmental and maternal effects. Archiv für Hydrobiologie Supplement **90**:453–473.

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

Gabriel, W. 1993. Models on diel vertical migration. Archiv für Hydrobiologie, Beihefte Ergebnisse der Limnologie **39**: 123–136.

Gabriel, W., and B. Thomas. 1988. Vertical migration of zooplankton as an evolutionary stable strategy. American Naturalist **132**:199–216.

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

Giske, J., D. L. Aksnes, and B. Førland. 1993. Variable generation times and Darwinian fitness measures. Evolutionary Ecology **7**:233–239.

Giske, J., R. Rosland, J. Berntsen, and Ø. Fiksen. 1997. Ideal

free distribution of copepods under predation risk. Ecological Modelling **95**:45–59.
Glazier, D. S. 1992. Effects of food, genotype, and maternal size and age on offspring investment in *Daphnia magna*. Ecology **73**:910–926.
Gurney, W. S. C., E. McCauley, R. M. Nisbet, and W. W. Murdoch. 1990. The physiological ecology of *Daphnia:* a dynamic model of growth and reproduction. Ecology **71**: 716–732.
Hallam, T. G., R. R. Lassiter, J. Li, and L. A. Suarez. 1990. Modelling individuals employing an integrated energy response: application to *Daphnia*. Ecology **71**:938–954.
Harvell, C. D. 1990. The ecology and evolution of inducible defences. Quarterly Review of Biology **65**:323–340.
Houston, A., C. Clark, J. McNamara, and M. Mangel. 1988. Dynamic models in behavioural and evolutionary ecology. Nature **332**:29–34.
Lampert, W. 1993. Phenotypic plasticity of the size at first reproduction in *Daphnia:* the importance of maternal size. Ecology **73**:1455–1466.
———. 1994. Phenotypic plasticity in the size at first reproduction in *Daphnia magna*. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **25**:2362–2365.
Larsson, P., and S. Dodson. 1993. Chemical communication in animals. Archiv für Hydrobiologie **129**:129–155.
Loose, C. J. 1993. *Daphnia* diel vertical migration behavior: response to vertebrate predator abundance. Archiv für Hydrobiologie, Beihefte Ergebnisse der Limnologie **39**:29–36.
Loose, C. and P. Dawidowicz. 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. Ecology **78**:2255–2263.
Lynch, M. 1980. The evolution of cladoceran life histories. Quarterly Review of Biology **55**:23–42.
Machácek, J. 1991. Indirect effects of planktivorous fish on the growth and reproduction of *Daphnia galeata*. Hydrobiologia **225**:193–197.
———. 1993. Comparison of the response of *Daphnia galeata* and *Daphnia obtusa* to fish-produced chemical substance. Limnology and Oceanography **38**:1544–1550
———. 1995. Inducibility of life history changes by fish kairomone in various developmental stages of *Daphnia*. Journal of Plankton Research **17**:1513–1520.
Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. Ecology **67**:1127–1138.
Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey, USA.
McCauley, E., W. W. Murdoch, R. M. Nisbet, and W. S. C. Gurney. 1990. The physiological ecology of *Daphnia:* development of a model of growth and reproduction. Ecology **71**:703–715.
McGurk, M. D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Marine Ecology Progress Series **34**:227–242.
McNamara, J. M. 1991. Optimal life histories: a generalisation of the Perron-Frobenius Theorem. Theoretical Population Biology **40**:230–245.
Reede, T. 1995. Life history shifts in response to different levels of fish kairomones in *Daphnia*. Journal of Plankton Research **17**:1661–1676.
Reede, T., and J. Ringelberg. 1995. The influence of a fish exudate on two clones of the hybrid *Daphnia galeata X hyalina*. Hydrobiologia **307**:207–212.
Riessen, H. P. 1992. Cost-benefit model for the induction of an antipredator defence. American Naturalist **140**:349–362.
Riley, G. A. 1956. Oceanography of the Long Island Sound 1952–1954. II Physical oceanography. Bulletin of the Bingham Oceanographic Collection **15**:15–46.
Ringelberg, J. 1991. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). Journal of Plankton Research **13**: 17–25.
Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York, New York, USA.
Rosland, R., and J. Giske. 1994. A dynamic optimization model of the diel vertical distribution of a pelagic planktivorous fish. Progress in Oceanography **34**:1–43.
Sibly, R. M. 1989. What evolution maximizes. Functional Ecology **3**:129–135.
Sibly, R. M., and P. Calow. 1986. Why breeding earlier is always worthwhile. Journal of Theoretical Biology **123**: 311–319.
Sih, A. 1987. Predators and prey life styles: an evolutionary and ecological overview. Pages 203–224 *in* W. C. Kerfoot and A. Sih, editors. Predation—direct and indirect impact on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.
Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
Stibor, H. 1992. Predator-induced life-history shifts in a freshwater cladoceran. Oecologia **92**:162–165.
Taylor, B. E., and W. Gabriel. 1992. To grow or not to grow: optimal resource allocation for *Daphnia*. American Naturalist **139**:248–266.
Tjossem, S. F. 1990. Effects of fish chemical cues on vertical migration behavior of *Chaoborus*. Limnology and Oceanography **35**:1456–1468.
Tollrian, R. 1995. Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia pulex*. Ecology **76**:1691–1705.
Weider, L. J., and J. Pijanowska. 1993. Plasticity of *Daphnia* life histories in response to chemical cues from predators. Oikos **67**:385–392.
Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, Connecticut, USA.