

Predator-Prey Games in Multiple Habitats Reveal Mixed Strategies in Diel Vertical Migration

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ABSTRACT: Prey and predators continuously react to each other and to their environment, adjusting their behavior to maximize their fitness. In a pelagic environment, organisms can optimize their fitness by performing diel vertical migrations. We applied a game-theoretic approach to investigate the emergent patterns of optimal habitat selection strategies in a multiple-habitat arena. Our setup allows both players to choose their position at day and at night in the water column. The model reproduces features of vertical migrations observed in nature, including residency at depth or at the surface, vertical migrations, mixed strategies, and bimodal distributions within a population. The mixed strategies appear as a consequence of frequency-dependent processes and not of any intraspecific difference between individuals. The model also reveals a curious feature where natural selection on individuals can provoke distinct regime shifts and precipitate an irreversible collapse in fitness. In the case presented here, the increasing voracity of the predator triggers a behavioral shift in the prey, reducing the fitness of all members of the predator population.

Keywords: diel vertical migration, game theory, habitat selection, predator-prey interactions, deep scattering layer, optimal strategies.

Introduction

Diel vertical migration (DVM) is a behavior exhibited by a large number of marine species, from plankton to marine mammals. The most conspicuous of these are the migrations carried out by mesopelagic fish (O'Driscoll et al. 2009; Dypvik et al. 2012), krill (Onsrud et al. 2004; Zhou and Dorland 2004), copepods (McLaren 1963; Frost and Bollens 1992; Hays et al. 2001), and jellyfish (Kaartvedt et al. 2007). These migrations are particularly evident in the daily variations in the depth of the deep scattering layer (Barham

1966; Isaacs et al. 1974), the signature of aggregations of acoustically reflective marine organisms that typically alternate between a surface layer during nighttime hours and a deeper layer during daylight hours. While deep scattering layers are ubiquitous features of the world's oceans, the patterns they exhibit vary considerably from place to place and over seasons (Plueddemann and Pinkel 1989; Klevjer et al. 2016). For instance, there are large variations in the depth of the deep daylight layer—from a few dozen to several hundred meters. Further, there is seldom a single well-defined scattering layer, and a wide variety of daily patterns is observed. For instance, there can be multiple strata displaying different vertical cycles, double layers that remain resident near surface and at depth with daily exchange, layers that disperse and reaggregate, and any number of combinations of these. With the advent of more advanced acoustics that are able to track individual organisms (Kaartvedt et al. 2007, 2008), the picture becomes even more complex, with individuals of apparently the same species displaying quite different behaviors.

While these patterns are of interest in themselves and in the trophic interactions they mediate (Bollens et al. 2011), they also contribute to the biological pump and have an important consequence for the biogeochemistry of the world's oceans (Longhurst and Harrison 1989; Steinberg et al. 2000; Bianchi et al. 2013a). Vertically migrating organisms actively transport organic carbon out of the surface ocean, often to depths of 100 m or more, where it is respired and excreted by the migrator itself or consumed by their predators—giving rise to a drawdown of carbon from the surface ocean (Ducklow et al. 2001; Hansen and Visser 2016), an associated depletion of surface nutrients (Dam et al. 1995; Steinberg et al. 2002), and a depletion of subsurface oxygen (Bianchi et al. 2013a). The importance of DVM in ocean biogeochemistry in part stems from the sheer numbers of organisms involved. In particular, the fact that these patterns show up in acoustic profiles indicates that a significant fraction of the pelagic bio-

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mass is involved. Indeed, it has been estimated that the vertical migration of zooplankton constitutes one of the largest mass movements of biomass on Earth (Hays 2003). The daily cycles in the distribution of biomass into different-depth strata of the oceans, the mechanisms that drive this partitioning, and how they are affected by biotic and abiotic factors are thus questions of some relevance for the carbon, nutrient, and oxygen dynamics of the ocean.

As with many phenomena in behavioral ecology, the imperative for DVM can be seen in a fitness trade-off between growth and mortality risk (Lima and Dill 1990). For zooplankton grazers, this is a balance between feeding on their phytoplankton prey at the surface and avoiding the attention of visual predators. The optimal strategy is thus to feed at the surface at night and take refuge at depth during the day (Zaret and Suffern 1976), where the cost of migration and lost growth potential are offset by increased survivorship. Different patterns can be explained in part by different zooplankton species, as each species' migration contributes to its fitness trade-off in a somewhat different way (Stich and Lampert 1981).

The predators that in some sense provoke the migration of grazers have their own imperatives to optimize fitness in turn; they can follow their prey or not or adopt some other distinct migration pattern depending on, for instance, water clarity, competition with nonvisual predators, and their own mortality risk. This triggers a cascade of interlinked migration patterns throughout the food web (Bollens et al. 2011). Indeed, seen in this light, it becomes evident that in a predator-prey system the optimal choice of strategy for one affects the optimal choice of strategy for the other (Hugie and Dill 1994) and vice versa. That is, there is a game of strategies being played out between predators and prey that ultimately shapes the patterns of DVM that emerge in nature.

In ecology, game theory has been widely used to describe everything from sex ratios (Fisher 1930; Maynard Smith 1976) to distribution of competitors (Sih 1998; Cressman et al. 2004) and social arrangements (Reeve and Holldobler 2007). In this work, we extend the predator-prey game from a two-habitat arena (Iwasa 1982; Gabriel and Thomas 1988; Sainmont et al. 2013) into a multiple-habitat arena in which prey and predators can adjust their position in a water column divided into several layers and are not obliged to simply choose between the surface and some deep habitat. This radically increases the number of potential competing strategies.

In addition to implications for the biogeochemistry of the oceans, the multiple-habitat arena also allows us to capture the vertical variability of the proximate causes of DVM, namely, food availability and light intensity. In particular, the trade-off will be different in strata of different depths even without frequency dependence.

Methods

We consider two populations of fixed size: one of prey (N) and one of predators (P). These populations live in a water column divided into M layers of Δz (m) thickness, ordered from the shallowest to the deepest. Each organism is free to move within the water column. To illustrate the model, we cast it in terms of zooplankton grazers as prey and planktivorous fish as predators. The fish rely on vision and thus light to locate their zooplankton prey. The resources for prey are located in the surface simulating phytoplankton. This setting is one of the most common in the pelagic ocean, but it should be noted that the method outlined here can be tailored to any trophic arrangement given suitable mechanistic descriptions of the growth, interaction, and mortality terms.

We define the matrices $\mathbf{n} = n_{ij}$ and $\mathbf{p} = p_{ij}$ as the frequency of ij strategies in prey and predator populations, respectively, that is, the strategy in which the individual chooses its daytime position in layer j and its nighttime position in layer i . By definition, n_{ij} and p_{ij} conform to the identities

$$\begin{aligned} \sum_{i=1}^M \sum_{j=1}^M n_{ij} &= 1, \\ \sum_{i=1}^M \sum_{j=1}^M p_{ij} &= 1. \end{aligned} \quad (1)$$

In terms of abundance, if we write the mean concentration of prey and predators throughout the water column as N_0 (m^{-3}) and P_0 (m^{-3}), then the prey and predator concentration in layer i at nighttime is

$$\begin{aligned} N_{i,\text{night}} &= MN_0 \sum_{j=1}^M n_{ij}, \\ P_{i,\text{night}} &= MP_0 \sum_{j=1}^M p_{ij}, \end{aligned} \quad (2)$$

with similar expressions for the daytime concentrations.

In terms of time, the day is divided between a fraction σ of daylight hours, and a fraction $1 - \sigma$ of darkness, neglecting the periods of dawn and dusk. The general depth-varying factors governing the fitness of individuals in the respective populations are the potential growth rate of the prey and the mortality risk posed by the predators. Depth variations in potential prey growth rates reflect, for instance, the vertical distribution of phytoplankton food resource or temperature. For convenience, we write individual growth rate as $g'(z) = g_{\max}g(z)$ (day^{-1}), where $g(z)$ is a dimensionless function indicating the depth structure and g_{\max} (day^{-1}) is the maximum growth rate that can vary depending on temperature and resource (phytoplankton) abundance.

The ability of the visual predator to detect prey depends on light intensity $L(z, t)$ ($W m^{-2}$) equal to $L_{\max} \exp(-\kappa z)$ during daytime and $\rho L_{\max} \exp(-\kappa z)$ during nighttime. We assume a uniform extinction coefficient κ (m^{-1}). We note that the factor ρ is not necessarily 0, as illumination by moonlight can be significant for visual predators (Bollens and Frost 1991; Webster et al. 2013). The clearance rate β ($m^3 s^{-1}$) of the predator is defined to mimic a saturation condition at high light intensities (Aksnes and Utne 1997; Titelman and Fiksen 2004; Bianchi et al. 2013b). Defining the constant b_{\max} ($m^3 day^{-1}$) allows us to write the clearance rates as $\beta_{\text{day}} = b_{\max} b_{\text{day}}(z)$ and $\beta_{\text{night}} = b_{\max} b_{\text{night}}(z)$, where b_{day} and b_{night} are two dimensionless functions given by

$$\begin{aligned} b_{\text{day}}(z) &= \frac{L_{\max} \exp(-z\kappa)}{L_0 + L_{\max} \exp(-z\kappa)}, \\ b_{\text{night}}(z) &= \frac{\rho L_{\max} \exp(-z\kappa)}{L_0 + \rho L_{\max} \exp(-z\kappa)}, \end{aligned} \quad (3)$$

where L_0 ($W m^{-2}$) is the half-saturation light intensity.

The fitness of a specific strategy ij is defined as the difference between the specific growth rate and the potential mortality rate that an organism is exposed to over a daily cycle. For migrating animals, an extra term modeling the cost of migration is added. For simplicity, we assume feeding interactions to follow a type I (linear) functional response, as in the natural environment, organisms are generally undersaturated in food supply (Kjørboe 2011).

For the prey, net growth for strategy ij is

$$G_{ij}^N = g_{\max}((1 - \sigma)g_i + \sigma g_j) - c_N \delta_{ij}, \quad (4)$$

where the net migration cost is assumed to be a linear function of the migration distance, with c_N the cost to migrate 1 m and $\delta_{ij} = \Delta z |i - j|$.

For this strategy, the corresponding mortality risk from visual predators is proportional to the probability (i.e., sum of frequencies) of predators being in the same layer at the same time:

$$\begin{aligned} D_{ij}^N &= (1 - \sigma)\beta(i, \text{night})P_{i, \text{night}} + \sigma\beta(j, \text{day})P_{j, \text{day}} \\ &= b_{\max} MP_0 \left((1 - \sigma)b_{\text{night}, i} \sum_{k=1}^M p_{ik} + \sigma b_{\text{day}, j} \sum_{k=1}^M p_{kj} \right). \end{aligned} \quad (5)$$

Mortality risk for prey is conversely a component of the potential growth rate for the predator. For the strategy ij , this growth rate can be written

$$G_{ij}^P = b_{\max} \eta MN_0 \left((1 - \sigma)b_{\text{night}, i} \sum_{k=1}^M n_{ik} + \sigma b_{\text{day}, j} \sum_{k=1}^M n_{kj} \right) - c_P \delta_{ij}. \quad (6)$$

In this, η represents the conversion efficiency—how much a single prey contributes to the reproduction rate of a preda-

tor. As with prey, we include a cost of migration proportional to migration distance. Finally, for closure, we require a mortality risk for predators. We choose a density-dependent function to reflect reduced fitness at high abundances to mimic possible interference with each other and attraction of top predators at high concentration (Hixon and Carr 1997):

$$D_{ij}^P = \mu MP_0 \left((1 - \sigma) \sum_{k=1}^M p_{ik} + \sigma \sum_{k=1}^M p_{kj} \right). \quad (7)$$

In summary, the fitnesses of prey and predator following strategy ij are

$$\begin{aligned} F_{ij}^N(\mathbf{p}) &= g_{\max}((1 - \sigma)g_i + \sigma g_j) - c_N \delta_{ij} \\ &\quad - b_{\max} MP_0 \left((1 - \sigma)b_{\text{night}, i} \sum_{k=1}^M p_{ik} + \sigma b_{\text{day}, j} \sum_{k=1}^M p_{kj} \right), \end{aligned} \quad (8)$$

$$\begin{aligned} F_{ij}^P(\mathbf{n}, \mathbf{p}) &= b_{\max} \eta MN_0 \left((1 - \sigma)b_{\text{night}, i} \sum_{k=1}^M n_{ik} + \sigma b_{\text{day}, j} \sum_{k=1}^M n_{kj} \right) - c_P \delta_{ij} \\ &\quad - \mu MP_0 \left((1 - \sigma) \sum_{k=1}^M p_{ik} + \sigma \sum_{k=1}^M p_{kj} \right). \end{aligned} \quad (9)$$

These fitness functions describe a noncooperative game where all individuals within each population are trying to maximize their fitness. This game is solved when a Nash equilibrium is reached, which means that no organism has an advantage in unilaterally changing its strategy. In such a solution, only a subset of all strategies might be populated (i.e., those for which $n_{ij} > 0$ and $p_{ij} > 0$), and at equilibrium, all populated strategies within the prey and predator populations will have identical fitness

$$F_{ij}^N(\mathbf{p}) = F_0^N \text{ for all } n_{ij} > 0 \text{ and } F_{ij}^P(\mathbf{n}, \mathbf{p}) = F_0^P \text{ for all } p_{ij} > 0, \quad (10)$$

while all unpopulated strategies will have inferior fitness

$$F_{ij}^N(\mathbf{p}) \leq F_0^N \text{ for all } n_{ij} = 0 \text{ and } F_{ij}^P(\mathbf{n}, \mathbf{p}) \leq F_0^P \text{ for all } p_{ij} = 0. \quad (11)$$

The system has polymorphic-monomorphic equivalency (Broom and Rychtář 2014), discussed further in the appendix (available online). That is, the matrices \mathbf{n} and \mathbf{p} denote the frequency distribution of strategies but are mute on how these distributions arise, in terms of either different proportions of the population playing pure strategies (polymorphic) or all individuals playing the same mixed strategy (monomorphic), or indeed some combination of these two extremes. Any individual playing against resident (\mathbf{n}, \mathbf{p}) is indifferent to

whether these represent polymorphic or monomorphic strategies.

We find the Nash equilibrium of the system numerically by solving the replicator equation (Schuster and Siegmund 1983; Hofbauer and Sigmund 2003). Essentially, each sub-population of strategy ij is allowed to grow according to its growth rate (i.e., fitness) before renormalization to satisfy constraint (1). For details, see the appendix. In general, not all situations solved with replicator dynamics lead to a steady-state solution. In this particular case, all simulations of the replicator dynamics converged to a stable equilibrium. We ensured this by iterating over a large number of time steps

(typically 10^6) and different initial conditions and assessed stability by estimating the variance in fitness and strategies.

The MATLAB code for running the discussed examples is deposited in the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.19n37d1> (Pinti and Visser 2018).

Results

We choose a set of parameters (table 1) that are illustrative for a planktonic system of a zooplankton grazer (the prey) feeding on a phytoplankton resource and preyed on in turn

Table 1: Glossary of parameters

| Variable | Description | Value (default) | Unit |
|--|--|-----------------------|---------------------------------|
| b_{\max} | Absolute maximum clearance rate (voracity) of predator | 10^{-2} to 100 | $\text{m}^3 \text{day}^{-1}$ |
| g_{\max} | Maximum growth rate of prey | .1 | day^{-1} |
| N_0 | Average concentration of prey in water column | 5,000 | m^{-3} |
| P_0 | Average concentration of predator in water column | 1 | m^{-3} |
| M | Number of depth bins, leading to M^2 different pure strategies per trophic level | 30 | ... |
| β | Clearance rate of predator | ... | $\text{m}^3 \text{day}^{-1}$ |
| $b_{\text{day}}(z), b_{\text{night}}(z)$ | Vertical structure function for maximum clearance rate of predator at day and night | Equation (3) | ... |
| $g(z)$ | Vertical structure function for maximum growth rate of prey | Equation (12) | ... |
| L | Light intensity at depth z and time t | ... | W m^{-2} |
| L_{\max} | Typical light level at the surface during daylight hours | 100 | W m^{-2} |
| L_0 | Half-saturation light level for visual predator | 1 | W m^{-2} |
| μ | Density-dependent mortality rate of predators: if all predators are uniformly distributed throughout the water column, they each suffer a mortality of $\mu P_0 \text{day}^{-1}$; if they are all concentrated into a single bin, they each suffer a mortality of $M \mu P_0 \text{day}^{-1}$ | 10^{-3} | $\text{m}^3 \text{day}^{-1}$ |
| c_N | Cost in terms of growth rate of migrating 1 m for the prey | 10^{-5} | $\text{m}^{-1} \text{day}^{-1}$ |
| c_P | Cost in terms of growth rate of migrating 1 m for the predator | 10^{-5} | $\text{m}^{-1} \text{day}^{-1}$ |
| δ_{ij} | Migration distance for strategy ij | $\Delta z i - j $ | m |
| σ | Fraction of daylight hours per day | 0 to 1 (.65) | ... |
| κ | Attenuation coefficient for light | .07 | m^{-1} |
| ρ | Fractional difference between night and day light levels | 10^{-3} | ... |
| η | Predator growth efficiency | 10^{-2} | ... |
| z | Depth coordinate | 0 to 300 | m |
| Δz | Thickness of depth bins | 10 | m |
| H | Depth of the water column | 300 | m |
| z_0 | Depth of mixed layer | 50 | m |
| z_s | Thickness of mixed layer transition zone | 10 | m |
| G_{ij}^N, G_{ij}^P | Growth rate of prey (predator) following strategy ij | Equations (4) and (6) | day^{-1} |
| D_{ij}^N, D_{ij}^P | Death rate of prey (predator) following strategy ij | Equations (5) and (7) | day^{-1} |
| F_{ij}^N, F_{ij}^P | Fitness of prey (predator) following strategy ij | Equations (8) and (9) | day^{-1} |
| \mathbf{n}, \mathbf{p} | Frequency matrix of prey (predator) strategies | ... | ... |
| $N_{i,\text{night/day}}, P_{i,\text{night/day}}$ | Concentration of prey (predator) at night (or day) in the layer i | Equation (2) | m^{-3} |

Note: Values and equations were taken from the literature: detection distance (Bianchi et al. 2013b), light-related parameters (Aksnes and Utne 1997a), maximum growth rate (Hirst and Sheader 1997), and copepod rates and costs (Titelman and Fiksen 2004; Visser 2007).

by a visual predator such as a fish. The vertical variation in maximum prey growth rate is given by

$$g(z) = \frac{1}{2} \left(1 - \tanh \left(\frac{z - z_0}{z_s} \right) \right), \quad (12)$$

where z_0 is the depth of the surface mixed layer (hence resource availability) and z_s is the thickness of the transition zone to a depleted deep layer (Ji and Franks 2007). Figure 1 shows the vertical functional form of both of the growth conditions as well as the predator clearance rate for both day and night conditions.

Maximum Clearance Rate

Among many of the governing parameters, both environmental and those determining trophic interactions and efficiency, one that can exhibit large variation in nature is the maximum clearance rate of the predator. This is a function not only of light and the visual acuity of the predator but also of the conspicuousness of the prey (is it pigmented, does it have a full gut, is it moving?), the swimming behavior of the predator, and the escape ability of the prey. Figure 2 shows the change in predator-prey strategies as a function of b_{max} , the maximum clearance rate of the predator, all other parameters be-

ing held constant. It shows three general patterns of strategies:

Strategy 1. For very low clearance rates ($b_{max} < 0.02$), essentially both predators and prey exhibit no significant DVM and reside exclusively in the surface layer. They both alternate between a diffuse daytime distribution (fig. 2A, 2B) and are more concentrated during nighttime (fig. 2C, 2D). During this phase, the fitness of the prey decreases while that of the predator increases with increasing b_{max} (fig. 2E, 2F).

Strategy 2. For intermediate clearance rates ($0.02 < b_{max} < 1.6$), both prey and predators start to migrate, alternating between a deep daytime depth and a shallow nighttime depth. This pattern is most clear in the prey, where the whole population subscribes to DVM, albeit to slightly different depths. For the predator, however, while the major part of the population follows the prey between the surface and depth, there is a small fraction that remains resident in the surface and another fraction that follows the prey at night but chooses some intermediate depth during the day. This small fraction at intermediate depth is a consequence of the game, as it prevents prey from remaining higher in the water column during daytime to “cheat.” It would not be encountered in analysis without game theory. The depths of both the nighttime surface layer and the deep daytime layer gradually deepen as

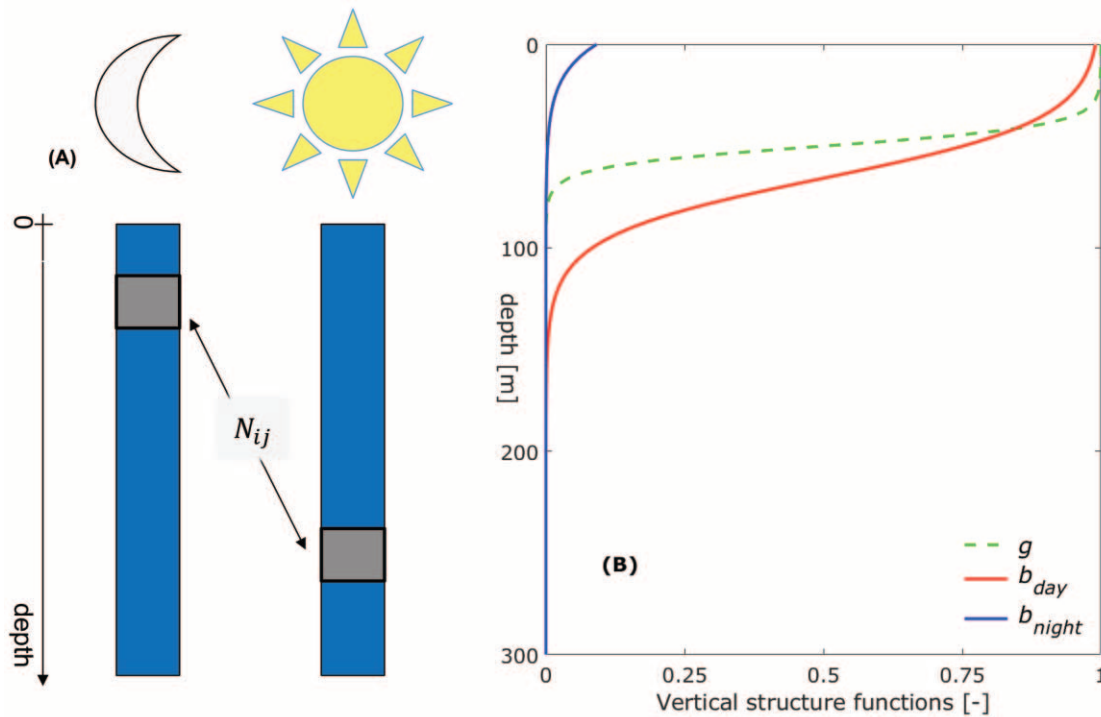


Figure 1: A, Prey following the strategy ij will alternate between the layer i at night and the layer j during daytime. B, The vertical structure function of the growth g (green dashed line), the clearance rate during daytime b_{day} (red) and during nighttime b_{night} (blue). A summary of the parameters used to plot these profiles is given in table 1.

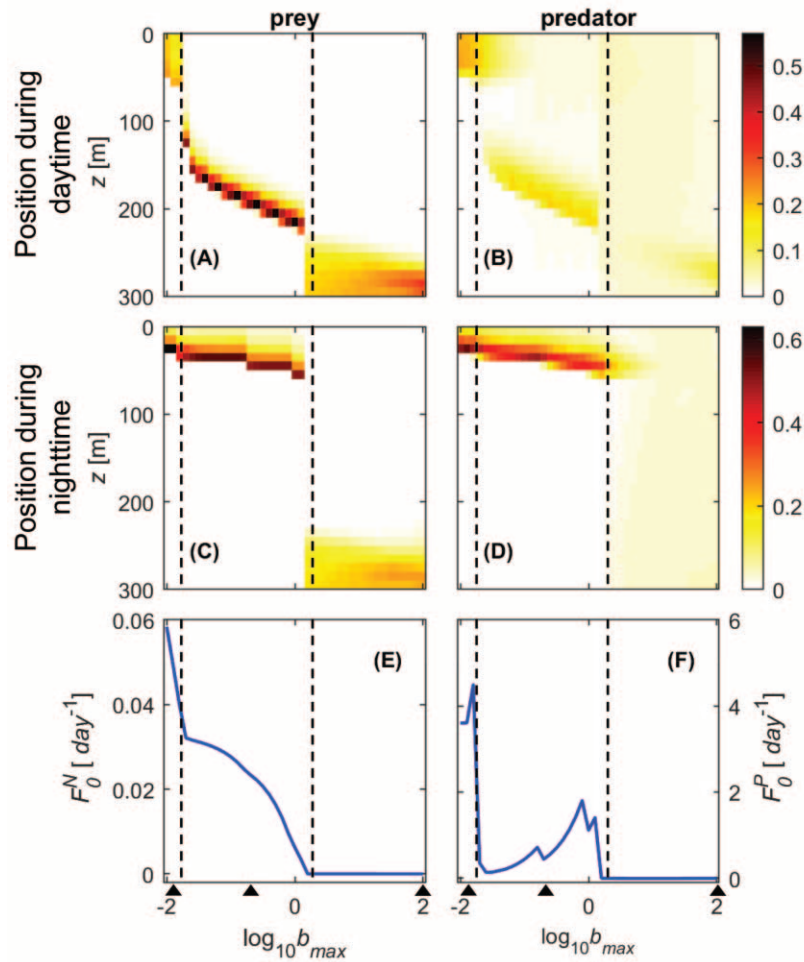


Figure 2: Vertical distribution of the prey during day (A) and night (C) and the corresponding distribution for predators during day (B) and night (D) for a range of predator maximum clearance rate b_{max} from 0.01 to 100 $\text{m}^3 \text{day}^{-1}$. Parameter values are set according to the values given in table 1. The variation of fitness for the prey (E) and predator (F) is given as a function of the predator maximum clearance rate b_{max} corresponding to vertical distribution patterns given above. Small dark triangles show the value of b_{max} for which the strategy occupancy diagrams are plotted (fig. 3). Dashed lines show the theoretical migration regime shifts.

b_{max} increases. In this phase, while the prey fitness (fig. 2E) continues to decrease with increasing b_{max} , it does so at a lower rate than when $b_{max} < 0.02$. The predator fitness (fig. 2F) suffers a significant decrease at the point where the prey start migrating. Thereafter, the predator maximum fitness increases again with increasing b_{max} .

Strategy 3. For large values of clearance rate ($b_{max} > 1.6$), prey and predators both essentially stop migrating, with prey retreating to a permanent residence at depth (fig. 2A, 2C) and predators becoming uniformly distributed in the water column throughout the day (fig. 2B, 2D). For this range of b_{max} , the maximum fitness for both prey and predator drops to zero (fig. 2E, 2F).

In figure 3, we present the strategy occupancy of prey and predators in the three different migration regimes. These ex-

amples are for the specific $b_{max} = 0.0126 \text{ m}^3 \text{day}^{-1}$ (fig. 3A, 3B), $b_{max} = 0.1995 \text{ m}^3 \text{day}^{-1}$ (fig. 3C, 3D), and $b_{max} = 100 \text{ m}^3 \text{day}^{-1}$ (fig. 3E, 3F). Although certain strategies are adopted by the majority of individuals, the full range of strategies for both predator and prey for which fitness is equal and maximized is quite extensive.

Transitions between different migration regimes for prey can be estimated from simple theoretical considerations of migrations between a feeding and a resting layer, for example, by calculating when the risk of remaining at the surface during daytime becomes greater than the net gain in growth (for details, see the appendix). With the parameter set used here, this results in approximate migration regime shifts at thresholds $b_{max} = 0.0167 \text{ m}^3 \text{day}^{-1}$ and $b_{max} = 2.7 \text{ m}^3 \text{day}^{-1}$, which is consistent with the values observed in figure 2.

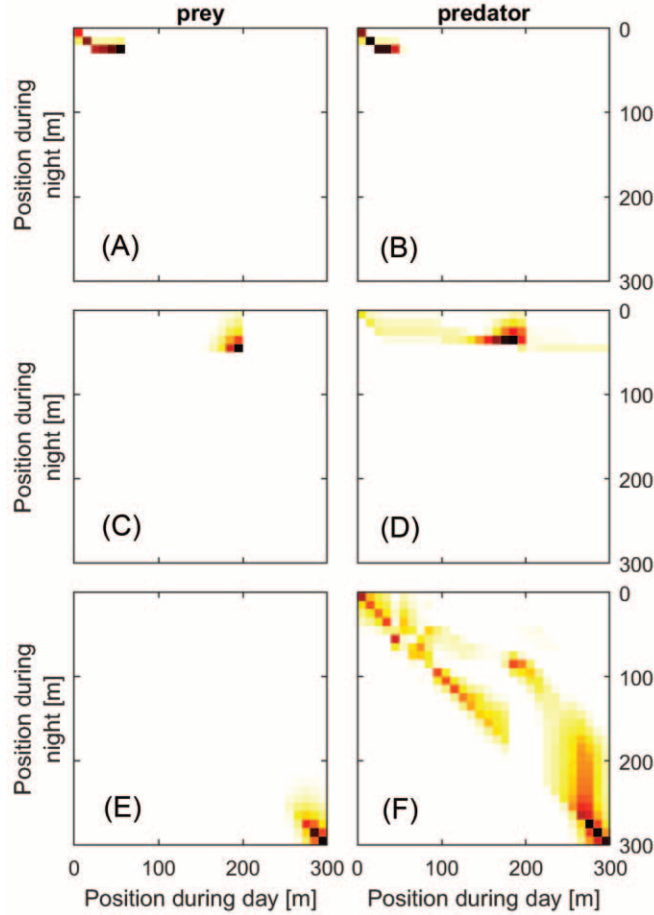


Figure 3: Strategy occupancy of prey (A, C, E) and predator (B, D, F) in the three different migration regimes. These examples are for the specific $b_{\max} = 0.0126$ (A, B), $b_{\max} = 0.1995$ (C, D), and $b_{\max} = 100$ (E, F).

Day Length

Day-night differences in light are a primary driver of DVM (Zaret and Suffern 1976; Hays 2003). Figure 4 illustrates the DVM strategies emerging for varying daytime fraction σ in this game. For most of the values of σ , results in terms of distribution during day and night in the water column change very little ($0.1 < \sigma < 0.9$); both prey and predator undertake regular DVM from the depth to the surface. However, the results are different for extreme values of σ . If σ is small (< 0.1), which means that there is almost no daytime, prey stay at the surface all the time. As the risk of being preyed on is very low and the resources maximum, it is not beneficial to migrate (fig. 4A, 4C). Predators also stay at the surface to catch prey where they are (fig. 4B, 4D). When the fraction of daytime is close to one (i.e., almost no night), prey stop migrating and spend all their time at depth, whereas predators distribute themselves evenly in the water column. This is a direct consequence of the fact that the players are distributed as to follow a Nash equilibrium; since there is plenty of light, preda-

tors would be able to catch any prey in the upper layers of the water column. The predators remove the possibilities for the prey to escape the game and be in more profitable water layers by being evenly distributed in the water column. This situation also corresponds to a minimum fitness for the prey, as the predator confines them at depths with the slower growth. The fitness of the prey decreases linearly as σ increases (fig. 4E); they are staying less and less at the surface and therefore benefit less and less from the resources they can find there. The fitness of the predator also decreases linearly with the day length. When the day length increases, prey spend more time in the depth and cannot be captured as easily as in the mixed layer, even at night. Indeed, this can be summarized from the ratio of predator clearance rates $b_{\text{day}}(200 \text{ m}) \approx 10^{-2} b_{\text{night}}(50 \text{ m})$.

Seasonality

Daytime fraction σ alone is only one of several seasonally varying factors driving DVM. Additional factors include the max-

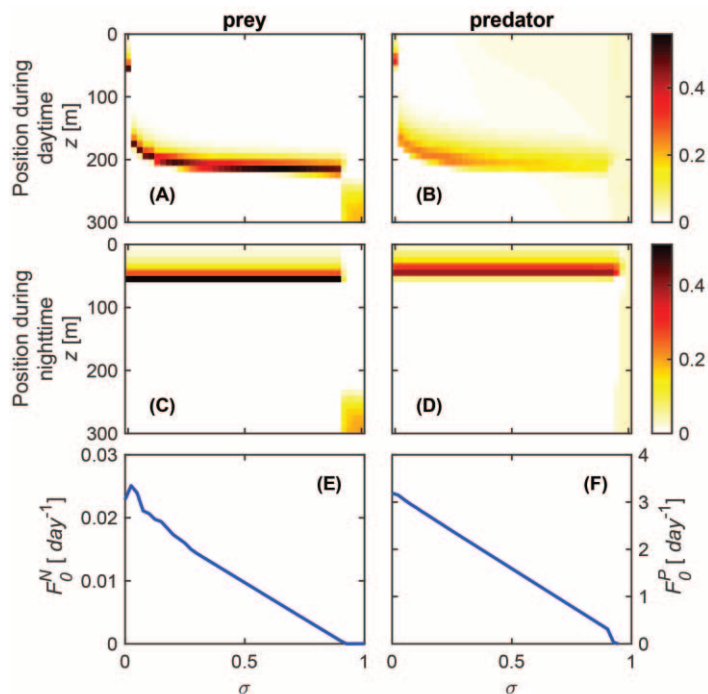


Figure 4: Vertical distribution of the prey during day (A) and night (C), the corresponding distribution for predators during day (B) and night (D), and the associated prey (E) and predator (F) fitnesses for a range of daylight fractions σ from 0 (total 24-h darkness) to 1 (total 24-h light).

imum irradiance L_{\max} , the mixed layer depth z_0 , the maximum growth rate for the prey g_{\max} , and the average prey concentration in the water column N_0 . We select typical patterns of the seasonal variation of these (table 2) to illustrate the DVM patterns that emerge (fig. 5). From shallow DVM in the winter months, the DVM almost disappears in the summer where organisms are almost evenly scattered in the water column. This corresponds to a strong fitness minimum for both species.

Discussion

Game Theory as a Way to Investigate Migration Patterns

Our method based on game theory principles is effective, as it can reproduce the main migration patterns observed in nature. Among all the known regimes of DVM (normal, residency, reverse migration), only reverse migration (i.e., surface at night, depth during the day) is not reproduced by our model—a migration pattern arising from additional trophic levels or the presence of nonvisual predators (Ohman 1990).

Moreover, the model reproduces the DVM patterns of both prey and predators, who can choose to follow their prey or not depending on the ensuing benefit. To our knowledge, this is the first time that a model provides the distribution of two trophic levels in a multilayered water column. Several models

looked at DVM (Fiksen and Giske 1995; Giske et al. 1997; De Robertis et al. 2000; Batchelder et al. 2002; Fiksen et al. 2005; Hansen and Visser 2016), but only a game-theoretic setup enables consideration of the movements of two trophic layers (Fiksen et al. 2005). There exists some game-theoretic setups focusing on DVM, but they either considered the migration of only one trophic layer (Gabriel and Thomas 1988) or divided the water column in only two layers—namely, surface and depth (Iwasa 1982; Sainmont et al. 2013)—thus giving a very crude approximation of the positions and strategies of the players.

Mixed Strategies Emerge from Frequency-Dependent Processes

Our model also illustrates the importance of frequency-dependent processes, as they drive the emergence of mixed strategies. That is, even though players within a population are identical, they display different strategies. The distribution of individuals among strategies ensures that all players within a population have identical fitness—the defection of any one player from a given strategy will invariably reduce its fitness. Indeed, this variation of strategies within a population has been observed but is usually explained as state dependent (maturity, hunger) or as a manifestation of personality syndromes (boldness, aggression; Ohman 1990). We show

Table 2: Seasonal values of the parameters used to produce figure 5

| Parameter | January | February | March | April | May | June | July | August | September | October | November | December |
|----------------------------|---------|----------|--------|--------|--------|--------|--------|--------|-----------|---------|----------|----------|
| σ | .39 | .44 | .50 | .56 | .61 | .64 | .63 | .58 | .52 | .46 | .40 | .37 |
| L_{\max} ($W\ m^{-2}$) | 81.25 | 120.0 | 175.0 | 211.25 | 250.83 | 293.75 | 296.25 | 248.75 | 188.75 | 120.42 | 82.92 | 65.0 |
| z_0 (m) | 80 | 100 | 60 | 30 | 10 | 10 | 10 | 10 | 10 | 20 | 30 | 50 |
| N_0 (m^{-3}) | 33,750 | 45,000 | 12,500 | 7,500 | 2,500 | 7,500 | 1,250 | 22,500 | 2,500 | 15,000 | 11,250 | 6,250 |
| g_{\max} (day^{-1}) | .35 | .35 | .63 | .88 | 1.0 | .63 | .55 | .55 | .55 | .63 | .5 | .5 |
| L_0 ($W\ m^{-2}$) | .5 | .5 | .5 | .5 | .5 | .5 | .5 | .5 | .5 | .5 | .5 | .5 |

Note: Solar irradiance was calculated using the Solar Electricity Handbook (Boxwell 2017), and other variables were taken from the literature: prey average concentration (Sardou et al. 1996), prey maximum growth rates and chlorophyll (Morel and André 1991), and mixed layer depth (D'Ortenzio et al. 2005).

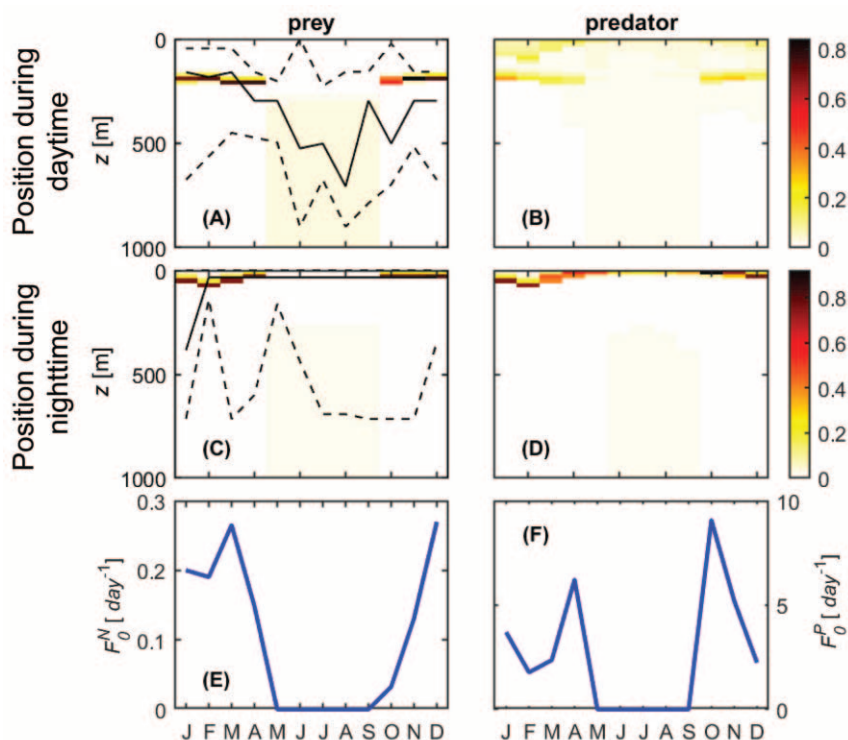


Figure 5: Variations in the vertical distribution of the prey during day (A) and night (C), the corresponding distribution for predators during day (B) and night (D), and the associated prey (E) and predator (F) fitnesses during an annual cycle. The solid (respectively, dashed) lines in A and C show the mean (minimum and maximum) observed depth of *Meganctiphanes norvegica* (Sardou et al. 1996).

here that mixed strategies are a feature of the underlying interactions and are not due to a variability in trade-offs experienced by different members of populations. This is one of the strengths of our approach, as these frequency-dependent processes and thus mixed strategies cannot be addressed in a fixed environment with optimal fitness techniques based on simpler rules, such as Gilliam's rule, or even with more complex life-history optimization (e.g., dynamic programming but without a game-theoretic approach).

Clearance Rates and Behavior Changes

The different migration regimes as a function of predator clearance rate demonstrated by our model can be validated from field findings. For instance, different clearance rates for predators can be related to prey size (reduced detectability of smallest prey and thus reduced clearance; Aksnes and Utne 1997), so these results can be compared to observed size-dependent DVM patterns (Ohman and Romagnan 2016). Indeed, observed size-dependent DVM patterns (Sardou et al. 1996) indicate that intermediate-sized prey exhibit the largest migration amplitude, while small prey remain resident in the surface, and large prey remain resident at depth. While other

factors can be involved, this pattern is entirely consistent with our model results where size can be equated with clearance rate.

Clearance rate can also be influenced by the predator's visual range and hence changes in water turbidity. Observations of the vertical movement of marine organisms in response to an inflow of turbid water (Frank and Widder 2002) showed that smaller organisms (small euphausiids) migrated upward, whereas larger organisms (large euphausiids, salps, myctophids) did not change their distribution. As for observed size-dependent patterns (Ohman and Romagnan 2016), this is consistent with an upward migration in response to a decrease in risk, whereas larger organisms with a relatively smaller decrease in risk did not change their behavior. While this behavior can be empirically related to organisms following a specific isolume (Schmitz et al. 2004), the functional rationale can be posited in terms of reduced risk for which irradiance serves as an easily sensed proxy. In a similar manner, different migration patterns of the krill *Meganctiphanes norvegica* in different Norwegian fjords can be related to different concentrations of dissolved organic matter (Onsrud and Kaartvedt 1998), in effect changing the clearance rate of their predators.

Changes with Seasonality

The equilibrium distributions for extreme values of σ point out that variation in day length cannot explain the observed seasonality in DVM in and of itself. Indeed, the only place where such fractions of daylight can occur is the high Arctic, where many more factors come into play (e.g., diapause during the polar night is as much about temperature and low primary production as it is about darkness and predator avoidance; Varpe 2012).

We investigated the seasonal variation (table 2; fig. 5) in a temperate water column, specifically, the northwestern Mediterranean. This enabled us to compare our results with the monthly study of DVM (Sardou et al. 1996) exhibited by the krill *M. norvegica*. The general pattern produced by the model is in broad agreement with field findings (fig. 5). Observed monthly distributions of the predatory fish are also in general agreement. Predators gather at the surface at night and perform DVM throughout the year, except during summer where both predator and prey are scattered through the water column. Predators follow a bimodal distribution during the day (200 m depth and the surface) between October and April. Such bimodal distributions have been exhibited before, for example, with the analysis of acoustic scattering layers (Klevjer et al. 2016).

Nash Equilibrium, Evolutionary Stable Strategy, and Ideal Free Distribution

The coupling presented here provides a way to assess optimal distributions of prey and predators in terms of Nash equilibria. For a game with a single player, the ideal free distribution is the Nash equilibrium of the habitat selection game, and provided that the fitness is negatively density dependent, it is also an evolutionary stable strategy (ESS; Cressman and Křivan 2006; Křivan et al. 2008; Křivan 2014). However, for two or more players, the Folk theorem (Cressman 2003) states that a stable equilibrium of the replicator equation is a Nash equilibrium but is not necessarily an ESS, the very definition of which is clouded for two-species games with more than two strategies as considered here (Křivan et al. 2008). As we consider the equilibrium distribution of the population at a given period and no group of the population will change its behavior at the same time, we believe that the replicator equation gives a reasonable representation of nature. Trophic rearrangements and seasonal variations of environmental parameters surely occur, but we assume that organisms have learned through evolution to deal with these changes. Of greater concern is the fact that our model might have several Nash equilibria or can oscillate around equilibria. To check this, for each set of parameters used, several runs with different initial conditions were performed. No significant differences between runs were observed, which validates the robustness of our

model in providing us with stable equilibria mimicking animal distribution in the water column. Moreover, our results were quite stable with little (or no) oscillations across equilibrium points, both for the fitness and the distribution. Figure A1 (available online) displays an example of convergence to the equilibrium with the replicator equation. The variances in fitness over the last 20,000 iterations were very low, ranging between 10^{-3} and 10^{-11} .

Natural Selection Triggers Fitness Collapse

A curious consequence of the frequency-dependent processes described here is that evolution by natural selection can drive a species to a collapse in realized fitness. After all, evolution is shaped by the advantage an individual gets from adaptations, and it would seem that an individual would benefit from having a superior attribute, for example, a higher clearance rate, which would enable it to capture more prey. This trait would thus be favored and would then spread within the predator population. However, this can induce a sharp decline in realized predator fitness (fig. 2F)—in a sense, they become too accomplished for their own good. Furthermore, such a change is irreversible in that a reduction in clearance rate for an individual always reduces its fitness compared to its conspecifics and thus cannot be evolutionarily favored. The proximate cause for this is the switch in behavior of the prey as increasing predator voracity drives them to seek refuge in a process akin to behaviorally mediated trophic relationships (Schmitz et al. 2004). It remains unclear as to how this process would play out in an evolutionary setting that includes population dynamics.

Conclusion and Perspectives

DVM is more than just a key behavioral component of marine life; it has far-reaching effects on the productivity, community structure, and population dynamics of marine ecosystems (Cushing 1951; Hays 2003), as well as the ocean's biogeochemistry (Longhurst et al. 1990; Bianchi et al. 2013a). Our work provides a mechanistic understanding of DVM and particularly the cascading migrations of the upper trophic layers (Bollens et al. 2011) that also play a significant role in the biological pump. It is becoming increasingly evident that the active transport of carbon by consumers such as zooplankton (Jónasdóttir et al. 2015; Hansen and Visser 2016) and fish (Davison et al. 2013) constitute an important component of the biological pump. Our model provides a tool to dynamically describe the vertical positioning of these consumer species in terms of readily prescribed (or modeled) environmental parameters. Furthermore, the modeling framework can be readily expanded to include additional consumer populations with different feeding modes (e.g., tactile predators such as jellyfish). A clear conclusion that can be drawn

from this work is that behavior is an important factor in determining how marine ecosystems function and that optimality of behavior, as we see in DVM, is strongly controlled by a strategic payoff between predators and their prey.

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