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The influence of food availability, predation risk, and metabolic costs on the evolutionary stability of diel vertical migration in zooplankton

WILFRIED GABRIEL and BERNHARD THOMAS

With 3 figures in the text

Introduction

Diel vertical migration of zooplankton implies that during daytime the richer food resources of the upper water layers are not used and that egg developmental time is prolonged due to the lower temperature experienced by the animals. To find ultimate causes for the migratory behaviour, these two disadvantages have to be offset by fitness components that increase because of vertical migration. Several hypotheses have been proposed: metabolic advantages and better utilization of resources (McLAREN 1963 and 1974, KERFOOT 1970, ENRIGHT 1977, ENRIGHT & HONNEGER 1977), avoidance of starvation (GELLER 1986), and avoidance of visual predators (ZARET & SUFFERN 1976, WRIGHT et al. 1980). Field data (e.g. GLIWICZ 1986) support the predator evasion hypothesis.

In Lake Constance STICH & LAMPERT (1981) observed different migratory behaviour in two coexisting and morphologically very similar *Daphnia* species: one migrated but the other did not. Because they differed only slightly in reproductive and metabolic parameters (STICH & LAMPERT 1984), the conditions when vertical migration is an evolutionarily stable strategy must be evaluated. Doing so may determine whether the coexistence of these two strategies can be understood from a theoretical point of view. By modelling the interaction of algae, zooplankton, and predators and using evolutionary game theory, GABRIEL & THOMAS (1988) found that either vertical migration, no vertical migration, or a mixture of both strategies can all be evolutionarily stable. Using this general model we investigate the influence of food availability, predation risk, and metabolic costs on the favoured strategy.

The model

The data on diel vertical migration suggest that physical factors (day length, water temperature), biotic interactions (food availability, grazing rate, predation risk), and physiological constraints all may influence the choice of the optimal strategy and its evolutionary stability. Therefore, the model calculates the payoff difference between migrating and non-migrating animals depending on the following parameters: relative night length (T_n) in parts of 24 hours, algal density (A_0) in units of food concentration relative to the incipient limiting level (McMAHON & RIGLER 1965), partial intrinsic growth rate (r_p) of the algae (intrinsic growth rate that would have to be applied in the absence of zooplankton), density (N) and maximal filtration rate (γ) of zooplankton (N and γ are normalized in a way that $N\gamma$ is the corresponding intrinsic death rate of the algae), egg developmental time (τ_v in case of vertical migration and τ_s without migration), conversion efficiency of food into reproduction taking into account mortality caused by non-visual predators (β_v in case of vertical migration and β_s without migration), and predation risk (p as probability of being eaten in a time period of one day). GABRIEL & THOMAS (1988) calculated the payoff difference between the migratory and non-migratory strategies as a function of these parameters and the relative frequency ($= x_s$) of non-migrating animals. Using these formulas (but putting $x_s = 1$) one can easily calculate the level of predation risk at which the payoffs are equal for both strategies:

$$p_{\text{tot}} = (a_d + a_n(1 - \beta_v w / \beta_s)) / (a_d(1 + 1.5 \tau_s) + a_n 1.5 \tau_s)$$

with

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

and with a_d and a_n as the ingestion rates during day (d) and night (n). Below the incipient limiting level one gets

$$a_d = \gamma A_o [\exp\{(r_p - \gamma x_s N)(1 - T_n)\} - 1] / (r_p - \gamma x_s N)$$

$$a_n = A_o \exp\{(r_p - \gamma x_s N)(1 - T_n)\} [1 - \exp\{-\gamma N T_n\}] / N$$

and above incipient level A_{lim}

$$a_d = \gamma A_{lim} (1 - T_n)$$

$$a_n = \gamma A_{lim} T_n$$

We call this calculated predation level p_{tol} the tolerable predation risk. These results imply that at lower predation risks vertical migration is disfavoured, but at higher predation risks vertically migrating phenotypes can successfully invade the population and establish a stable portion of the population or, with further increasing predation risk, competitively exclude the non-migrating ones. Here we study the influence of the model parameters on the evolutionary stability of vertical migration in terms of this tolerable predation risk. If not indicated differently, the following parameter values are used: $A_o = 0.5$, $\gamma = 0.55$, $r_p = 0.35$, $N = 1.0$, $T_n = 0.4$, $\beta_s = 10.0$, $\beta_v = 11.0$, $\tau_s = 5.0$, $\tau_v = 10.0$.

Results and discussion

Any benefit for the non-migratory strategy increases the tolerable predation risk p_{tol} above which vertical migration is the favoured strategy, and, vice versa, any reduction in

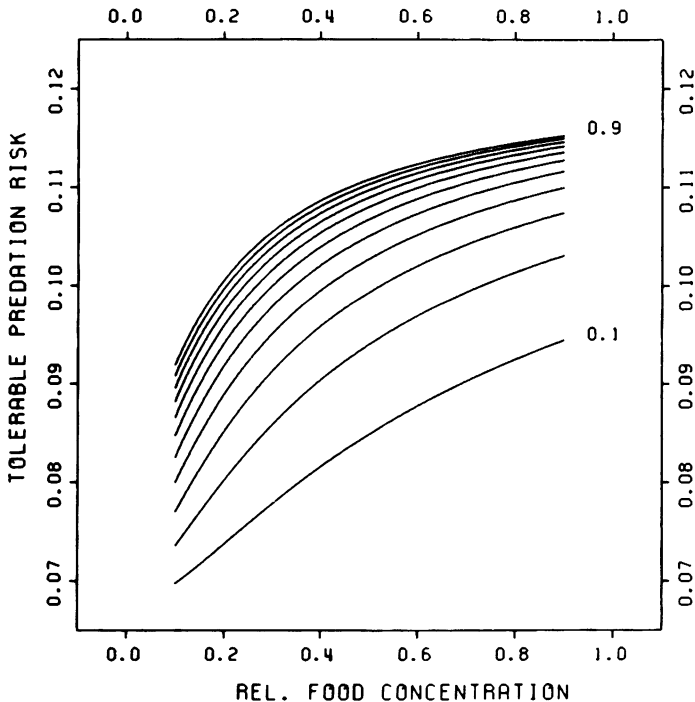


Fig. 1. Tolerable predation risk as a function of relative food concentration. The maximal filtration rate is varied from 0.1 to 0.9.

payoff for non-migration in relation to migration lowers p_{tol} . Therefore, the changes of the tolerable predation risk with variation of model parameters indicates whether the associated selective forces are in favour of vertical migration. Either an improved maximal filtration rate or an increased algal density (when below the incipient limiting level) lead to higher fitness due to enhanced reproductive output irrespective of the strategy chosen, but Fig. 1 shows that the profit for non-migrating animals is relatively higher than for migrating ones. Fig. 2 demonstrates that a change of the night length can increase or decrease the advantage of a strategy, dependent on the actual parameter values, but a higher partial algal growth rate always increases the relative payoff more for non-migrating than for migrating animals. Fig. 3 illustrates the influence of egg developmental time and the conversion efficiency of food uptake into reproduction. The longer the egg developmental time of migrating animals or the shorter the egg developmental time of non-migrating ones, the higher is the tolerable predation risk. In the case of non-migration, it also easily follows from the equations that food conversion efficiency (β_s) is always positively correlated with the tolerable predation risk. However, for vertical migration (β_v) the relationship between p_{tol} and β_v is more complicated, since the factor w is itself dependent on β_v (w corrects for the fact that fitness not only depends on total reproductive output within a time period but also on the frequency at which the reproduction occurs). For vertically migrating animals the advantage of the relative payoff due to increased food conversion efficiency is smaller as the egg developmental time is longer. The numer-

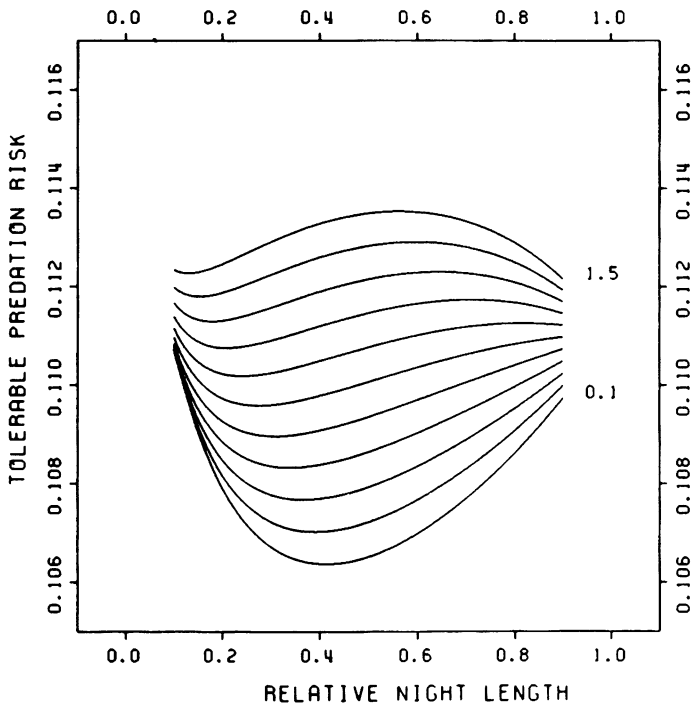


Fig. 2. Tolerable predation risk as a function of relative night length. The partial growth rate of algae is varied from 0.1 to 1.5.

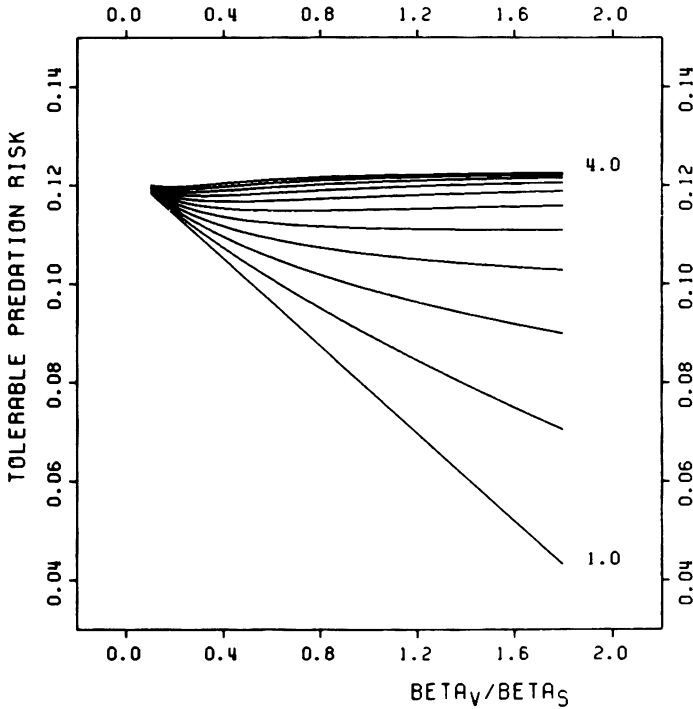


Fig. 3. Tolerable predation risk as a function of β_v/β_s , which is the ratio of the conversion efficiencies β of food into reproduction of migrating (v) and non-migrating (s) animals (β_s is kept fixed and β_v varies). The ratio of egg developmental time periods τ_v/τ_s is varied from 1.0 to 4.0 keeping τ_s fixed.

ical values of tolerable predation risks are of course dependent on the parameter values chosen, but the qualitative behaviour is independent of the parameter set. The tolerable predation risk increases with algal density and is maximal if β_v is small compared with β_s at high food concentrations. This maximal obtainable p_{tol} can be predicted from

$$\max(p_{\text{tol}}) = 1/(1 - T_n + 1.5 \tau_s)$$

The value of $\max(p_{\text{tol}})$ is mainly a function of τ_s and is only slightly modified by T_n ($T_n < 1.0$, $\tau_s > 1.0$). One may also ask whether vertical migration could also be advantageous in the absence of visual predators in the upper water layers. This would be equivalent to $p_{\text{tol}} \leq 0$. Fig. 3 shows that even under quite equal temperature conditions for migrating and non-migrating animals ($\tau_s/\tau_v \cong 1$), this is possible only if vertical migration is accompanied by an enormous gain in efficiency of conversion of food into reproduction. Therefore, it is extremely unlikely that metabolic advantages by themselves are ultimate causes of vertical migration in zooplankton. The main selective force for vertical migration seems to be the reduction of mortality, but the tolerable level of predation risk is a function of food availability and metabolic parameters.

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