

Diel vertical migration arising in a habitat selection game

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Abstract Predator and prey react to each other, adjusting their behavior to maximize their fitness and optimizing their food intake while keeping their predation risk as low as possible. In a pelagic environment, prey reduce their predation mortality by adopting a diel vertical migration (DVM) strategy, avoiding their predator during their peak performance by finding refuge in deep layers during daylight hours and feeding at the surface during the night. Due to the duality of the interaction between prey and predator, we used a game theory approach to investigate whether DVM can be a suitable strategy for the predator as well as the prey. We formulated three scenarios in plankton ecology in order to address this question. A novel finding is that mixed strategies emerge as optimal over a range of the parameter space, where part of the predator or prey population adopts a DVM while the rest adopt one or other “sit and wait” strategies.

Keywords Predator–prey interaction · Habitat selection · Game theory · Diel vertical migration · Zooplankton

Introduction

One of the most conspicuous features of marine pelagic ecosystems is the daily vertical migration exhibited by large numbers of organisms including fish (Beamish 1966), krill (Bollens et al. 1992; Zhou and Dorland 2004), jellyfish (Kaartvedt et al. 2007), copepods (McLaren 1963; Hays et al. 2001; Bollens and Frost 1989), and protists (Eppley 1968). Indeed, it has been argued that this vertical migration constitutes one of the largest concerted movements of biomass on earth (Hays 2003; Angel and Pugh 2000). This migration is not only important in shaping trophic interactions in the marine ecosystem, but it also contributes to the biological pump, influencing the rate at which carbon is drawn down from the atmosphere and sequestered in the deep ocean (Steinberg et al. 2000; Ducklow et al. 2001), with implications for global climate.

The imperative for vertical migration can be largely found in predator–prey interactions (Zaret and Suffern 1976). As in all predator–prey interactions, both predators and prey attempt to maximize their food intake (to fuel growth and reproduction) while at the same time seeking to minimize their mortality due to predation. In pelagic waters, prey can find refuge in deeper, darker waters, where the predator’s visual acuity is reduced (Aksnes and Giske 1993; Fortier et al. 2001). Therefore, the diel vertical migration (DVM) of zooplankton between the surface layers at night and the deeper waters during the day has largely been attributed to the trade-off between the availability of food and the necessity of avoiding predators (Lampert 1989; Dill 1987).

Diel vertical migration of zooplankton has been widely studied in fjords (Frost 1988; Bollens et al. 1992; Onsrud and Kaartvedt 1998), shelf seas (Krause and

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Radach 1989; Irigoien et al. 2004; Durbin et al. 1995), as well as open ocean systems (Hays 1996; Hattori 1989). In general, three patterns emerge: normal migration, reverse migration, and no detectable migration. These different patterns may be exhibited by the same population at different times. For instance, in the population of the copepod *Pseudocalanus newmani* in Dabob Bay, Washington, USA, different DVM patterns are correlated with the presence or absence of their predators (the copepod *Euchaeta elongata*, the chaetognath *Sagitta elegans*, and the euphausiids *Euphausia pacifica*) as well as the abundance of planktivorous fish (Ohman 1990) which target these predatory zooplankton in turn. In the same area, seasonal and interannual variation in the migratory behavior of the copepod *Calanus pacificus* yield significantly different mortality rates in migrating and nonmigrating copepods (Frost 1988). Further, while in general, populations move vertically according to some daily rhythm, it is also conspicuous that not all individuals do the same (Hays et al. 2001). Differing proportions of populations may migrate or remain in residence in surface or deep habitats. Indeed, detailed measurements of the vertical migratory behavior of individual jellyfish *Periphylla periphylla* (Kaartvedt et al. 2007) show asynchronous migrations by individuals sporadically throughout the day and night. These differences in migratory behavior have been ascribed to the different states (e.g. age, size, maturity, gut-fullness, and reserves) of individuals (Hays et al. 2001) and the subsequent trade-offs these individuals are faced with in maximizing their fitness.

Different methods to model the trade-offs inherent in DVM have been proposed over the years, such as dynamic programming (Mangel and Clark 1986; Fiksen and Giske 1995; Fiksen et al. 1998; Titelman and Fiksen 2004), life history theory (McLaren 1963), and genetic algorithms (Fiksen 2000; Eiane and Parisi 2001; Strand et al. 2002). However, most of these predator–prey interaction studies focused almost entirely on the prey, with the assumption that only the prey adapts its behavior. Lima (2002) argued that the entire predator–prey interaction should be taken into account, and that the predator adapts its behavior to the prey as much as vice versa. The predators should thus be able to follow the prey and react to their potential behavioral adjustments in order to maximize their hunting activity. Game theory has emerged as one of the best approaches for investigating how prey and predator interact, because it considers the characteristics and goals of both actors. While dynamic programming, life history theory, and genetic algorithms optimize individual's behavior on

long time scale, game theory often focus on short time scale; the day-to-day business of foraging in a risky environment. Finally, as a practical matter, game theory methods involve a low computational cost.

Game theory was introduced in ecology as the ideal free distribution (Fretwell and Lucas 1969), and Iwasa (1982) was the first to use game theory to explain the interaction between predators and prey and their distribution between two habitats. However, his results were not evolutionarily stable (Gabriel and Thomas 1988) and did not include DVM as a possible strategy. Gabriel and Thomas (1988) proposed a model that reaches the evolutionary stable state, but did not described the predator behavior. Afterward, Hugie and Dill (1994) presented a game theory using populations of fixed size and studied the interference and dilution effects in habitat choice, without including the DVM strategy. Later, Luttbegg and Sih (2004) used genetic algorithms to show that the relative importance of intra and interspecific competition is ruled by the fitness calculation, while Flaxman and Reeve (2006) explored the reasons for deviations from ideal free habitat selection.

As in the Hugie and Dill's study (1994), we investigate an inter- and conspecific game where prey and predator can choose between staying at the surface or going into the deep, and we add the possibility of a DVM strategy. We explore under which conditions DVM is the best strategy for the predator or the prey and, by contrast, under which conditions staying in one environment is the best strategy. To this end, three scenarios were analyzed: (1) Only the prey could perform DVM; (2) Prey and predator could both perform DVM; and (3) Presence of a top predator in the system. Some examples from the literature are used to illustrate the model.

Method

We consider a prey population (N) and a predator population (P) in a water column, which is divided into a surface habitat (S) and a deep habitat (D). Each individual chooses between the two habitats in order to maximize its fitness. Three strategies are investigated: staying at the surface (S), staying in the deep (D), or performing a DVM, by seeking refuge in the deep layer during the day and ascending to the surface at night (m). Migrating individuals are in the deep when it is light, which it is a fraction σ of the time, and at the surface when it is dark, a fraction $1 - \sigma$ of the time. We assume that the population size remains constant

and focus on the distribution of individual between strategies at a given time. The proportion of individuals that adopt each strategy is denoted as N_S , N_D , and N_m for the prey, and as P_S , P_D , and P_m for the predators:

$$\begin{cases} N_S + N_D + N_m = 1 \\ P_S + P_D + P_m = 1 \end{cases} \quad (1)$$

We evaluate fitness as the difference between specific growth rate and mortality rate. We choose a type I functional response for simplicity, assuming that the predator remains under-satiated at all times. For the prey, the specific growth rate is density independent and equals λ_S for an individual which adopts the “surface” strategy S , and λ_D for an animal which adopts the “deep” strategy D . A migrating prey individual experiences a time-averaged growth rate $\sigma\lambda_D + (1 - \sigma)\lambda_S$. In turn, a prey individual’s instantaneous predation risk is found as $V \cdot P$, where P is the proportion of predators present in the prey’s habitat at this instant, and the factor V is denoted predator voracity. This voracity differs between night and day and between the surface and the deep, and is an aggregate parameter which is affected by total predator abundance and relative habitat sizes, relative speed of movement between predator and prey, and detection distance. Time-averaged predation risks will be computed in the following in three different scenarios.

For the predator, the instantaneous growth rate is proportional to $V \cdot N$, where V is the local voracity and N is the fraction of prey occupying the predator’s habitat.

Note that the fitness of an individual is independent of its conspecifics and a linear (strictly, affine) function of the densities of the other species; i.e., we make the same simplifying assumptions of density independence and Holling type I functional response as in the classical Lotka–Volterra model of population dynamics.

Scenario 1: Only the prey can perform DVM

In this first scenario, the preys are able to choose the DVM strategy, while the predators only have the choice between remaining in the surface or the deep habitat (i.e., we enforce $P_m \equiv 0$). The fitness of a prey in the deep is the difference between growth rate and predation mortality, i.e., $F_{N_D} = \lambda_D - V_d P_D$. A prey which stays at the surface has a growth rate of λ_S and encounter surface predators which have a time-averaged voracity of $\sigma V_l + (1 - \sigma)V_d$ (voracity V_l in presence of light, and V_d in darkness). Prey performing DVM are

always in the dark and therefore encounter predators with constant voracity V_d , but with a time-averaged relative abundance $\sigma P_D + (1 - \sigma)P_S$. In summary, the fitness of prey adopting the different strategies are:

$$\begin{cases} F_{N_S} = \lambda_S - (\sigma V_l + (1 - \sigma)V_d)P_S \\ F_{N_D} = \lambda_D - V_d P_D \\ F_{N_m} = \sigma(\lambda_D - V_d P_D) + (1 - \sigma)(\lambda_S - V_d P_S) \end{cases} \quad (2)$$

Similarly, a surface predator has a voracity V_l in the day-time where it encounters prey with abundance N_S , and a voracity V_d in the nighttime where the prey abundance is $N_S + N_m$. A predator in the deep has constant voracity V_d and experiences a time-averaged prey abundance $N_D + (1 - \sigma)N_m$. In summary, the fitness of the two predator strategies are:

$$\begin{cases} F_{P_S} = (\sigma V_l + (1 - \sigma)V_d)N_S + (1 - \sigma)V_d N_m \\ F_{P_D} = V_d N_D + \sigma V_d N_m \end{cases} \quad (3)$$

Scenario 2: Prey and predator can both perform DVM

In this scenario, both prey and predator may perform a DVM. That is, we allow the predator to match the prey distribution daily, as suggested by Lima (2002). Predators performing DVM forage in the surface at night, in the deep during daytime, and all day long on the vertically migrating prey (Eq. 4). Since migrating predators are always in the dark, their voracity is constant V_d . From the point of view of the prey, migrating predators gives rise to an extra term in the predation risk (Eq. 2): $(1 - \sigma)V_d P_m$ for surface prey, $\sigma V_d P_m$ for deep prey, and $V_d P_m$ for migrating prey. Thus, the fitness of prey strategies become:

Prey:

$$\begin{cases} F_{N_S} = \lambda_S - (\sigma V_l + (1 - \sigma)V_d)P_S - (1 - \sigma)V_d P_m \\ F_{N_D} = \lambda_D - V_d P_D - \sigma V_d P_m \\ F_{N_m} = \sigma(\lambda_D - V_d P_D) + (1 - \sigma)(\lambda_S - V_d P_S) - V_d P_m \end{cases} \quad (4)$$

Predator:

$$\begin{cases} F_{P_S} = (\sigma V_l + (1 - \sigma)V_d)N_S + (1 - \sigma)V_d N_m \\ F_{P_D} = V_d N_D + \sigma V_d N_m \\ F_{P_m} = (1 - \sigma)V_d N_S + \sigma V_d N_D + V_d N_m \end{cases} \quad (5)$$

Scenario 3: Presence of a top predator in the system

In the last scenario, we investigate the impact of a third trophic level on top of the predator–prey system considered so far. This top predator is only allowed to forage on the intermediate predator and is assumed to stay at the surface ($T_S = 1$) all the time, but is given different foraging efficiencies in the day and the night. The fitness of prey in the scenario is that in the previous scenario, i.e., Eq. 4. For surface and migrating intermediate predators, a predation risk is amended:

Predator:

$$\begin{cases} F_{P_S} = (\sigma V_l + (1 - \sigma)V_d)N_S + (1 - \sigma)V_dN_m \\ \quad - (\sigma W_l + (1 - \sigma)W_d)T_S \\ F_{P_D} = V_dN_D + \sigma V_dN_m \\ F_{P_m} = (1 - \sigma)V_dN_S + \sigma V_dN_D + V_dN_m \\ \quad - (1 - \sigma)W_dT_S \end{cases} \quad (6)$$

Since top predators have fixed strategies, their fitness does not influence model results, but we include it for completeness:

$$F_{T_S} = \sigma W_l P_S + (1 - \sigma)W_d(P_S + P_m) \quad (7)$$

Solution

The fitness functions define a noncooperative game, where individuals play against individuals of their own species as well as individuals of the other species. To solve this game, we identify the Nash equilibrium, where no individual can gain an advantage by changing strategy. The Nash equilibrium is found numerically by solving the replicator equation until steady state (Schuster and Sigmund 1983; Hofbauer and Sigmund 2003); see Appendix for details.

Results

Our primary interest was to investigate the migration patterns emerging as a result of differing factors contributing to the fitness trade-offs or the various actors. To facilitate intercomparison, the model was set up so that the prey's available food in the deep, predation efficiency in the deep, and top predator efficiency in the dark were all assumed to stay constant ($\lambda_D = 0.2$, $V_d = 0.1$, and $W_d = 0.05$). The simulations were set for a daylight hour proportion $\sigma = 0.65$ per day. The effect of changes in prey's growth rate (λ_S), in predation voracity (V_l), and the top predator efficiency in the

surface and in light hours (W_l) were investigated in the different scenarios.

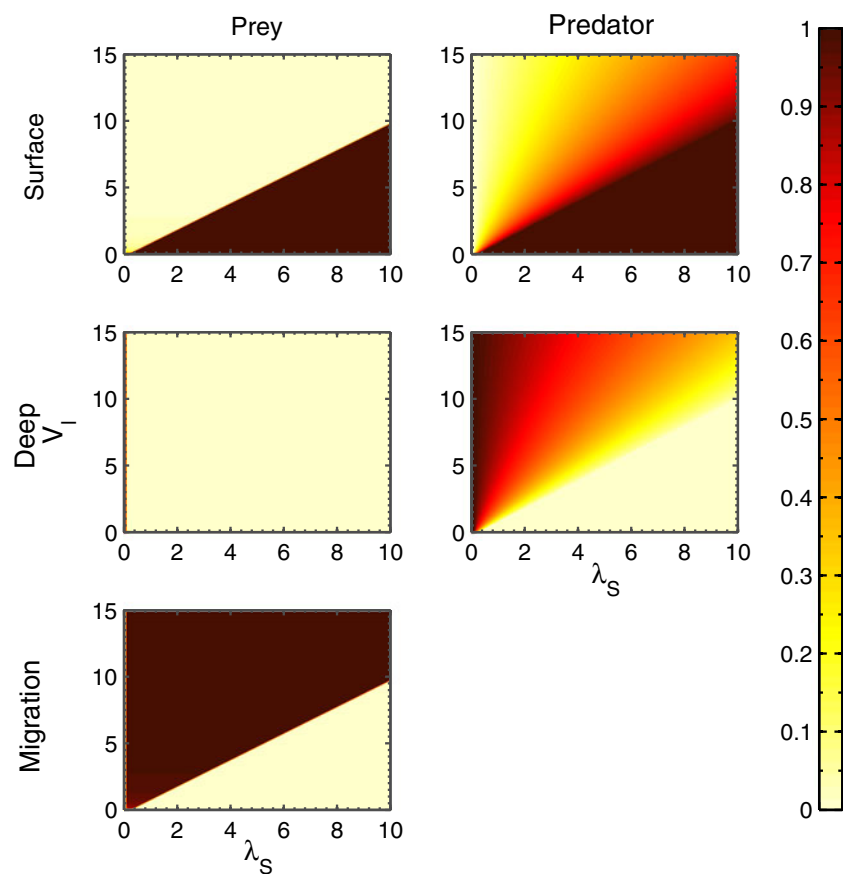
Scenario 1: Only the prey could perform DVM

Prey had the choice between staying at the surface, in the deep or performing a diel vertical migration (i.e., staying at the surface during the night and in the deep during the day). The DVM strategy for the prey was advantageous so long as the predators' voracity was relatively high compared to the prey's growth rate (Fig. 1). In the opposite situation, i.e., when the growth rate at the surface was very high compared to the predator voracity, the prey favored the surface, no matter what the distribution of the predator was. Further, the whole prey population chose the same strategy, all remaining in the surface (low risk, high growth) or performed diel migration (high risk, low growth). In the meantime, the proportion of predators at the surface increased when the prey's growth rate (λ_S) increased (matching the observation made by Hammond et al. 2007) and all the predators remained at the surface when all the prey were there (Fig. 1). Therefore, apart from the case where all the prey were concentrated in the same habitat, the predator tend to match the prey resources and not their own resource distribution, a feature which Sih (1998) and Flaxman and Lou (2009) also observed.

Scenario 2: Prey and predator could both perform DVM

Now, predators were given the possibility of following their prey in a DVM between the deep layer during daylight hours and the surface layer at night. Although, the DVM strategy was not purely favorable for the predator, as they could not benefit from their high visual performance (they stay in the deep layer, where the light cannot penetrate during the day, and come to the surface when it is dark), the DVM strategy allowed the predators to match the prey distribution and migration. Optimal prey strategies were similar to scenario 1, with largely the whole prey population choosing the same strategy, all remaining in the surface (low risk, high growth) or performing diel migration (high risk, low growth, Fig. 2). Unlike the first scenario, the predators did not choose to remain in the deep habitat. This result can easily be understood by the absence of a migration cost and the absence of prey in this habitat at night. Unsurprisingly, when all the prey remained in the surface under high growth, low risk, so too did the predators while DVM becomes a suitable strategy for both predator and prey when food levels drop and predator performance increases. However, while the

Fig. 1 Proportion of individuals in the different strategies, with the prey in the *left column* and the predators in the *right column*, in the case where the prey are the only ones able to perform the DVM. On the x-axis, we varied the prey's growth rate in the surface, and on the y-axis the daylight predator voracity. The *first row* represents the proportion of individuals that choose the strategy of staying in the surface. The *second row* shows the proportion that chose the deep strategy, and the *bottom row* represents those that chose the DVM strategy



switch in strategies for prey encompasses very nearly the whole population at once, the predator population exhibits a more mixed response with variable fractions of the population choosing one strategy or the other.

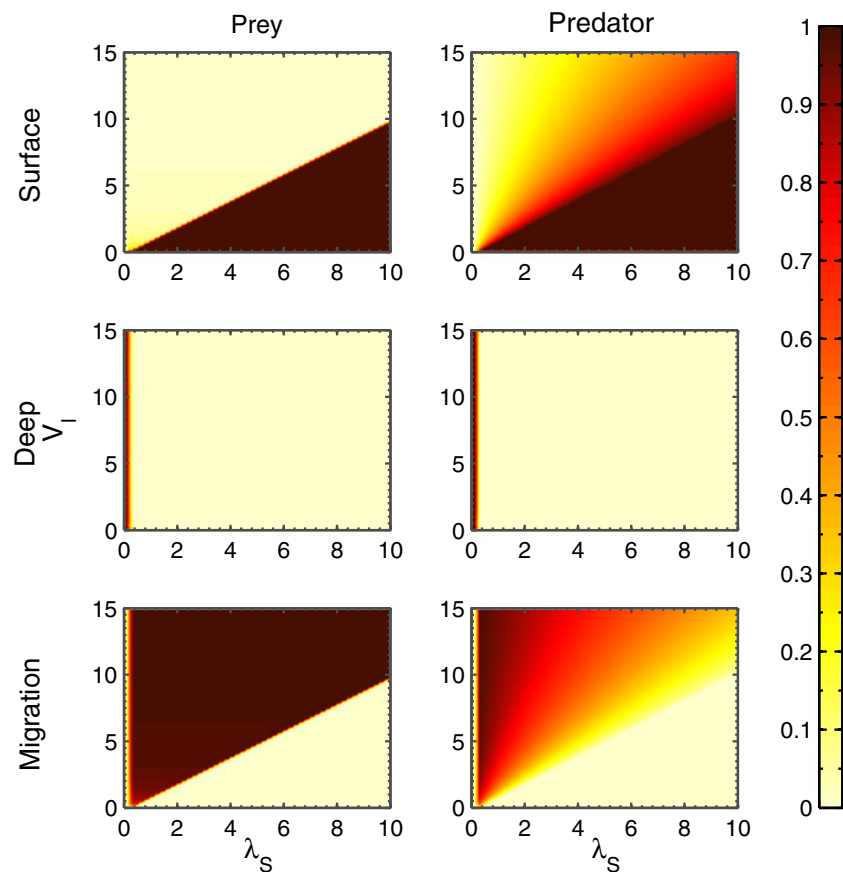
Scenario 3: Presence of a top Predator in the system

The system includes a top predator above the prey–predator system, which is assumed to forage only on the intermediate predator. Introducing a top predator into the predator–prey system opens new opportunities for the prey (Fig. 3 compared to Fig. 2), “the enemies of my enemy is a friend” situation (Fiksen 2000). The prey can now freely match their resources when the predation risk from the top predator is sufficient to deter the intermediate predator. In such circumstances, the intermediate predator will perform DVM and the prey can stay freely in the surface (see Fig. 3 and bottom right corner of each panel in Fig. 4, showing high W_I values and low V_I values). However, when the intermediate predator is more efficient than the top predator, the intermediate predator prefers to sustain the mortality risk and will divide between staying in the surface and migrating (top of the panel in Fig. 3 and

bottom left corner of each panel in Fig. 4, low value of W_I). When the intermediate predators become too efficient at foraging on the prey, the preys look for refuge in the DVM strategy, leading the intermediate predator to follow them partially in their migration (top of each panel in Figs. 3 and 4).

It is interesting to observe that when the prey and intermediate predator both display mixed strategies, e.g., high voracity V_I and prey growth rate λ_S in Fig. 3, the proportions of the different strategies are determined indirectly, by the game played by the other species. For example, the proportions of the prey strategies are independent of the prey growth rate λ_S but depend only the voracity V_I of their predators (Fig. 3, top left panel). What explains this somehow counterintuitive phenomenon is that the prey proportions are determined by the requirement that the predator strategies must have same fitness: Clearly, the prey growth rate λ_S does not directly affect predator fitness and therefore does not affect prey distribution. Similarly, the proportions of predator strategies are determined by the requirement that the prey strategies have same fitness, and is therefore essentially given by the ratio V_I/λ_S , which explains the diagonal isoproportion lines in Fig. 3, top right

Fig. 2 Proportion of individuals in the different strategies, with the prey in the *left column* and the predators in the *right column*, in the case where prey and predators can both perform the DVM. On the x-axis, we varied the prey's growth rate in the surface, and on the y-axis the daylight predator performance. The *first row* represents the proportion of individuals that choose the strategy of staying in the surface. The *second row* shows the proportion that chose the deep strategy, and the *bottom row* represents those that chose the DVM strategy



panel. This phenomenon of indirect control is related to the well-known Lotka–Volterra equations, where the equilibrium abundance of prey is independent of its own growth rate but not independent of predator mortality (e.g., Edelstein-Keshet 2004, p. 220).

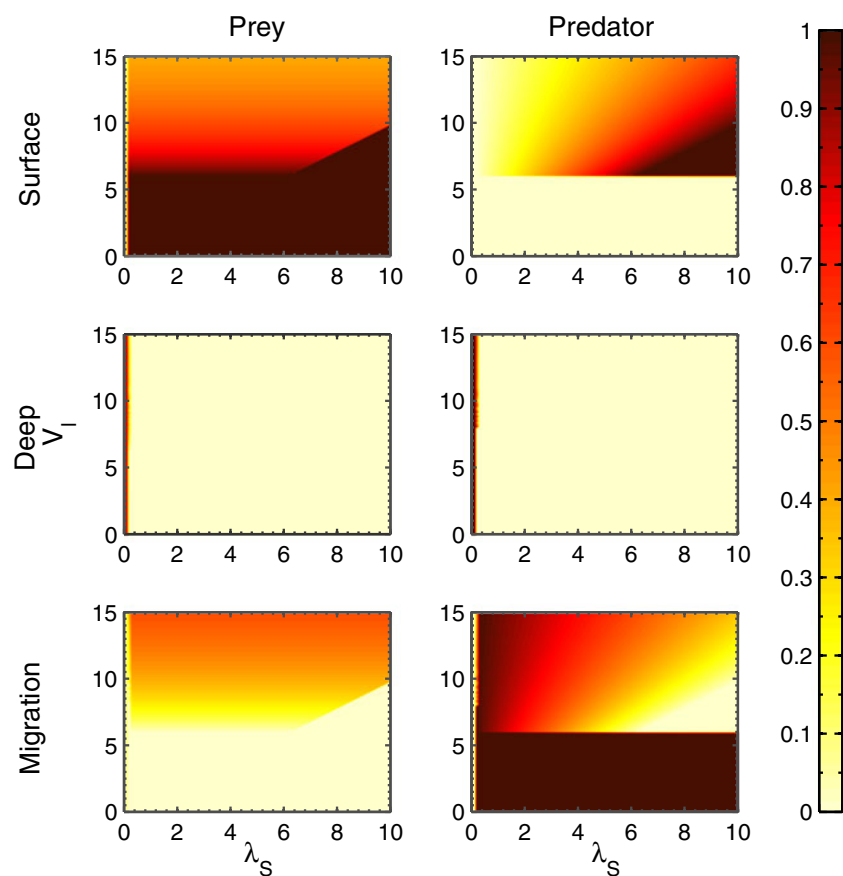
Discussion

Our game theoretic model of diel vertical migration, predicated on the fitness trade-offs incurred by predators and prey, reproduces the main features observed in nature; that prey select DVM when risk in surface waters during the day outweighs the added benefit of resource acquisition. Moreover, it predicts DVM as an optimal strategy for predators as well, when following migrating prey provides an added benefit either in feeding opportunity (scenario 2) or in mitigating their own predation risk (scenario 3). This coupling of DVM behavior between trophic levels echoes the “cascading migration” concept forwarded by Bollens et al. (2011). While the proximate causes of DVM may be more complex than presented here (e.g., temperature effects on metabolic rates (Fiksen and Giske 1995),

turbulence, risk, and feeding opportunities (Visser et al. 2009)), the modeling framework presented here provides a means of assessing evolutionary stable strategies across trophic guilds. A particular feature of the model is the emergence of mixed strategies, where parts of the population assume different strategies. This may at first seem puzzling, as there is no inherent density dependence included in the various fitness trade-offs. There are, however, functional density dependencies mediated by trophic interactions; DVM in prey is dependent not just on the performance of predators, but the proportion of the predator population adopting a specific strategy. When predators come under the risk of predation themselves, mixed strategies become apparent in the prey population as well. That is, mixed strategies are a feature of the underlying interactions, and not just due to demographic variance and the somewhat different trade-off options experienced by individual members of the population (Ohman 1990).

The king penguins *Aptenodytes patagonica* in the Kerguelen islands are a good example of inter- and conspecific competition between predators and prey. Studies of the depth dive of the king penguins have shown that they perform deep dives during daylight

Fig. 3 Distribution of the prey (*left column*) and the predator (*right column*) in the different strategies (surface, deep, and DVM) under the presence of a top predator which forage on the middle predator. On the x-axis, we varied the prey's growth rate in the surface (λ_S), and on the y-axis the intermediate predator foraging voracity in the surface during daylight hour (V_I). The top predator foraging voracity is fixed at $W_I = 6.0$. The *first row* represents the proportion of surface strategy, in the *middle*, the deep strategy, and in the *bottom*, the diel vertical migration strategy while the *top predator* (not represented) is assumed to stay in the surface

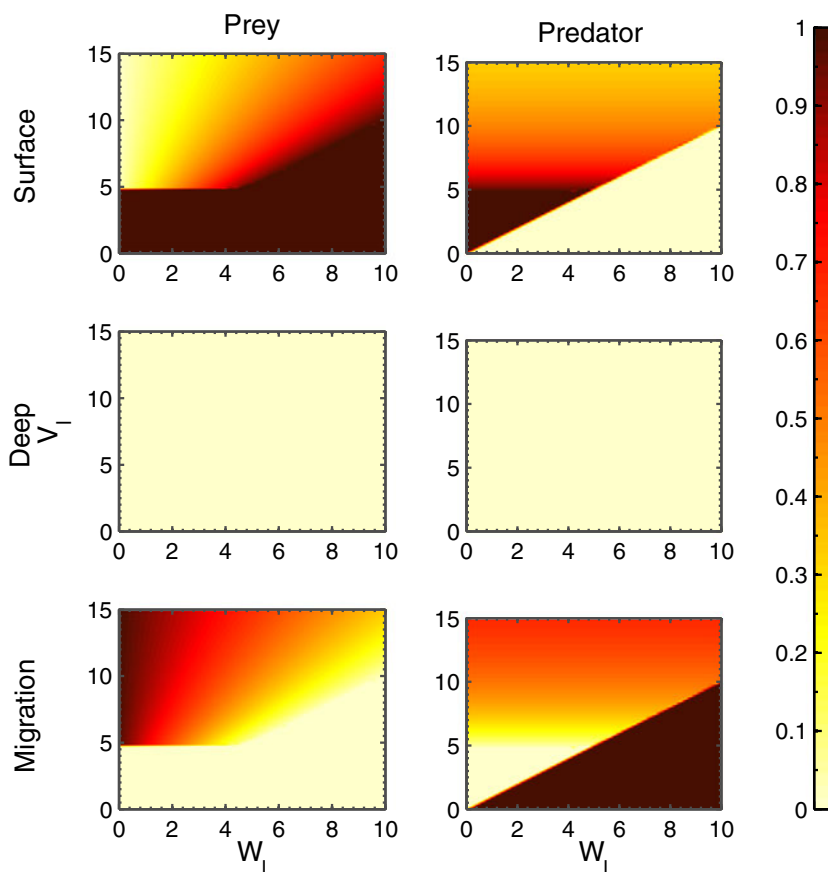


versus shallow ones during the night (Bost et al. 2002; Hays 2003). This pattern follows the DVM of the myctophid fish, their main prey, at the Kerguelen islands, throughout the summer (Bost et al. 2002). During their deep dives in daytime, the penguins reduce their time at the surface by 1/3, thus reducing their searching time at shallow waters. It can thus be an advantage for an individual prey to risk staying at the surface, but if the density of prey at the surface becomes too high, the penguins will not perform deep dives any longer as the deep dives are energetically costly due to the necessity to return regularly to the surface to breathe (Hays 2003). At dusk, the penguins' visual performance at the surface layer diminishes and the fish ascend to the surface, inducing shallower dives from the penguins. Although the shallow dives require less energy, the poor rate of prey capture, due to the darkness results in a lower ingestion rate. The prey are therefore safer at the surface at night than in the deep during the day (Hays 2003). The myctophid fish, along with the abundant species of *Protomyctophum*, *Gymnoscopelus*, and *Electrona* are known to perform a DVM in this area (Bost et al. 2002) and are assumed to follow their main prey (copepods, amphipods, and euphausiids) in

their vertical pattern (Koz 1995) while avoiding the dangerous surface layers during the daylight hours. Although the myctophid fish can forage all day and night on the copepods, amphipods, and euphausiids, we can assume that those prey, actively feeding in the surface at night, are easier to locate and therefore predate, even in the ambient darkness compared to during their resting mode in deep. A comparable behavior of the penguins had been found in some mesopelagic fish like the big-eye tuna (*Thunnus obesus*) or the swordfish (*Xiphias gladius*) which perform diel vertical migration to track the zooplankton in the deep during the day while performing short excursions to shallower depth to warm up and therefore maintain the advantage of high muscle temperature (Dagorn et al. 2000).

As a second example for the prey and predator performing DVM, we consider the *C. pacificus* copepods in the deep basin Dabob Bay, Washington, USA. *C. pacificus* feed mainly on the phytoplankton and are predated by visual planktivorous fish (Frost 1988; Ohman 1990). We compare the dynamics of the system between 2 years: in April 1979, the concentration of chlorophyll a was relatively low (70 mg chl.a.m⁻² in the upper 30 m, Frost 1988), while in April 1985, it

Fig. 4 Distribution of the prey (*left column*) and the predator (*right column*) in the different strategies (surface, deep and DVM) under the presence of a top predator which forage on the middle predator. On the x-axis, we varied the top predator voracity during daylight hour (W_I), and on the y-axis the intermediate predator foraging voracity in the surface during daylight hour (V_I). The prey's growth rate in the surface is fixed at $\lambda_S = 5.0$. The *first row* represents the proportion of surface strategy, in the *middle*, the deep strategy, and in the *bottom*, the diel vertical migration strategy while the *top* predator (not represented) is assumed to stay in the surface



was more than three times higher ($250 \text{ mg chla.m}^{-2}$). In presence of low food, the model predicts the prey to migrate even with low predation, while in high food availability (and therefore a potential high growth rate), the prey will choose to stay in the surface unless the predation risk gets very high, which match the observations from Frost (1988).

In the same area, the system consisted by *P. newmani*, the carnivorous copepod *E. elongata*, and a visual planktivorous fish is a good example of the three level interaction: the copepod *E. elongata*'s main prey is the *Pseudocalanus* spp., while they, in turn, are mainly predated on by fish. In July 1979, an high abundance of planktivorous fish (three-spine stickleback *Gasterosteus aculeatus* and the juvenile chum salmon *Onchorhynchus keta*) was observed at one station while the other had a low fish abundance (Ohman 1990). In the presence of the planktivorous fish, the model predicts that the middle predator migrates while the prey takes the opportunity to stay in the surface, matching the observation for the *P. newmani* and *E. elongata* (Ohman 1990). In low level of top predation, the model predicts that the middle predator mainly stays in the

surface while the prey will perform a DVM, which conforms to observations (Ohman 1990). Precisely, how this migration pattern may change when prey are exposed to mixed predators (e.g., visual and rheotactic, Visser et al. 2009) remains to be explored, although the basic modeling framework would stay the same.

The fitness measure used in this paper was, it can be argued, the simplest possible choice. First, fitness of an individual is usually measured either as the total reproductive output over the remaining life time (e.g., Hugie and Dill 1994; Visser 2007), or as the specific growth rate of the subpopulation to which the individual belongs (e.g., the present study). See Mylius and Diekmann (1995) for a discussion of the relationship between these two measures. In our case, where we have not posed a complete model of population dynamics, there is no reason to prefer the one or the other except analytical simplicity. For this reason, we have focused on the specific growth rate; initial investigations indicate that our conclusions remain unaltered if we had instead used the reproductive output.

Additionally, our fitness measure has the property that the fitness of an individual is independent of the

strategy played by its conspecifics, if one fixes the strategies of the other species. Stated differently, the specific growth rates show no direct density dependence. This structure was also used by Iwasa (1982), and was criticized in Hugie and Dill (1994) because it does not lead to Nash equilibria which are evolutionarily stable strategies: Once the predators follow the equilibrium strategy, there is no selection for any prey strategy, and vice versa. A symptom of this is that we have to modify the replicator equation (Appendix) for our iteration to always converge to the equilibrium. However, for many real systems, it is plausible that some weak direct density dependence is present, even if it is less tractable to parametrize and quantify this density dependence. If we had included in our model a weak density dependence, then this would stabilize the equilibrium but only shift it marginally. For this reason, in the interest of a minimal model, we have investigated the model without density dependence.

The main assumption behind this model is that prey behave linearly to the amount of food available and to the capacity of the predator to forage them. However, the animal's behavior in nature is influenced by its internal state, as well as environmental factors: on the one hand, it will prefer to risk high predation pressure rather than starve, while a full gut will favor a safer strategy. Thus, individuals can be pushed to deviate from the ideal repartition between habitat (Alonzo 2002) but at a cost of increase competition between conspecific (Flaxman and Reeve 2006). Further, spending time in the deep habitat, either by adopting a deep strategy or a DVM, often results in a reduced growth rate or slower egg development due to a lower ambient temperature. Organisms are often preyed on by different kinds of predators (tactile, visual hunters) and therefore must make a trade-off in their behavior to avoid their most dangerous predators, while still maintaining a high feeding rate. High plasticity in the vertical pattern has been observed in some species of zooplankton as a function of their different predator abundance (Frost and Bollens 1992), thus showing the wide range of responses zooplankton can produce in relation to predation pressure.

Although it was not investigated here, some organisms also perform reverse DVM. This pattern has been observed for small organisms, especially when their main predators use tactile sense and are themselves preyed by high-performance visual hunters (Frost and Bollens 1992; Ohman 1990). We also assumed a clear compartmentalization in the food chain. However, predators often forage more than one trophic level distant. The different migration patterns emerging

from scenario 2 and 3 and the results from Rosenheim (2004) show the link between trophic relationships and the behaviors they mediated.

Conclusion

Whereas prior investigations of predator–prey interaction using game theory mainly focused in static ways on the predator–prey distribution between two habitats, we show here that DVM between two habitats with different characteristics can be a sustainable strategy under conditions in which predation pressure and food availability are balanced. A game theory approach allows equal consideration of both the predator's and prey's behavior, each pursuing their own goals and responding to environmental conditions and the behavior of conspecific and interspecific players in order to find the best strategy. These considerations reproduce many of the features of DVM observed in nature as well as leading to the emergence of mixed strategies as a possible evolutionary stable state and cascading behavioral effects that project beyond the nearest trophic levels.

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Appendix

Solution scheme

The Nash equilibrium of the game can be found algebraically, by requiring that all strategies which are adopted by a positive fraction of animals share the same fitness, and that all strategies which are not adopted, have no greater fitness. This leads to a set of linear equations. However, this approach is somewhat tedious, because one must treat the boundaries (i.e., solutions where some strategies are not adopted) separately. A more convenient and flexible approach is to use that the Nash equilibrium is necessarily an equilibrium of the replicator equation (see Hofbauer and Sigmund 2003, for background and a precise converse statement).

With this approach, the replicator equation governs the dynamics of the fractions of the different strategies as follows: The fitness of prey (Eq. 2) and of predator (Eq. 3) are used as growth rates of the subpopulations which adopt each strategy. These dynamics do not necessarily mimic real population dynamics, but is merely

a computational method to identify the Nash equilibrium, by marching the replicator equation forward in time until steady state. We formulate the replicator equation in discrete time. In a first step, populations grow according to their fitness:

$$\begin{cases} N'_S(i+1) = N_S(i) + N_S(i)F_{N_S}^+ dt \\ N'_D(i+1) = N_D(i) + N_D(i)F_{N_D}^+ dt \\ N'_m(i+1) = N_m(i) + N_m(i)F_{N_m}^+ dt \\ P'_S(i+1) = P_S(i) + P_S(i)F_{P_S}^+ dt \\ P'_D(i+1) = P_D(i) + P_D(i)F_{P_D}^+ dt \\ P'_m(i+1) = P_m(i) + P_m(i)F_{P_m}^+ dt \end{cases} \quad (8)$$

In the next step, the abundance proportions are renormalized so as to sum to one:

$$\begin{cases} N_S(i+1) = \frac{N'_S(i+1)}{N'_S(i+1) + N'_D(i+1) + N'_m(i+1)} \\ N_D(i+1) = \frac{N'_D(i+1)}{N'_S(i+1) + N'_D(i+1) + N'_m(i+1)} \\ N_m(i+1) = \frac{N'_m(i+1)}{N'_S(i+1) + N'_D(i+1) + N'_m(i+1)} \\ P_S(i+1) = \frac{P'_S(i+1)}{P'_S(i+1) + P'_D(i+1) + P'_m(i+1)} \\ P_D(i+1) = \frac{P'_D(i+1)}{P'_S(i+1) + P'_D(i+1) + P'_m(i+1)} \\ P_m(i+1) = \frac{P'_m(i+1)}{P'_S(i+1) + P'_D(i+1) + P'_m(i+1)} \end{cases} \quad (9)$$

This completes the recursion, which is then iterated until steady state.

Stabilization

The Nash equilibrium is an equilibrium of the replicator dynamics, but not necessarily an asymptotically stable equilibrium. Since our model of fitness does not include a direct dependence of the density of conspecifics, the replicator dynamics may display periodic dynamics which cycle around the Nash equilibrium, similar to the classic Lotka–Volterra system. To stabilize the Nash equilibrium and dampen out these cycles, we modify the replicator equation as follows: We add a proportion “a” of the difference between the last two time steps

of the predators proportion in the surface ($P_S(i-1) - P_S(i-2)$), to the proportion of prey in the surface (N_S):

$$N'_S(i+1) = N_S(i) + N_S(i)F_{N_S}^+ dt + a(P_S(i) - P_S(i-1)) \quad (10)$$

This computational stabilization mimics damping in physical systems and does not change the system equilibrium value, as at equilibrium, the predator proportion does not change anymore ($P_S(i) = P_S(i-1)$), so $P_S(i) - P_S(i-1) = 0$). Again, we stress that this is merely a computational method for identifying the Nash equilibrium, so an ecological interpretation of this damping term is not necessary.

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