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VERTICAL MIGRATION OF ZOOPLANKTON AS AN EVOLUTIONARILY STABLE STRATEGY

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Many taxa of freshwater and marine zooplankton are present in the upper waters only at night. During or around sunrise they swim long distances downward, and at dusk they ascend again. Debate continues about the ultimate and proximate causes of this widespread behavior. The study of phototactic responses (Siebeck 1960; Ringelberg 1964) has shown that changes in relative light intensity may trigger diel vertical migration. Leaving the warm and food-rich surface waters may be disadvantageous to the animals because growth and reproduction are affected by food intake whereas egg developmental time is inversely related to temperature. Several hypotheses of the mechanisms counterbalancing this possible fitness disadvantage have been proposed.

The occurrence and the intensity of vertical migration vary between lakes and within and between species. The situation in Lake Constance (West Germany, Austria, and Switzerland) is especially interesting, since morphologically similar, coexisting congeneric species show contrasting patterns of vertical migration. One species, *Daphnia hyalina*, migrates; the other, *D. galeata*, does not (Stich and Lampert 1981; Geller 1986). Both this discovery and further experimental studies (Stich and Lampert 1984) have cast doubt on arguments based solely on metabolic advantages or increased efficiency in the utilization of resources (McLaren 1963, 1974; Kerfoot 1970; Enright 1977; Enright and Honegger 1977). In addition, damage from direct solar radiation (Huntsman 1925; Hairston 1976) is unlikely to be of great importance in the evolution of this phenomenon. Speculations on a starvation-avoidance strategy (Geller 1986) still lack experimental confirmation. A more plausible explanation is that migratory behavior is a response to predators that hunt by sight (Zaret and Suffern 1976; Wright et al. 1980; Stich and Lampert 1981; Ohman et al. 1983; Clark and Levy 1988). Recently, Gliwicz (1986) has supported this hypothesis with data demonstrating a gradual increase in the amplitude of diel vertical migration correlated with an artificially

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imposed augmentation of predators. These investigations all suggest that diel vertical migration is an adaptive strategy for avoiding predation.

Weider (1984) has shown that the behavior of diel vertical migration has a strong genetic component. We assume that the frequency of phenotypes with different migratory behavior influences their relative fitness. Evolutionary game theory may aid in the investigation of the conditions under which diel vertical migration is an evolutionarily stable strategy (ESS; Maynard Smith and Price 1973; Maynard Smith 1974, 1982; Thomas 1984).

ON IWASA'S GAME MODEL FOR ZOOPLANKTON MIGRATION

To our knowledge, Iwasa (1982) was the first to employ methods of evolutionary game theory in explaining vertical migration of zooplankton. He designed a game between a predator (fish) and prey (herbivorous zooplankton) in which two types of behavior ("strategies") are considered for both fish and zooplankton: staying in the upper or lower layer of water. From this habitat-selection game he derived several interesting features about the distributions of both species between the water layers. The main results of the game appear in good agreement with empirical findings, but its theoretical grounds seem problematic.

In Iwasa's model, the fitness of one species is determined solely by the behavior of the other species. For example, fish fitness is assumed to depend on zooplankton availability in either layer but is not affected by the behavior of conspecifics. Similarly, the payoffs—in terms of fitness—for zooplankton are not influenced by the frequencies of zooplankton strategies. Therefore, the model describes a game between populations without self-interaction. A general theorem about "asymmetrical" games or, likewise, interacting populations states that mixed equilibria (different strategies coexist in one or both populations) cannot be evolutionarily stable in the absence of self-interaction (Pohley and Thomas 1979; Selten 1980; Schuster and Sigmund 1981). This holds at least for linear models like Iwasa's; some of his most interesting statements are thus based on an equilibrium that is not evolutionarily stable. In particular, this game model does not provide a valid explanation for a situation in which fish and zooplankton migrate between two layers in a way that maintains fixed equilibrium portions of fish and zooplankton in each layer.

The prerequisite for self-interaction for mixed evolutionarily stable equilibria is intuitively evident from the following argument. To determine whether an equilibrium is evolutionarily stable, one must ask what would happen if the equilibrium were perturbed, for example, if by chance zooplankters of a given strategic type should increase above equilibrium. The condition of evolutionary stability demands that, in this case, the deviation should be counterbalanced; that is, an excess of this strategic type should be "punished" by a reduction in the payoff associated with this strategy. In Iwasa's habitat-selection game, however, the payoff terms for zooplankton strategies depend *only* on the frequencies of fish in the corresponding layer. Consequently, at an equilibrium point for fish strategies, both zooplankton strategies fare equally well, whatever their frequencies are, and an excess of one strategic type would not lower its fitness. Moreover, if the

distribution of fish strategies deviates from its equilibrium, then the payoffs for the zooplankton strategies are again dependent only on the frequencies of fish strategies but independent of the actual proportions of zooplankton strategies. That is, if one zooplankton strategy is inferior at a certain proportion of fish strategies, then this strategy would be "punished," regardless of whether its frequency is below or above equilibrium. In particular, if it were below its equilibrium value, it would further decrease rather than re-approach the zooplankton equilibrium. The corresponding argument holds for fish strategies.

It may be objected that, if the zooplankton frequencies were to drift away from their equilibrium values as described above, the payoff for fish strategies would change. Thus, it could be imagined that the fish frequencies may be driven into a range where zooplankton strategies might recover their equilibrium. At this point, however, intuitive arguments do not lead us any further, and we have to rely on a mathematical treatment of the problem, which states that, in this case, strategy coexistence cannot be evolutionarily stable. In fact, a dynamic simulation for such a model shows that deviations from the equilibrium distribution are not compensated for (see Schuster and Sigmund 1981).

In this paper, we present a model that includes both interaction with a predator *and* self-interaction. For convenience, the model will be formulated for zooplankton only. This is because, in agreement with the empirical findings, we assume that vertical migration indeed protects the zooplankton from fish predation in upper waters; hence, it will be assumed that fish do not migrate vertically. Predation protection in lower waters may occur either because zooplankton in deeper water layers are invisible to fish that forage by sight or because the oxygen depletion becomes intolerable to planktivorous fish. Fish species that have learned to follow the vertical migration of zooplankton are not considered explicitly in our model and are treated like other (strategy-dependent) mortality factors.

CONCEPTUAL BASIS OF THE MODEL

We attempt to explain diel vertical migration by a game-theoretical approach that concentrates on the zooplankton population, that is, its metabolic, reproductive, and feeding conditions, and its mortality caused by predation. We assume that vertical migration is a behavioral response to various selective forces and physiological constraints. Food intake, metabolic costs, reproduction, and risk of predation depend on the strategy chosen. Because most planktivorous fish hunt by sight, light conditions strongly influence the predation mortality of zooplankton. The risk of fish predation is therefore highest during daytime in the upper water layers. The density of edible algae may be altered by zooplankton in that vertical migration reduces grazing pressure on the algae (Lampert and Taylor 1985). In addition, migrating animals experience a lower average temperature than nonmigrating ones; this increases the egg developmental time but may also reduce metabolic costs.

To study the combined effect of these variables and their relations we simply consider two genetically determined ethotypes, namely, migrating and nonmigrating zooplankters, which may, in principle, both occur in a zooplankton popula-

TABLE 1
COMPARISON OF ZOOPLANKTON STRATEGIES

Water Layer	Day	Night
Upper	s, stationary strategy high food high temperature accelerated development predation risk from fish	s, stationary strategy v, migrating strategy high food high temperature accelerated development <i>no</i> predation risk from fish
Lower	v, migrating strategy low food low temperature retarded development <i>no</i> predation risk from fish	(no zooplankton)

tion. We believe that the basic results derived from this simplifying approach would not differ qualitatively if a more finely grained distinction had been made, although this finer distinction of intermediate ethotypes might be necessary for a comparison with data from real populations. These behavioral types are implemented as "strategies" in a two-strategy model. It is not the number of strategies that makes a valid model. It is only economic to implement model complexity where it is needed: we deal with few strategies but spend more effort on detailed interaction and on the payoff consequences of other determinants. We also consider two distinct water layers and assume that nonmigrating animals always stay in the upper layer but migrating animals are in the lower layer during the daytime and in the upper layer at night (see table 1). Here, "daytime" is defined as a period during which fish forage by sight in the upper layer, whereas at night there is relatively little or no fish predation. We explicitly implemented the mortality caused by daytime fish predation in the upper layer. Aside from fish predation, we consider only global components of strategy-dependent mortality, for example, different rates of juvenile and adult mortality caused by invertebrate predators. The interaction of zooplankton with its algal food is calculated in some detail. Like vertical migration, algal growth also exhibits a diurnal cycle. We restrict the time of algal growth to the daytime (as defined for the zooplankton). Furthermore, we assume that available food in the lower layer is, at most, only enough to meet metabolic requirements. We calculate the success, or payoffs, for different strategies with respect to the following additional determinants (see table 2): actual algal density, grazing rate, abundance of zooplankton, day length, intensity and frequency dependence of fish predation, conversion of ingested food to reproductive output (mortality besides fish predation included), and the dependence of egg developmental time on water temperature.

Interaction within a zooplankton population does not consist of individual encounters as in simple games but is, rather, "against the field" (Maynard Smith 1982; Pohley and Thomas 1983). Interaction consists mainly of food competition

TABLE 2

MODEL PARAMETERS AND SUBSCRIPTS

MODEL PARAMETERS AND SUBSCRIPTS	
Subscript	
d	during the day
n	during the night
v	v strategy: diel vertical migration
s	s strategy: stationary, no migration
Parameter	
a	food uptake
a_d	during the day (s strategy only)
a_n	during the night (v and s strategies)
A	algal density
A_{lim}	algal density above which the food uptake is independent of algal density (incipient limiting level)
D	population density of zooplankton feeding in the upper water layer
N	total population density of zooplankton
p	predation risk from fish (and other optically oriented predators)
r_p	potential growth rate of algae (in the absence of feeding zooplankton)
$\bar{S}(S_v, S_s)$	relative payoffs measured in successful reproductive output (but corrected for fitness contributions due to different intergenerational periods)
T_n	length of night (in parts of 24 h)
w	slow-breeding correction factor
$x(x_s, x_v)$	relative part of a strategy present in the total population
$\beta(\beta_s, \beta_v)$	conversion factor of food uptake to successful reproductive output (mortalities other than fish predation taken into account)
γ	maximal grazing rate of zooplankton
ΔS	$S_s - S_v$, payoff difference between nonmigrating and migrating zooplankton
$\tau(\tau_v, \tau_s)$	egg developmental time

in different layers and a modulation of fish predation, both dependent on the frequencies of the zooplankton ethotypes present. We measure the payoffs of the two strategies relative to each other with respect to a time period of 24 h on a scale that represents fitness in terms of successful reproductive output equivalent to intrinsic growth rates.

In principle, game-theoretical analysis may reveal evolutionary stability in any of the following situations: no migration at all, vertical migration of the whole population, and a mixture of migrating and nonmigrating individuals within a population (i.e., neither of the strategies is an evolutionarily stable strategy [ESS] on its own). In addition, both the migratory and the stationary strategies may be ESS's exclusively, providing the possibility that the whole population may be turned to the alternative behavior if occasional fluctuations are strong enough. The aim of the model is to evaluate boundary conditions and essential determinants that imply evolutionary stability in any of these situations. The ESS-theoretical approach has the advantage that general conclusions can be drawn without explicit simulation of complex population dynamics.

EVOLUTIONARY STABILITY

We analyze the simple situation for an evolutionarily stable strategy (ESS) of one zooplankton population with two strategies: diel vertical migration (strategy

with subscript v) and no migration (strategy with subscript s for stationary). Let x_v and x_s denote the (relative) frequencies of v and s types in a population. Since $x_v + x_s = 1$, we may use x_s as the independent variable to describe the population state. The payoffs from either strategy may depend on the population state and are thus denoted by $S_s(x_s)$ and $S_v(x_s)$, respectively. Accordingly, let

$$\Delta S(x_s) = S_s(x_s) - S_v(x_s) \quad (1)$$

denote the difference between the payoffs of the strategies. Originally, an ESS could not be invaded by rare mutants once it had become established in the population. Assuming a pure, nonmigrating population (i.e., $x_s = 1$), the stationary strategy s would be evolutionarily stable if, whenever a few mutants of type v reduce x_s by a small quantity ϵ from 1 to $1 - \epsilon$, we would still have $S_s(1 - \epsilon) > S_v(1 - \epsilon)$. That is, because selection acts against it, strategy v cannot invade a population of s types. The corresponding interpretation holds for evolutionary stability of strategy v .

A population may achieve a state of evolutionary stability in another way: an evolutionarily stable polymorphism, or population state, is characterized by a stable balance of selective forces on either type expressed by a payoff equilibrium at some frequency \hat{x}_s :

$$S_s(\hat{x}_s) = S_v(\hat{x}_s). \quad (2)$$

Stability requires that deviations from this equilibrium frequency result in a disadvantage to the type whose frequency is enhanced over its equilibrium value. In our case, this condition can be expressed as

$$(x_s - \hat{x}_s) \Delta S(x_s) < 0 \quad (3)$$

for x_s close to \hat{x}_s . In generic cases, this simply means that $\Delta S(x_s)$ must have a negative slope at \hat{x}_s . The formalism for multi-strategy models was described by Pohley and Thomas (1983). Hence, we can investigate our model for evolutionarily stable strategies (ESS's, in the sense of evolutionarily stable states; see Thomas 1984) by identifying one of the following conditions:

$$\begin{aligned} s \text{ is an ESS if } \Delta S(x_s = 1) &> 0; \\ v \text{ is an ESS if } \Delta S(x_s = 0) &< 0; \\ \hat{x}_s \text{ is an ESS if } \Delta S(x_s = \hat{x}_s) &= 0 \text{ and } d\Delta S(\hat{x}_s)/dx_s < 0. \end{aligned} \quad (4)$$

This is most easily done by plotting graphs of $\Delta S(x_s)$ versus x_s after evaluating the strategy-dependent payoff functions S_s and S_v . A crucial point for this calculation is the food uptake of zooplankton: the ingested food is an important fitness component, and the interaction of zooplankton with its algal food implies zooplankton self-interaction modulated by the frequencies of the two strategies.

ALGAL DENSITY AND FOOD UPTAKE

According to experimental studies on feeding physiology (McMahon and Rigler 1965; Lampert 1977), ingestion and assimilation rates increase linearly with food

concentration until maximal values are reached at a certain level of food concentration. If food concentrations are increased above this so-called incipient limiting level (Fry 1947, cited in McMahon and Rigler 1965), food uptake remains constant. Therefore, the interaction of zooplankton with its algal food has to be modeled differently for low and high food concentrations.

At low food concentrations we describe the dynamics of algal density (A) by formally separating the interaction with the zooplankton from all other influences. We assume that

$$dA/dt = r_p A - \gamma D A, \quad (5)$$

with r_p as a "partial" intrinsic growth rate, which would apply to the algae in the absence of the zooplankton; D is the density of the actual feeding part of the zooplankton population; and γ is the maximal filtration rate. With these definitions, A and D must be normalized such that γD corresponds to an intrinsic death rate of the algae caused by the zooplankton. For our study, it is not necessary to consider the long-term behavior of algae, since we are interested only in payoff analysis based on a representative time period of 24 hours. (Note that 24 hours is also the minimum period that has to be taken into account since this period is fundamental to the description of zooplankton strategies.) With equation (5), we implicitly assume that at low concentrations all positive and negative effects on algal growth besides zooplankton grazing can be taken into account by a single variable r_p . Thus, r_p can hardly be constant over longer time periods, but it is the advantage of a local ESS analysis that we do not have to consider long-term dynamics. The ingested food per animal (a) in a time interval T is obtained by integration over the product of algal density with filtration rate:

$$a = \int_0^T \gamma A(t) dt. \quad (6)$$

Let A_0 denote the algal density at sunrise, and $T_n < 1$ the length of the night (we use 24 hours as the time unit so that $1 - T_n$ gives the daylight fraction). Let N denote the total zooplankton density, and x_s the nonmigrating part of the population, which implies that $D = x_s N$ is the proportion of zooplankton feeding during daylight in the upper layer. Integration of equations (5) and (6) yields the food intake per animal during daylight:

$$a_d = \gamma A_0 \{ \exp[(r_p - \gamma x_s N)(1 - T_n)] - 1 \} / (r_p - \gamma x_s N). \quad (7)$$

For simplicity, we assume that only the zooplankton under consideration are feeding on the algae represented by A or that other zooplankton have distinct food niches or are negligible with respect to A . Thus, neglecting metabolic losses of the algae, we can approximate $r_p = 0$ at night. Integrating equations (5) and (6) under this condition starting from the calculated algal density at sunset, we determine the total food intake during the night:

$$a_n = A_0 \exp[(r_p - \gamma x_s N)(1 - T_n)] [1 - \exp(-\gamma N T_n)] / N. \quad (8)$$

At high food concentration (at or above the incipient limiting level), the food uptake during the day (a_d) and night (a_n) is independent of the actual algal density.

If the algal density at the incipient limiting level is denoted by A_{lim} , then a_d and a_n are simply given by

$$a_d = \gamma A_{\text{lim}}(1 - T_n) \quad \text{for } A \geq A_{\text{lim}}, \quad (9a)$$

$$a_n = \gamma A_{\text{lim}} T_n \quad \text{for } A \geq A_{\text{lim}}. \quad (9b)$$

PAYOFFS

The relative advantages of the two strategies can be compared without an absolute fitness scale. To calculate relative payoffs in terms of successful reproductive output for a time interval of 24 h, we must convert the food uptake into reproduction. For this purpose we use a general, but strategy-dependent, parameter, β . Since we do not differentiate age classes, this parameter gives an average over a whole subpopulation with the same strategy, and it may also comprise other strategy-dependent factors like juvenile mortality and life span. The food-conversion factor β mainly reflects energy for metabolism and somatic growth.

To compare the two strategies, however, it is not sufficient just to count the reproductive output, since fitness also depends on the time span in which this output is released. For example, let us hypothesize that lower metabolic costs compensate for the reduced food uptake resulting from migration. Then, migrating and nonmigrating zooplankton would produce an equal number of eggs over a certain time period, but they would differ in clutch sizes and time intervals between releases of the clutches. This occurs because the egg developmental time is inversely related to temperature. As a result, an animal living at a lower average temperature waits longer to hatch eggs carried in the brood pouch. The nonmigrating zooplankton with the shorter egg developmental time (and also shorter pre-reproductive period) thereby realizes a higher intrinsic growth rate by its earlier release of its offspring (releasing 20 eggs after 10 days results in lower fitness than releasing 10 eggs every 5 days). The expected number of descendants per migrating animal including itself after one intergenerational period is simply $1 + n$, if n is the number of eggs produced in one clutch. For fitness comparisons, we must calculate the corresponding number for a hypothetical faster-breeding animal that releases n offspring in the same time span but distributed over k clutches, such that each clutch consists of n/k juveniles. If we assume that offspring reach maturity after one of these shorter intergenerational periods, then the expected number of descendants for a time interval equivalent to the intergenerational period of the slower breeders (k times the intergenerational time of the faster breeders) is given by the geometric series

$$1 + \frac{n}{k} \sum_{l=0}^{k-1} \left(1 + \frac{n}{k}\right)^l = 1 + \frac{n}{k} \frac{(1 + n/k)^k - 1}{(1 + n/k) - 1} = \left(1 + \frac{n}{k}\right)^k. \quad (10)$$

(This result can also easily be derived from the equivalent difference equations.) To calculate the strategy-dependent payoffs in terms of reproductive output, we must account for the influence on fitness of the time between two clutches. If the payoff for nonmigration is unchanged, we must adjust the payoff for migration

according to the different numbers of expected descendants ($1 + n$ against $[1 + n/k]^k$) by applying the (slower-breeder) correction factor w :

$$w = (1 + n)/(1 + n/k)^k. \quad (11)$$

Since the migrating animals are not exposed to fish predation, the different breeding times associated with the two strategies cannot necessitate an additional fitness correction because implications of predation are different. Mortality not caused by fish that forage by sight must be considered separately for each strategy in β_v and β_s .

The payoffs for diel vertical migration and no migration are the sum of payoffs obtained during the day and night:

$$\begin{aligned} S_s &= S_{s,n} + S_{s,d}; \\ S_v &= S_{v,n} + S_{v,d}. \end{aligned} \quad (12)$$

According to the model assumption, there is no fish predation at night. The corresponding payoffs are given by the amount of ingested food, a_n , times the strategy-specific conversion into reproduction (β):

$$\begin{aligned} S_{s,n} &= \beta_s a_n, \\ S_{v,n} &= \beta_v a_n w, \end{aligned} \quad (13)$$

with w from equation (11) as the factor that corrects for the unequal periods of egg development, τ_s and τ_v , of the strategies s and v . We simplify the situation by assuming that egg developmental time τ equals the time between molts and the accompanied release of juveniles. By putting $k = \tau_v/\tau_s$ and $n = \beta_v a_n \tau_v$ in equation (11), we can calculate w as

$$w = (1 + \beta_v a_n \tau_v)/(1 + \beta_v a_n \tau_s)^{\tau_v/\tau_s}. \quad (14)$$

During daylight, the predation risk diminishes the payoff for nonmigrating animals (strategy s). Let p be the probability of being eaten during daytime and a_d be the food ingested during this time. The payoff from feeding in the surface layer during the daylight is then $(1 - p)\beta_s a_d$. In case of predation, however, carried eggs and the material stored in the ovaries are also lost. The energy stored in these eggs was collected during daylight and at night over the time period τ_s . Since the average animal is in the middle of the molting phase, it has invested food for the ovaries over a time period of $\tau_s/2$. Therefore, we must subtract the total expected loss, that is, $\frac{3}{2}\beta_s \tau_s (a_n + a_d)$ weighted by probability p . Thereby, the payoff for nonmigrating animals during daylight is

$$S_{s,d} = (1 - p)\beta_s a_d - \frac{3}{2}p\beta_s \tau_s (a_n + a_d). \quad (15)$$

Because feeding conditions for migrating animals are poor from sunrise until sunset, the corresponding payoff is assumed to be negligible compared to the payoff from feeding at night. (In reality, it may even be negative if metabolic costs are not balanced by food uptake.) Thus, we can set

$$S_{v,d} = 0. \quad (16)$$

With these payoffs we quantify the fitness difference of nonmigrating and migrating animals as $\Delta S = S_s - S_v$. At low concentrations of algal food (below the incipient limiting level) and/or under density-dependent fish predation, the payoff functions are nonlinear with respect to the relative frequencies of the two strategies. For that reason, a simple game model with a constant-payoff matrix is not applicable (Pohley and Thomas 1983). Instead, we use the total payoff difference $\Delta S(x_s)$ for the analysis of evolutionary stability according to equation (4). This can be done most comprehensively by simple graphical means.

RESULTS

We present results on evolutionarily stable strategies and states for high and low food concentrations and discuss the influence of the model parameters on the favored strategy. The parameter values are estimated from the literature values for *Daphnia hyalina* and *D. galeata* (e.g., Stich and Lampert 1984; Stich 1985; Geller 1986) and therefore represent situations realized in nature. If not stated differently, we used the following parameter set: $\gamma = 0.55$, $r_p = 0.35$, $N = 1$, $p = 0.1$, $T_n = 0.4$, $\beta_s = 10$, $\beta_v = 11$, $\tau_s = 5$, $\tau_v = 10$, $A > A_{\text{lim}}$ or $A = 0.5A_{\text{lim}}$.

High Food Concentrations

Above the incipient limiting level, food uptake is not influenced by the relative frequencies of the two strategies; thus, frequency-dependent payoff functions can be caused only by fish predation. In the simplest case of high food concentration and constant predation pressure, we therefore expect a straight line parallel to the x_s -axis for the graphical representation of the payoff difference, ΔS . That is, the payoff difference, ΔS , is independent of frequency; this does not necessarily mean, however, that payoffs themselves are independent of frequency. It is the differences that matter here. For values of ΔS above zero, the stationary strategy s is evolutionarily stable; below zero, only strategy v (diel vertical migration) can be established. In fact, the favored strategy is determined by physiological parameters and metabolic requirements of the zooplankton species, the difference in the average temperature perceived according to the two strategies, the length of the night phase, and the intensity of the predation pressure, whatever its frequency. For example, with increasing fish predation, the advantage of strategy s can be reduced drastically (fig. 1), such that at a certain predation pressure (corresponding to the zero line) strategy v becomes an ESS. Similar figures can be produced by changing other model parameters.

Figure 2 illustrates the situation under the assumption of frequency-dependent predation risks. The predation pressure is chosen such that for $x_s = 1$, when all zooplankton are nonmigrating (stationary), strategy s is favored. Moreover, with decreasing x_s , the total amount of prey for the fish is reduced. A negative slope can be achieved only if the predation risk per zooplankton increases with zooplankton density. This seems to be quite unrealistic but could, in principle, be caused by learning and by highly prey-selective predators. If the predation risk decreases with zooplankton abundance, the advantage of s strategists increases with their frequency, resulting in a positive slope in the figure.

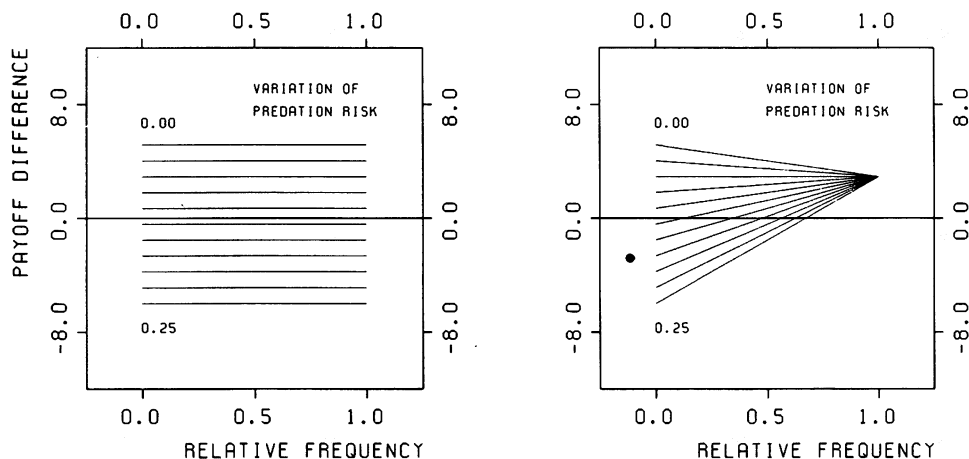


FIG. 1 (*left*).—The payoff difference ΔS between strategy s (no vertical migration) and strategy v (diel vertical migration) as a function of the relative frequency of strategy s , x_s . The concentration of algal food is high ($A > A_{lim}$). The predation risk for the zooplankton, p , is taken to be independent of its abundance and varied between 0 and 0.25 in increments of 0.025. Values of the other model parameters: $\gamma = 0.55$, $r = 0.35$, $N = 1$, $T_n = 0.4$, $\beta_s = 10$, $\beta_v = 11$, $\tau_s = 5$, $\tau_v = 10$.

FIG. 2 (*right*).—Same as figure 1, but with predators' foraging density dependent on zooplankton density. The predation risk at $x_s = 1$ (high prey density) is fixed at $p = 0.05$ and increases or decreases linearly with x_s to values between 0 and 0.25 at $x_s = 0$.

The intersecting points with equal payoffs for the two strategies, however, are unstable equilibria by equation (4): for lower x_s values the advantage of the v strategy increases from generation to generation until the whole population participates in vertical migration. This means that both strategies are ESS's but exclude each other: a mixed population would be driven to a pure s -type or v -type population depending on the starting frequencies. Similarly, random fluctuations could by chance reverse selection conditions (with respect to frequencies) and thus lead to the establishment of the opposite strategy. The condition for a stable mixture of strategies (negative slope at $\Delta S = 0$) can be fulfilled only if, at high frequencies of x_s , strategy v is superior to strategy s , causing the payoff difference ΔS at $x_s = 1$ in figure 2 to drop below zero. In addition, vertically migrating zooplankton would have to realize a higher payoff than nonmigrating ones at low frequencies of x_s (or at high frequencies of x_v). Therefore, at high food concentrations, the model predicts pure strategies and allows stable mixtures of strategies only for special cases when the predation risk increases with prey abundance.

Low Food Concentrations

Below the incipient limiting level of food concentration, the payoffs depend on the relative frequency of strategies, as shown by the calculations of food uptake in equations (7) and (8). For reasons of clarity, we discuss only cases of constant predation risk. The additional effects of density-dependent predation pressure are equivalent to the results given above and would have to be superimposed. To

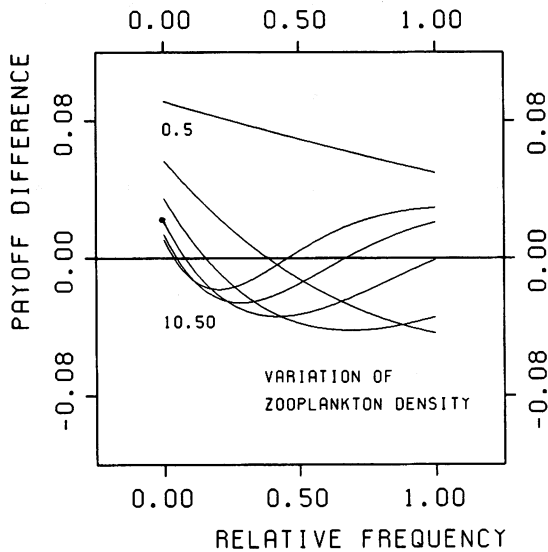


FIG. 3.—Frequency dependence of the payoff difference at low algal densities ($A = 0.5A_{lim}$). The predation risk is fixed at $p = 0.11$, and the abundance of zooplankton is increased from 0.5 to (unrealistically high values of) 10.5.

demonstrate what complex payoff functions can result from the interaction of zooplankton with its algal food, figure 3 shows payoff differences for various total zooplankton densities at unrealistic parameter values. Even if rarely realized in nature, inherent in the structure of the model are nontrivial results like two simultaneous equilibrium points: a stable one at low frequencies of x_s , and an unstable one at higher values of x_s . In this case, the starting frequency determines whether a mixture of strategies or a pure s strategy (nonmigrating) can establish an evolutionarily stable state.

Figure 4 shows the influence of increased predation risk. Without any predation risk, we obtain a negative slope because at low frequencies of nonmigrating zooplankton, the algae can grow better during the day; the resulting higher food availability during the day gives an additional advantage to s strategists. With increasing predation pressure, the slope changes to positive values; therefore, enhanced predation risk causes the greatest increases in the relative payoffs for migrating zooplankton if the number of nonmigrating animals is small. This change of slope occurs at the critical point of predation intensity where the payoff for strategy s becomes negative (in relative terms of the model) but its absolute value still increases with food availability. In general, there is always a maximum level of predation pressure that may be compensated for by other advantages; under still-higher mortality risks, only the strategy of vertical migration can be evolutionarily stable. At moderate levels of predation, each strategy can be an ESS, but for many (realistic) combinations of model parameters, strategy mixtures are also ESS's. Even without any fish predation, stable mixed populations

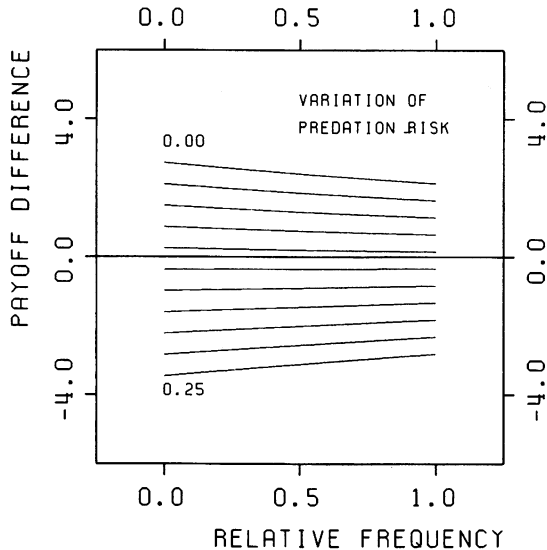


FIG. 4.—Same as figure 1 but at low algal densities ($A = 0.5A_{lim}$).

are possible in principle. This outcome requires extreme conditions, however, such as short days and high metabolic advantage for migrating animals.

A variation in one model parameter can cause a change from a single stable strategy to a stable mixture of strategies or even to the stability of the opposite strategy. The more sensitive the model is to such a parameter, the more easily may evolutionary stability switch to an alternative. One of the most sensitive parameters is egg developmental time. Figure 5 gives such an example where an 8% variation in egg developmental time τ_v , which corresponds to a variation in the average temperature perceived by v strategists, is sufficient to cause the change from one stable strategy over a stable mixture of strategies to the stability of the opposite strategy. Therefore, the region of a stable mixture of strategies may be sometimes restricted to narrow parameter bands.

Influence of the Model Parameters

The role of most model parameters on the strategy is intuitively clear and can also be derived easily from the formulas for ΔS . Any increase in β , the strategy-dependent conversion factor, raises the chances of its accompanied strategy, but a prolonged egg developmental time favors the opposite strategy. Higher predation pressure is always advantageous for strategy v . An improved maximal filtration rate increases the fitness of both strategies, but strategy s gains more than strategy v . Below the incipient limiting level, the relative payoff for strategy v decreases as food concentration increases, but a higher growth rate of the algae can be used better by animals that always stay in the upper water layer. High abundance of zooplankton has the opposite effect of high food availability, but at very high zooplankton abundances a frequency-dependent influence may favor the s strat-

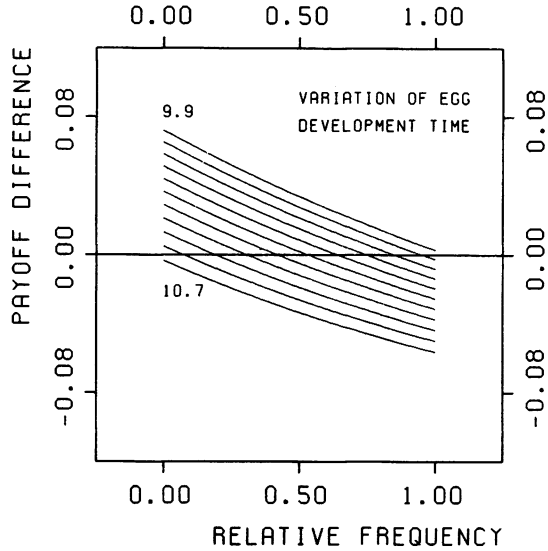


FIG. 5.—Shift in the stable equilibrium of strategy frequencies by variation of the egg developmental time, τ_v , from 9.9 to 10.7 days.

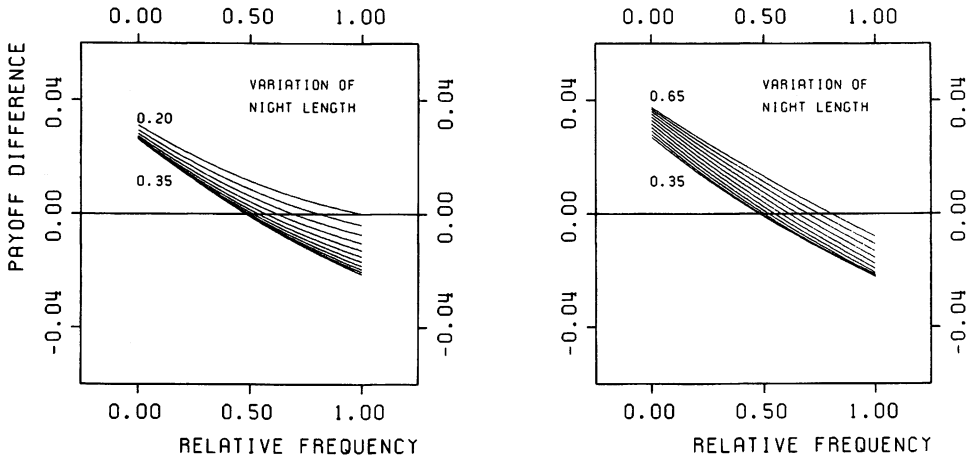


FIG. 6 (left).—Increasing advantage for vertical migration until an optimal length of the night. $T_n = 0.2, 0.215, \dots, 0.35$; $\beta_v = 8$.

FIG. 7 (right).—Decreasing advantage for vertical migration above the optimal length of the night. $T_n = 0.35, 0.38, \dots, 0.65$; $\beta_v = 8$.

egy with increasing frequency of x_s (see fig. 3). In a situation of stable mixtures of strategies, a lengthening of the night at first favors the v strategists (fig. 6). However, there exists a night length that maximizes the frequency of strategy v . Above this optimal value, a prolonged night disfavors vertical migration (fig. 7).

Even if we ignore the known and unknown correlations between the model parameters (e.g., a longer night phase reduces the average temperature of the migrating animals and, therefore, increases their egg developmental time), studies that alter a single factor are helpful in understanding the direction and relative importance of various selective forces. Accepting the simplifications of the model, which probably cause negligible errors compared to the scarcity of available experimental information, any particular situation in the field can be analyzed. The aim of the model, however, is directed more to the study of general tendencies and implications. For the same reason, we do not include further analyses of much more complicated payoffs that can be calculated, for example, frequency-dependent predation pressure at low food concentrations.

DISCUSSION

In natural populations, the abundance and growth rate of algae, the density of zooplankton, fish predation, day length, water temperature, and also the amplitude of vertical migration change markedly over the seasons of a year. The model, however, treats these parameters as constants. Therefore, the model predictions describe the selective forces acting in certain fixed environmental settings and in distinct periods of the annual cycle. It is plausible that the phenotypes of the two strategies can outcompete each other depending on the actual values of factors such as the intensity of fish predation. The most important result of this study is the existence of stable mixtures of strategies in a large range of realistic model parameters. This means that there are environmental conditions under which the advantage or the disadvantage of migration depends on the relative frequency of the strategies in a way that favors the coexistence of migrating and nonmigrating phenotypes. Especially under low predation pressure, the observed vertical migration patterns may be affected by a combination of several factors. The model supports the hypothesis that a change in strength and direction of the selective forces induces variation in the composition of the phenotypes. Clonal replacement is therefore an obvious explanation for the variation in the migration pattern during the year.

However, the model does not exclude the possibility that the migrating phenotype includes a change in behavior during the year triggered by external factors (or internal clocks). In fact, it does not consider such a situation. Nevertheless, the evolutionary stability of strategy v , depending on various conditions as discussed above, may equally well suggest the latter interpretation. An extended model might consider conditional strategies in the sense that finely grained field investigations and experiments would have to be conducted accordingly. Because of the difficulty in following single zooplankters, the available field data on vertical migration consider whole populations and not individuals. Therefore, one must be careful in interpreting the phenomena (see Pearre 1979*a,b*).

Even such striking results as the "evolution of vertical migration," as observed by Gliwicz (1986), can be explained in terms of our model. The existence of stable mixtures of strategies with (undetectable) low frequencies of migrating animals (or their immigration) would be sufficient to explain the observation of enhanced vertical migration following the increase in fish abundance. The coexistence of the migrating and nonmigrating, yet closely related, *Daphnia* species in Lake Constance can be understood without a niche-segregation argument. Slightly different metabolic parameters and/or predator-evasion probabilities are sufficient to establish their different stable strategies. If one treats the two species as one (hybrids can be found; Wolf and Mort 1986), then they could be genetically different representatives of the two strategies.

Only two distinct strategies are analyzed in our model. It is very likely, however, that intermediate strategies are responsible for different migration amplitudes in nature. This could be described by modifications of the model presented here; we believe that the level of simplicity chosen here is nevertheless powerful enough to obtain the desired interpretation of the ultimate and proximate causes of diel vertical migration. Our model is intended to stimulate more detailed experiments on the physiology and genetics of zooplankton.

SUMMARY

By applying evolutionary game theory, we calculate the differences in payoffs between diel vertical migrating and nonmigrating zooplankton. The results depend on the abundance and growth rate of the algae, the filtration rate and density of the zooplankton, the strategy-dependent efficiency of converting food into reproduction, temperature-dependent egg developmental time, day length, and predation pressure. In addition to regions where the two strategies exclude each other, it is also possible for a population to reach an evolutionarily stable equilibrium mixture of strategies. At high food concentrations, equilibrium is unlikely because it would require a predation risk increasing with prey abundance; but at low food concentrations, strategy mixtures can be stable for many combinations of realistic model parameters, even with density-independent mortality caused by fish predation. Temporal variation in the selective forces shifts this equilibrium point. Therefore, the model can explain seasonal changes and long-term trends in the pattern of diel vertical migration.

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LITERATURE CITED

Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* 131:271-290.

- Enright, J. T. 1977. Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. *Limnol. Oceanogr.* 22:856-872.
- Enright, J. T., and H. W. Honegger. 1977. Diurnal vertical migration: adaptive significance and timing. Part 2. Test of the model: details of timing. *Limnol. Oceanogr.* 22:873-886.
- Fry, F. E. J. 1947. Effects of the environment on animal activity. Publications of Ontario Fisheries Research Laboratory, 68. University of Toronto Press, Toronto, Ontario.
- Geller, W. 1986. Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): a starvation avoidance mechanism? *Arch. Hydrobiol. (Suppl.)* 74:1-60.
- Gliwicz, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature (Lond.)* 320:746-748.
- Hairston, N. G. 1976. Photoprotection by carotenoid pigments in the copepod *Diatomus nevadensis*. *Proc. Natl. Acad. Sci. USA* 73:971-974.
- Huntsman, A. G. 1925. Limiting factors for marine animals. I. The lethal effect of sunlight. *Contrib. Can. Biol. new ser.* 2:81-88.
- Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. *Am. Nat.* 120:171-180.
- Kerfoot, W. B. 1970. Bioenergetics of vertical migration. *Am. Nat.* 104:529-546.
- Lampert, W. 1977. Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. III. Production and production efficiency. *Arch. Hydrobiol. (Suppl.)* 48:310-335, 336-360.
- Lampert, W., and B. Taylor. 1985. Zooplankton grazing in a eutrophic lake: implications of diel vertical migration. *Ecology* 66:68-82.
- Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47:209-221.
- . 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.
- Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflicts. *Nature (Lond.)* 246:15-18.
- McLaren, I. A. 1963. Effects of temperature on the growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Board Can.* 20:685-727.
- . 1974. Demographic strategy of vertical migration by a marine copepod. *Am. Nat.* 108:91-102.
- McMahon, J. W., and F. H. Rigler. 1965. Feeding rate of *Daphnia magna* Straus in different foods labeled with radioactive phosphorus. *Limnol. Oceanogr.* 10:105-113.
- Ohman, M. D., B. W. Frost, and E. B. Cohen. 1983. Reverse diel vertical migration: an escape from invertebrate predators. *Science (Wash., D.C.)* 220:1404-1407.
- Pearre, S., Jr. 1979a. On the adaptive significance of vertical migration. *Limnol. Oceanogr.* 24:781-782.
- . 1979b. Problems of detection and interpretation of vertical migration. *J. Plankton Res.* 1: 29-44.
- Pohley, H.-J., and B. Thomas. 1979. On evolutionarily stable strategies in populations with subpopulations having isolated strategy repertoires. *BioSystems* 11:263-268.
- . 1983. Non-linear ESS-models and frequency dependent selection. *BioSystems* 16:87-100.
- Ringelberg, J. 1964. The positively phototactic reaction of *Daphnia magna* Straus: a contribution to the understanding of the diurnal vertical migration. *Neth. J. Sea Res.* 2:319-406.
- Schuster, P., and K. Sigmund. 1981. Coyness, philandering and stable strategies. *Anim. Behav.* 29:186-192.
- Selten, R. 1980. A note on evolutionarily stable strategies in asymmetric animal conflicts. *J. Theor. Biol.* 84:93-101.
- Siebeck, O. 1960. Untersuchungen über die Vertikalwanderung planktischer Crustaceen unter Berücksichtigung der Strahlungsverhältnisse. *Int. Rev. Gesamten Hydrobiol.* 45:381-454.
- Stich, H.-B. 1985. Untersuchungen zur tagesperiodischen Vertikalwanderung planktischer Crustaceen im Bodensee. Ph.D. diss. University of Freiburg, Freiburg, West Germany.
- Stich, H.-B., and W. Lampert. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature (Lond.)* 293:396-398.
- . 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under

- simulated food and temperature conditions of diurnal vertical migration. *Oecologia (Berl.)* 61:192-196.
- Thomas, B. 1984. Evolutionary stability: states and strategies. *Theor. Popul. Biol.* 26:49-67.
- Weider, L. J. 1984. Spatial heterogeneity of *Daphnia* genotypes: vertical migration and habitat partitioning. *Limnol. Oceanogr.* 29:225-235.
- Wolf, H.-G., and M. Mort. 1986. The genetic structure of large-lake *Daphnia* populations. *Evolution* 40:756-766.
- Wright, D., W. J. O'Brien, and G. L. Vingard. 1980. Adaptive value of vertical migration: a simulation model argument for the predation hypothesis. Pages 138-147 in W. C. Kerfoot, ed. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, N.H.
- Zaret, T. M., and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* 21:804-813.