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Oceanic diel vertical migrations arising from a predator-prey game^{*}

Uffe H. Thygesen · Toby A. Patterson

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Abstract The deep scattering layer is an ubiquitous aggregation of zooplankton and forage fish in the ocean. It features the striking phenomenon of diel vertical migration, where animals remain in deep, dark water in daylight hours and migrate upwards at dusk. The common explanation for this is that prey avoid vulnerability to visual predators. Here, we develop a game-theoretic explanation for the deep scattering layer and its diel vertical migrations, focusing on one generic predator species and one generic prey species. The model is formulated in continuous time and space, and by neglecting the cost of locomotion, it allows fine-grained predictions of vertical distributions. The Nash equilibrium features a distinct deep scattering layer which undertakes diel vertical migrations, the range of which increases with predator abundance. Maximum feeding rates are predicted to occur at dawn and dusk. Predator interference emerges from the game dynamics in the form of a complicated functional depen-

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dency of gross encounter rates on predator abundance. In turn, the growth rate of the prey decreases monotonically with predator abundance. In addition to providing a mechanistic explanation for the striking phenomenon of diel vertical migrations, the model yields quantitative predictions of vertical distributions and diel patterns in feeding intake, which may be compared with acoustic data, observed individual behavior, or stomach data.

Keywords Deep scattering layer · Diel Vertical Migration · Behavioral games · Nash Equilibrium

1 Introduction

Diel vertical migration (DVM) of organisms is a remarkable structuring feature of aquatic ecosystems: Small zooplankton and fish migrate towards the surface at dusk and then descend at the following dawn. In the open ocean, they spend the daylight hours at considerable depth where they make up what is termed the Deep Scattering Layer (DSL) - named for its acoustic properties which make it detectable using echo-sounding, so that the phenomenon is well documented across systems (Dypvik et al, 2012; Klevjer et al, 2016, for example). The dynamics of both epi- and meso-pelagic ecosystems, the largest habitats on the planet, are hugely influenced by this phenomenon, which in turn imparts global significance of DVM. This synchronous movement over a daily cycle is thought to constitute the largest transport of biomass of any migration on the globe (Hays, 2003). DVM is also considered to be a significant contributor to the global carbon cycle via the so-called biological pump (Ducklow et al, 2001) which cycles surface production into deep water.

Despite the huge impact of DVM on production cycles in the ocean, the details of its drivers are not entirely clear. The migrations must confer advantage in terms of growth and mortality, which combine into fitness. Several studies have supported the idea that residing in deep and crucially, dark, waters, during daylight is a strategy for avoiding visual predators, and in general terms, this hypothesis is accepted over alternative explanations, at least for zooplankton and in the open ocean (Hays, 2003; Lampert, 1989). During night-time, low light levels allow the organisms that constitute the deep scattering layer to forage in the more productive waters in the upper photic zone, with reduced risk of predation. A complicating factor is that animals may be visual predators while subjected to predation by other visual predators, so light implies both opportunity for growth and risk of death, and these two must be traded off against each other (Clark and Levy, 1988). A similar complication is the coexistence of different vertical strategies even within a species (Watanabe et al, 2006). In any case, it is likely that light levels are the main cue that initiate migrations, and several studies have compared

the movements and distributions of prey species with light levels (e.g., Murray et al (1912); Nilsson et al (2003)).

Given that diel vertical migrations are thought to be driven by predation risk, conferred as a function of light levels, it is not surprising that many empirical studies of ocean top predators and their vertical distribution over the diel cycle have shown pronounced changes in distribution which are congruent with DVM in the prey. In these instances, predators spend the day at depth and descend/ascend with dawn/dusk, in patterns that resemble those of prey migrations. Tracking both predators and preys within the same study, Josse et al (1998) observed the vertical movements of tuna and the sound scattering layer, and Sims et al (2005) observed basking sharks feeding on zooplankton. More commonly, we must compare observed motion of predators with our general assumption of prey behaviour. Examples include whale sharks (Meekan et al, 2015), swordfish (Takahashi et al, 2003), white shark (Jorgensen et al, 2012), and bigeye tuna (Evans et al, 2008).

Since the trade-offs faced by the prey depend on predator distributions, while predator behaviour can be expected to depend on prey distributions, the vertical distributions and migrations of organisms can only be understood as a game where each individual plays against both conspecifics and individuals of other species. A seminal work in this direction is that of Iwasa (1982). Here, the vertical dimension is reduced to two habitats, a surface habitat and a deep habitat, and the time axis is divided into a light period and a dark period. The model predicts diel vertical migrations, where the two species co-habitate the surface habitat at night while they distribute themselves over the water column during the day, where the prey show higher preference for the deep habitat than do the predators. Sainmont et al (2013), also including a third trophic level, allowed parts of the populations to perform migrations while others would stay stationary, and found equilibria where all strategies co-existed.

In this paper we formulate a game between predators and prey in continuous space and continuous time. This formulation requires the development of novel techniques for resolving the game, as well as the simplification following from neglecting the cost of locomotion, but in turn allows us to include mechanisms such as the variations in light intensity during the day and with depth, the thermal structure of the water column, and the effect of light levels on detection distances between predators and prey. In turn, the outcome of the game (the Nash equilibrium) is vertical distributions of each species at any point of time. From these we can derive quantities such as the depth range occupied by each species, swimming speeds, and temporal patterns of predator-prey encounters. Compared to previous game-theoretic models of vertical distributions, the continuous formulation allows more fine-grained predictions. The continuous space allows us to examine the vertical position of the deep scattering layer, while the continuous time allows us to examine the movements of the deep scattering

layer during dawn and dusk. We also scale up to predict system-level consequences, e.g. the sensitivity of prey behaviour and predation mortality to predator abundance.

We have in mind the game between prey such as myctophids or other oceanic forage fish, and predators such as tuna. However, we formulate the model generically, without specifying particular prey and predators explicitly. This allows us to obtain a fairly simple model with a limited number of parameters, while still generating predictions that can be compared qualitatively with data such as vertical distributions obtained from fisheries acoustics or individual vertical behaviour illuminated by electronic data storage tags. A key component in the game is the preference of the prey for the surface waters; without such a preference, the prey would descend to the bottom and remain there. While the prey in reality are likely feeding on resources with a particular vertical distribution, we do not wish to include lower trophic levels in our model. Therefore, we link the growth rate of the prey to the ambient water temperature, which means that the prey experiences higher growth rate in the mixed layer near the surface. We emphasize that this should be seen as a simple way of parametrizing the prey's preference for the layers closer to the surface.

Thus, the prey face a trade-off between growth rate and vulnerability to predation. At the same time, the prey must spread out; excessive prey concentrations at a single point would attract predators and result in high predation mortalities. From the point of view of the predator, a trade-off emerges between high light levels, implying that prey can be detected, and high prey abundances. At the Nash equilibrium, these trade-offs are resolved in the sense that the two species are, at each point in time, distributed vertically so that no single animal can see an advantage in deviating from its strategy.

The model we pose is dynamic in the sense that we resolve the diel cycle and compute the fitness of animals by averaging over this cycle, but it does not contain dynamic state variables of the organisms such as gut fullness or even vertical position. This simplification implies a computational efficiency that allows us to make high-resolution predictions and investigate sensitivity to parameters. In particular it allows us to scale up and predict system-level consequences of e.g. varying the abundance of the predators.

2 The vertical game between predators and prey

We consider a game in which each predator, and each prey, must at each instant choose a vertical position z in the water column. As in previous game-theoretic models of diel vertical migration (Iwasa, 1982; Sainmont et al, 2013), the prey must choose between surface layers which offer high growth rates but also high visibility to predators, and deeper layers which are relatively safe but offer slower

Fig. 1 The model components. Left panel: Temperature profile $T(z)$ and resulting growth rate $g_N(z)$ of the prey, as function of depth. Right panel: Detection distance between predators and prey as a function of time and depth.

growth. The predators, in turn, optimize their foraging success which involves a compromise between high light levels and high prey abundances.

We now detail the specification of growth and mortality for the two species; see figure 1. For the prey growth rate $g_N(z, t)$, for simplicity, we consider a single physical forcing factor, namely temperature, and assume a standard scaling between temperature and growth rate:

$$g_N(z, t) = g_0 Q_{10}^{(T(z)-T_0)/10} .$$

where g_0 is a reference growth rate at reference temperature T_0 , and Q_{10} defines the growth acceleration resulting from a 10 degrees temperature increase. In this growth model, only relative growth matters, so we take $g_0 = 1$ per year. The temperature $T(z)$ in turn depends on depth as in (Maury, 2005; Thygesen et al, 2016):

$$T(z) = T_0 - (p \cdot z + \Delta T_{\text{clin}}) \cdot \frac{z^\lambda}{z_{\text{clin}}^\lambda + z^\lambda} \quad ,$$

where T_0 is surface temperature, p is the temperature gradient below the thermocline, ΔT_{clin} is the temperature drop over the thermocline, z_{clin} is the depth of the thermocline, and λ controls the sharpness of the thermocline. The resulting temperature and growth profiles are seen in figure 1, left panel.

We keep the time argument in $g_N(z, t)$ for the sake of generality although the growth rate here is a constant function of time. This is a useful model of the vertical variation in growth which displays the right qualitative feature, namely decreasing growth rates with depth (compare also (Loose and Dawidowicz, 1994)). Specific studies could take into account the details of what the prey forages on and how, for example, by letting prey growth rate depend on plankton densities.

The mortality of the prey, and the foraging success of the predator, is given by a clearance volume $\beta(z, t)$ (volume per time), so that the rate of prey consumption at depth z and time t is given by the encounter rate $E(z, t)$:

$$E(z, t) = \beta(z, t)P(z, t)N(z, t) \quad ,$$

where $P(z, t)$ is the density of predators and $N(z, t)$ is the abundance of prey (both in numbers per volume). The encounter rate is given in number of encounters per volume per time. Note that we assume a type I functional response, i.e. first order mass action. The clearance volume β is given by the swimming speed U of the predator, assumed constant, and the distance $D(z, t)$ at which a predator detects its prey:

$$\beta(z, t) = U\pi D^2(z, t) + U\pi D_c^2 \quad . \quad (1)$$

Here, D corresponds to the distance of visual detection. The clearance term $U\pi D_c^2$ is introduced to ensure that the prey cannot escape predation completely, and can e.g. model direct contact between predators and prey. For the visual detection distance D , we follow Aksnes and Utne (1997) and assume that the detection happens when a given light intensity reaches from the prey to the predator. Specifically, the detection distance $D(z, t)$ is given implicitly as the solution to the equation

$$I(z, t)e^{-kD}D^{-2} = c(K + I(z, t))$$

where $I(z, t)$ is the light intensity at depth, k is the diffuse attenuation coefficient (assumed constant), and the right hand side determines the detection threshold. The logic of this expression is that the light is attenuated at rate k over a distance $D(z, t)$ from the prey to the predator, while spreading spherically, explaining the term $D^{-2}(z, t)$. The constant 4π involved in the surface area is absorbed in c . The detection threshold $c(K + I)$ depends on ambient light, which can be justified by appeal to a contrast threshold and a saturation in the visual response. The fact that the threshold grows with ambient light also ensures that the detection distance does not diverge as the light intensity increases, but since interactions tend to take place in low light regimes, this has limited effect. The light intensity at depth is $I(z, t) = I(0, t) \exp(-kz)$ while the light intensity $I(0, t)$ at the surface is found from the position of the sun and the moon, using a simplified model of the optics of the atmosphere, as implemented in R package `oce`. We ignore the angle of the light and refraction at the surface, assuming that the light is scattered diffusively near the surface. We acknowledge that this model of ocean optics and visual detection is coarse and simplistic, but argue that it catches the essential qualitative features; viz. high detection distances near the surface and during the day. The final distance of visual detection is seen in figure 1, right panel, and enters in the clearance volume in (1).

These encounters lead to an uptake rate per predator, for a predator at depth z and time t :

$$g_P(z, t) = N(z, t)\beta(z, t) \quad (2)$$

while we assume the mortality of the predator, μ_P , to be constant. In turn, the mortality rate for the prey at the same position is:

$$\mu_N(z, t) = \mu_0 + P(z, t)\beta(z, t) \quad (3)$$

where μ_0 is a constant mortality due to other causes than predation.

For the purpose of the subsequent analysis, we note that the prey growth rate $g_N(z, t)$ and the clearance volume $\beta(z, t)$ are positive, continuous and monotonically decreasing functions of depth z .

2.1 The dynamic equations of fitness and the Nash equilibrium

Previous game-theoretic studies of vertical migrations have been formulated discretely, which have led to algebraic conditions, possibly employing the replicator equation for computations (Sainmont et al, 2013, e.g.). In contrast, our continuous formulation is a special and simple case of mean-field game theory (Lasry and Lions, 2007), which leads to differential equations borrowing from the theory of dynamic optimization (Bertsekas, 2005; Houston and McNamara, 1999). Let $V_N(t)$ denote the fitness of

an individual prey at time t , defined as its expected energy uptake from time t and until the individual dies, assuming that the animal behaves optimally. We allow the animal to choose its vertical position z freely at each point in time and ignore the costs of locomotion. Thus the fitness evolves according to the Hamilton-Jacobi-Bellman equation

$$\dot{V}_N(t) + \sup_z [g_N(z, t) - \mu_N(z, t)V_N(t)] = 0 \quad , \quad (4)$$

where the dot in $\dot{V}_N$ indicates time derivative. This equation is complemented by the terminal condition $\lim_{t \rightarrow \infty} V_N(t) = 0$. The equation highlights the trade-off that the animal faces when choosing a depth z : The animal aims to maximize its growth rate $g_N(z, t)$ but at the same time minimize its mortality $\mu_N(z, t)$. The trade-off between these two conflicting objectives is quantified by its fitness $V_N(t)$: An animal with high fitness $V_N(t)$ should give priority to protecting its assets and thus minimize the mortality $\mu_N(z, t)$, while an animal with low fitness $V_N(t)$ should pay more attention to maximizing growth $g_N(z, t)$. In turn, for an optimal vertical trajectory $Z(t)$, which attains the supremum in (4) at each point in time, the solution to this equation can be written

$$V_N(t) = \int_t^\infty g_N(Z(s), s) \exp \left(- \int_t^s \mu_N(Z(u), u) du \right) ds$$

where the exponential denotes the probability of surviving from time t to time s . Thus, $V_N(t)$ is indeed the expected energy uptake in the remainder of the individual's life.

Inserting the particular form (3) of the prey mortality μ_N into (4), we obtain

$$\dot{V}_N(t) + \sup_z [g_N(z, t) - (\mu_0 + P(z, t)\beta(z, t))V_N(t)] = 0 \quad . \quad (5)$$

Likewise, let $V_P(t)$ be the fitness of an individual predator. If at depth z at time t , then its fitness evolves according to the equation

$$\dot{V}_P(t) + \sup_z [g_P(z, t) - \mu_P V_P(t)] = 0$$

with terminal condition $\lim_{t \rightarrow \infty} V_P(t) = 0$. Using the particular form (2) for the predator growth rate g_P , we obtain

$$\dot{V}_P(t) + \sup_z [\beta(z, t)N(z, t) - \mu_P V_P(t)] = 0 \quad . \quad (6)$$

We now consider the game that the individual predator plays against its conspecifics as well as against the prey. In this game, there is a continuum of players of each species, and each individual chooses a vertical trajectory $Z(t)$. From these trajectories, we can form the densities $P(z, t)$ and $N(z, t)$

of the two species, which in turn define the environment faced by each individual, and therefore the fitness functions $V_N(t)$ and $V_P(t)$ through the governing equations (5) and (6). We assume that the animals are long-lived compared to a single day, so that we can neglect fluctuations in the total abundance. Hence we consider $\bar{P} = \int_0^\infty P(z, t) dt$ and $\bar{N} = \int_0^\infty N(z, t) dz$ constant in time and positive.

We aim to identify a Nash equilibrium of this game, the defining property of which is that no individual player can obtain an advantage by changing strategy. Thus, a Nash equilibrium is obtained if and only if each prey at each time t chooses a vertical position for which the supremum in (5) is attained, and similarly, each predator chooses a vertical position for which the supremum in (6) is attained. Thus, the necessary and sufficient conditions for a Nash equilibrium are

$$P(z, t) \geq \frac{\dot{V}_N(t) + g_N(z, t) - \mu_0 V_N(t)}{\beta(z, t) V_N(t)} \text{ for every } z, t, \text{ with equality when } N(z, t) > 0 \quad , \quad (7)$$

$$N(z, t) \leq \frac{\mu_P V_P(t) - \dot{V}_P(t)}{\beta(z, t)} \text{ for every } z, t, \text{ with equality when } P(z, t) > 0 \quad . \quad (8)$$

We can now deduce some properties of the densities N, P at a given time t under a Nash equilibrium. First, from (8) we see that $P(z, t) > 0$ implies that also $N(z, t) > 0$, since $\mu_P V_P - \dot{V}_P > 0$. This conclusion hinges on the predator mortality μ_P being independent of depth z as well as some depth z' where $N(z', t) > 0$; then, the predators have no incentive to being in a place where there is no prey. Next, if $N(z, t) > 0$ and $z' < z$, then $N(z', t) > 0$ and $P(z', t) > 0$. To see this, note from (7) that $\dot{V}_N(t) + g_N(z, t) - \mu_0 V_N(t) \geq 0$. Since $g_N(z, t)$ decreases with z , it follows that $\dot{V}_N(t) + g_N(z', t) - \mu_0 V_N(t) > 0$ and therefore $P(z', t) > 0$, which in turn implies that $N(z', t) > 0$. In words, if prey are found at a given depth, then there must be predators at every location nearer to the surface, balancing the higher growth rates there, and these predators in turn require the presence of prey. The conclusion from this analysis is that at a Nash equilibrium, the prey and the predators will share a common habitat, which will be an interval $z \in [0, \bar{z}_t)$ with a limit $\bar{z}_t = \sup\{z \geq 0 : N(z, t) > 0\} \in (0, \infty]$ which may change with time.

We now inspect what happens at the limit $\bar{z}_t$. First, from (8) we see that $N(z, t)$ increases monotonically with depth for $z < \bar{z}_t$, and since $N(\cdot, t)$ integrates to $\bar{N}$, $\bar{z}_t$ must be finite. Moreover $N(z, t)$ must jump discontinuously to 0 at $\bar{z}_t$. In turn, from (7) we see that $\dot{V}_N(t) + g_N(z, t) - \mu_0 V_N(t)$ is positive for $z < \bar{z}_t$ and non-positive for $z > \bar{z}_t$. Since g_N is continuous, we conclude that

$$\dot{V}_N(t) + g_N(\bar{z}_t, t) - \mu_0 V_N(t) = 0 \quad . \quad (9)$$

Furthermore, letting $z \rightarrow \bar{z}_t$ in (7) we conclude that $P(z, t) \rightarrow 0$. Thus the predator density is a continuous function of z , also at the lower limit of the depth range.

In summary, the structure of a Nash equilibrium at a given time t is necessarily the following: Both species are constrained to a layer $z \in [0, \bar{z}_t]$ extending from the surface and to some finite depth $\bar{z}_t$. The prey are distributed such that a predator encounters the same number of prey regardless of depth, i.e. the prey density $N(z, t)$ increases with depth, scaling with $1/\beta(z, t)$. The prey density $N(z, t)$ then drops discontinuously to 0 at $\bar{z}_t$. In turn, the predators distribute themselves such that the growth of prey fitness is independent of depth, i.e. (7). Thus the predator density increases with the prey growth rate $g_N(z, t)$ and decreases with the clearance rate $\beta(z, t)$, as also found by Hugie (1999) in a discrete context. The density of predators $P(z, t)$ is a continuous function of depth; specifically, it vanishes at the lower limit of the depth range, i.e. $P(\bar{z}_t, t) = 0$.

2.2 Computational strategy for finding the Nash equilibrium

Here, we outline how to resolve the game computationally. The strategy is to search for densities $N(z, t)$ and $P(z, t)$ and corresponding fitness functions $V_N(t)$, $V_P(t)$ which satisfy the necessary and sufficient conditions (5), (6), (7), (8), restricting attention to densities $N(z, t)$ and $P(z, t)$ which have the properties which we deduced in section 2.1. Consider first the situation at a given time t , assuming the fitnesses $V_N(t)$ and $V_P(t)$ known. The objective of the calculations is to find the depth range $\bar{z}_t$, and then the rate of increase in fitness $\dot{V}_N(t)$ and $\dot{V}_P(t)$.

The condition for finding $\bar{z}_t$ is that the predator density integrates to the total predator abundance $\bar{P}$. Combining (7) and (9), we find

$$P(z, t) = \frac{g_N(z, t) - g_N(\bar{z}_t, t)}{\beta(z, t)V_N(t)} \text{ for } z < \bar{z}_t \quad (10)$$

and thus

$$\bar{P} = \int_0^{\bar{z}_t} P(z, t) dz = \int_0^{\bar{z}_t} \frac{g_N(z, t) - g_N(\bar{z}_t, t)}{\beta(z, t)V_N(t)} dz \quad .$$

Here, the total predator abundance $\bar{P}$ is a known parameter while the vertical range $\bar{z}_t$ must be found from this equation with a line search. It is easy to see that there can be at most one solution to this equation, since the right hand side is an increasing function of $\bar{z}_t$; for the specific model detailed in section 2, a solution is always found. Once the depth range $\bar{z}_t$ is known, the predator distribution is given from (10). Furthermore, we can find the rate of change $\dot{V}_N$ of the prey fitness from (9).

Next, the prey density

$$N(z, t) = \frac{\mu_P V_P(t) - \dot{V}_P(t)}{\beta(z, t)} \text{ for } z < \bar{z}_t \quad (11)$$

must integrate to the total prey abundance $\bar{N}$. Thus

$$\bar{N} = \int_0^{\bar{z}_t} N(z, t) dz = (\mu_P V_P(t) - \dot{V}_P(t)) \int_0^{\bar{z}_t} \frac{1}{\beta(z, t)} dz \quad .$$

From this expression, knowing $\bar{N}$, we can find the coefficient $\mu_P V_P(t) - \dot{V}_P(t)$ and thus the prey distribution $N(z, t)$. In turn, this also yields the rate of change $\dot{V}_P(t)$ of the predator fitness.

We now have a recipe for computing $\dot{V}_N(t)$ and $\dot{V}_P(t)$ from $V_N(t)$ and $V_P(t)$, i.e. two coupled ordinary differential equations for the fitnesses V_N and V_P . Solving these with the terminal conditions $\lim_{t \rightarrow \infty} V_N(t) = \lim_{t \rightarrow \infty} V_P(t) = 0$, we establish densities N , P , and fitnesses V_N , V_P which satisfy the conditions (5), (6), (7), (8), and therefore constitute a Nash equilibrium. We note that this construction also guarantees that the Nash equilibrium is unique, under the reasonable assumption that the ordinary differential equations for V_N and V_P have unique solutions.

To avoid a lengthy time-marching of these equations, we make a slow-fast approximation of the fitness dynamics, consistent with our assumption that the total abundances $\bar{N}$ and $\bar{P}$ are constant throughout the day. Thus also fitness fluctuations during a single day can be neglected. We can then compute the total growth and mortality of a prey over a day, which gives the fitness of the prey:

$$V_N = \frac{\int_0^1 \int_0^\infty N(z, t) g_N(z) dz dt}{\int_0^1 \int_0^\infty N(z, t) (\mu_0 + \beta(z, t) P(z, t)) dz dt}$$

Since the vertical distributions $N(z, t)$ and $P(z, t)$ depend on the prey fitness V_N , although this is suppressed in the notation, this is a nonlinear equation in V_N which is solved numerically using a standard nonlinear solver. We have not investigated theoretically if a unique solution can be guaranteed to exist, but the numerics do not indicate any problems. A similar expression could be written for the fitness V_P of the predators, but since the spatial distribution of predators does not depend on their fitness, it is not necessary to compute this.

2.3 Model parameterization

The model parameters are given in table 1. Results are shown for an oceanic position at 20 degrees south, on the prime (Greenwich) meridian, on May 3, 2017. Here, the sun rose at 6:55 in the morning (local time), and set at 16:58 in the afternoon. The moon, being 48 % illuminated, rose at 13:30 and set at 0:20 on May 4, 2017.

Symbol	Description	Value	Unit
<i>Prey growth and base mortality:</i>			
g_0	Reference growth rate	1	Per year
Q_{10}	Temperature coefficient	2.3	-
μ_0	Base prey mortality	1	Per year
<i>Thermal structure:</i>			
T_0	Surface temperature	27	°C
p	Deep temperature gradient	0.008	°C/m
ΔT_{clin}	Thermocline drop	4.5	°C
λ	Thermocline steepness	4	-
<i>Predator-prey encounters:</i>			
U	Predator speed	1	m/s
D_c	Direct contact distance	0.25	m
k	Light attenuation	0.03	1/m
c	Light detection threshold	10^6	m^{-2}
K	Level of light saturation	10^3	lx

Table 1 Model parameters

3 Results

3.1 Diel vertical migrations and the deep scattering layer

The model predicts diel vertical migration of both predators and prey at the Nash equilibrium (figure 2). These migrations are predicted to occur at dusk and dawn in accordance with empirical observations of the migration of the deep scattering layer (Dypvik et al, 2012; Klevjer et al, 2016) and of many pelagic predator species (Evans et al, 2008; Jorgensen et al, 2012; Meekan et al, 2015; Takahashi et al, 2003). Therefore both species occupy the mixed layer at night while both are predicted to reside beneath the thermocline during the day (figure 3). Qualitatively, the positioning of both species follows the light - i.e., as the illuminance at the surface increases, the animals descend. However, the animals do not maintain constant light levels in time (figure 4), and the average light levels experienced by the animals depend on parameter values. The fluctuations in mean log-illuminance in figure 4 can be translated to a vertical distance of roughly 130 m to a given isolumen.

At each point in time, the model predicts prey to be quite concentrated in the water column, so that the prey does indeed form a deep scattering layer. For the particular parameters in figure 2 and at noon, the 75 % deepest prey are found in a range of 85 meters. The prey is most concentrated at dawn and dusk, where this range is reduced to 51 meters. The predators sit slightly higher in the water column than the prey, as one would expect since the individual predator faces a trade-off between light

and prey abundance. Also, the predators are less concentrated than the prey, for example, at noon, the lower 75 % of the predators cover a range of 145 meters. On the particular run shown in figure 2, the moon is half full and sets at midnight, which results in a slight upwards migration of both species.

The encounter rates between predator and prey change markedly during the day. The pattern depends on the particular parameters. For the parameters in figure 2, the encounter rates peak sharply at dawn and dusk (figure 4), while encounter rates at noon and midnight are roughly similar. In contrast, at very low predator densities, the predation pressure is not large enough to cause marked vertical migrations, and then feeding occurs predominantly during the day (not shown).

Since the model contains no dynamics of digestion and no constraints or penalties on migration speeds, the mechanism giving rise to these peaks in feeding rates is that the mixed layer near the surface offers higher prey growth. As the light levels increase, the prey prefer to stay in the mixed layer as long as possible, even with elevated mortality. Once the light level have passed a threshold, the prey effectively evacuate the mixed layer. At this point they may as well go very deep, since the sensitivity of prey growth to depth is reduced below the mixed layer.

In further experimenting with the model, we examined the effect of changes in cloud cover from day to day and found that the deep scattering layer resides nearer to the surface on cloudy days, in agreement with observations.

3.2 Swimming speeds

Since the model does not take into account the cost of migration, it is relevant to compute the swimming speeds that the Nash strategies would require. The model itself does not specify the motion of an individual animal, only the distribution of animals at each time, but a plausible minimal hypothesis is that animals maintain their ordering. Thus, a specific individual from the prey population is characterized by a constant number n in the interval $[0, \bar{N}]$, giving the number of conspecifics above it, so that its vertical position $Z(t)$ at each time t satisfies

$$\int_0^{Z(t)} N(z, t) dz = n \quad .$$

Differentiating with time, we obtain the swimming velocity

$$\frac{d}{dt} Z(t) = - \frac{\int_0^{Z(t)} \frac{\partial N}{\partial t}(z, t) dz}{N(Z(t), t)} \quad .$$

Swimming speeds can thus be computed readily from the abundances using numeric differentiation and integration. We find, unsurprisingly, that the maximum swimming speed occur around dawn

Fig. 2 Simultaneous diel vertical migrations in the Nash equilibrium. Relative densities (in per cent of the population per meter) as function of time and depth, for $\bar{P} = 10^{-6} \text{ m}^{-2}$. Left panel: Prey. Right panel: Predators.

and dusk; for the parameters in figure 2, they amount to approximately 0.2 m/s for both predators and prey.

3.3 Scaling with predator abundance

We can now investigate the sensitivity of the model to various parameters. Here, we focus on the predator abundance. Figure 5 shows how population-level properties and rates vary, as the predator abundance is varied orders of magnitude. First, the depth range (defined as the maximum depth

Fig. 3 Vertical distributions in the Nash equilibrium. Relative densities (in per cent of the population per meter) as function of depth, shown at noon and at midnight, for $\bar{P} = 10^{-6} m^{-2}$. The prey (left) and predators (right) show qualitatively similar distributions, where they reside in the upper layers during the night (grey shaded) and seek deeper habitats during the day (white).

311 occupied by a prey during the diel cycle, $\max_t \bar{z}_t$) increases with predator abundance (figure 5, top
 312 panel). Without any predators, all the prey would sit at the surface, where the growth is highest. Since
 313 the growth rate is almost constant over the upper mixed layer, even a small predator population will
 314 cause the prey to initiate diel vertical migrations, distributing themselves over the upper mixed layer
 315 during the daytime, but still concentrating near the surface at night. As the predator population is
 316 increased, the prey first push to the lower part of the mixed layer, where growth rates are reduced,

Fig. 4 Diel fluctuations in rate of feeding of a predator (black), and in the mean light levels experienced by prey (blue) and predators (red), for $\bar{P} = 10^{-6} \text{ m}^{-2}$.

but soon begin to migrate below the mixed layer during the daytime. The range of these migrations increases with predator abundance. At very high predator densities, the prey spread out over large depth ranges below the mixed layer during the daytime.

The encounter rates, or equivalently, the predation mortality experienced by the prey, vary with the predator abundance in a complex way (figure 5, middle panel): Initially, the predation mortality increases steeply with the predator density. The initial linear relationship soon decelerates as the prey adapt behaviorally to the presence of predators, sacrificing growth for safety. At predator densities around 10^{-8} m^{-2} , a peak occurs after which the predation mortality decreases with increasing preda-

tor densities. This phenomenon may appear counter-intuitive but can emerge also in simple one-sided optimization models where the prey can adapt to predators. Here, the shift coincides with the on-set of a dense deep scattering layer in the daytime which is below the thermocline.

The prey growth rate decreases with predator abundance, since the prey adapt behaviourally to the presence of predators: More predators make the prey migrate deeper, which results in a reduced growth rate (figure 5, bottom panel). This prediction is robust and universal, in contrast to the non-monotonic relationship between the predator abundance and the predation mortality experienced by the prey (figure 5, middle panel).

From the point of view of the predator, the vertical migrations of the prey imply substantially decreased hunting success. The behavioral adaptation of the prey, as predator abundance is increased, there implies an emerging predator interference in the sense that the uptake per predator decreases markedly with the number of predators.

4 Discussion

The game theoretic model demonstrated here has successfully replicated the phenomenon of diel vertical migration which results in a deep scattering layer during the daytime, and the model predictions fit well with many results found in empirical studies which have thoroughly documented the phenomena. While diel vertical migrations have previously been studied from the game theoretic perspective, this is the first analysis which employs both continuous time and continuous space. This allows a modelling framework of higher fidelity, of which a noticeable feature is the way detection distances depend on time and depth. This in turn allows predictions such as the dynamics of the migration around dawn and dusk, the extent to which the organisms track isolumines, and the effect of the moon on nighttime vertical profiles. All these features allows the model to be confronted quantitatively with data on vertical distributions obtained with echosounders, or on individual vertical movements obtained with archival tags.

The model predictions hinge on the assumption of a Nash equilibrium, where all prey experience identical fitness regardless of their vertical position, as do all predators. This assumption, in games with similar structure, has previously been criticized (Gabriel and Thomas, 1988; Hugie and Dill, 1994) because the equilibrium is not evolutionary stable: At the equilibrium, all predators experience the same fitness; thus, there is no evolutionary incentive to uphold the equilibrium strategies, and consequently the system may drift away from equilibrium. However, an argument in favour of the Nash equilibrium is that weak intraspecific interactions (i.e., density dependence) will stabilize the

Fig. 5 Population-level quantities as function of predator abundance. Top panel: Depth ranges. Depth intervals which contain the lowest 75 % of the prey population at noon (white) and midnight (grey). Middle panel: Predation mortality of the prey for the Nash equilibrium (solid) and, for reference, for a fixed-strategy solution (dashed) where the vertical distributions do not change as predator abundance increases. Bottom panel: Prey growth rate and predator growth rate, relative to the maximum growth rate, for the Nash equilibrium (solid) and for the same fixed strategies.

Nash equilibrium without shifting it markedly (Sainmont et al, 2013). Also, at least for static games, the Nash equilibrium can be reached by animals performing fitness taxis in the sense of (Heilmann et al, 2018). This assumes that animals can sense local gradients in fitness landscapes, and in particular assess the mortality risk they are exposed to. It is a daunting question which cues are available to migrating animals as well as to which degree evolution has shaped behavioural responses that resemble

those of an optimal decision-maker, and also the implications of variations between individuals of the same species are unclear. Still the Nash equilibrium appears to be a reasonable starting point for the analysis.

One peculiarity of the Nash equilibrium in this game theoretic approach is the indirect reasoning. For example, the vertical distribution of the prey is given by the constraint that all predators must experience the same hunting success. In contrast, the constraint that prey distributions must be optimal does not directly lead to predictions, because the predator distribution is an unknown factor in this constraint. These indirect arguments can seem unintuitive; the situation is reminiscent of population dynamic models such as the Lotka-Volterra system, where e.g. the equilibrium prey abundance is found by requiring that the predator growth rate vanishes. Similar indirect effects appear also in single-species optimization models; for example, Fiksen and Jørgensen (2011) found that the growth rate of a fish larvae was largely independent of the abundance of its planktonic food, whereas its mortality decreased with food availability due to behavioral adaptation.

The model makes a number of more detailed predictions about the nature of the deep scattering layer and the diel vertical migrations of predator and prey: First, predators concentrate slightly higher in the water column than do the prey. There is not much data to determine if this prediction is in agreement with actual behaviour or not, although some indication of this is visible in (Josse et al, 1998). Moreover, prey abundance should increase with increasing depth, until it drops discontinuously to zero. We would not expect such a discontinuity in real data, where more than two species interact, intraspecific variability between individuals exists, and animals are imperfect decision makers. Despite these differences between reality and the idealised model, acoustic observations of the scattering layer typically show fairly sharp edges of the layer (Klevjer et al, 2016).

The model predicts relatively small fluctuations in mean light levels, i.e. each animal stays fairly close to a given isolumen. This is consistent with empirical findings. However, details in the parameters - and in particular, the decrease in growth rates compared with the attenuation of light - determine if the animals are predicted to be found in lighter regions during the day than during the night, or the converse.

An interesting prediction from the model is that a significant part of trophic encounters take place around dawn and dusk, a well-known phenomenon across many systems. In the model, the reason for this is that the prey are inclined to stay in the mixed layer and benefit from the higher growth rates even at the onset of dawn, resulting in increasing encounter rates. At some point the light reaches a critical level where the prey evacuate the mixed layer, resulting in decreased growth as well as decreased encounter rates. Thus, the model explanation for feeding at dawn and dusk is the stratification of the

water column, and not dynamics of migration or of digestion, since these components are absent in our model.

Beyond supplying a mechanistic explanation for a striking phenomenon in the oceans with global implications, one can envision that the model can predict how changes in parameters lead to changes in vertical distributions and migration patterns. This offers the potential of investigating how environmental change leads to changes in behaviour and thus changes in trophic couplings as well as system-level rates such as carbon sequestration. We note that animal behavior is a key component in the ecosystem dynamics, and that the adaptive nature of this behavior is rarely included in coarse-scale ecosystem models. Here, we have examined the effects of varying the predator abundance. Some of these effects appear obvious, e.g., that the prey migrate deeper as predators become more abundant, while it is more surprising that the prey's mortality depends non-monotonically on the predator abundance. This emergent interference competition between predators is a reminder that the dynamics of populations emerge from the decisions made by individuals, and that behavioural adaptations imply that mass-action analogies can be misleading.

At a technical level, the main contribution of the current work has been to extend previous game-theoretic models of vertical distributions in the oceans to continuous time and continuous space. This required novel methods for resolving the game, combining analytic reasoning with numerical computation, i.e. sections 2.1 and 2.2. The framework allows us to pose mechanistic model components for the variation in detection distance as function of time and depth, and thus to let encounter rates be given by light availability. This yields predictions applicable to a particular geographical location and date, of characteristics such as how the vertical range varies during the day. This in turn allows a more direct comparison of model predictions with data such as acoustic surveys or depth measurements from individual predators. While this contribution has focused on the theoretical development and generic predictions, future works should focus on specific systems and more quantitative comparisons of model predictions and data.

The model we have proposed is simplistic and generic, and it is possible to envision multiple extensions. Firstly, the model postulates a fixed growth rate of the prey. An obvious extension is to include further trophic levels, for example to mimic a system comprised of zooplankton, forage fish, and a top predator. We note that Hugie and Dill (1994) recommended four trophic levels. For such a model, an interesting question is when the trophic levels migrate in phase, and when e.g. the zooplankton will migrate in counterphase.

The model includes a local type I functional response. An interesting extension would be to include density dependent effects at each layer. A type II functional response in uptake rate - modelling prey

handling time - will give the prey a further incentive to aggregate. For some prey species including sprat, the phenomenon of diel vertical migrations occurs simultaneously with schooling (Nilsson et al, 2003), which changes the game even further. A type II functional response, where the saturation is caused by handling times, can easily be included in the model. However, if the explanation of the saturation is the capacity of the gut and digestion times, then the model must be extended with gut fullness as a state variable.

Similarly, the vertical position of each animal is not a state variable in our model: At each instant, the animal is free to choose any vertical position, and the cost of swimming is not included in the fitness. We note that the predicted maximum vertical swimming speeds from section 3.2, viz. 0.2 m/s, are unnoticeable for a predator such as a tuna. In contrast, Dypvik et al (2012) observed maximum swimming speeds of individual glacier lanternfish around 0.18 m/s, while the speeds of the layers were a factor 5 smaller. Although these observed swimming speeds are comparable to our predictions, we hypothesize that the difference between the observed speed of the individual and that of the population indicates that these animals are not limited by swimming speeds in their vertical migrations. For even smaller prey such as krill, limits on swimming speeds and the cost of swimming are likely to affect vertical migrations: For the centimeter-sized *Euphausia pacifica*, Torres and Childress (1983) found that swimming at 1-2 body lengths per second doubled the oxygen requirements compared to rest. Also, in a model study of optimal vertical migration for copepods, Hansen and Visser (2016) predicted that larger animals migrate further than smaller animals, because the relative importance of locomotion costs decreases with increasing size. Thus, we argue that costs and constraints on migrations are a factor for planktonic prey but less so for fishes, and therefore that our model applies to predator-prey interactions among fishes but less so to the planktonic domain. An extension of our model framework would be to include the vertical position as a dynamic state variable and the vertical velocity as a decision variable. This would turn the model into a deterministic mean field game (Lasry and Lions, 2007), for which the analysis would be much more demanding.

Finally, an interesting topic of future work would be to parametrize the model for specific systems. Interesting systems to investigate would be basking sharks feeding on zooplankton (Sims et al, 2005), Southern Bluefin Tuna or Bigeye Tuna feeding on the various species that compose the Deep Scattering Layer, or mackerel feeding on capelin in the North Atlantic. To calibrate the model for a particular system, the critical component is the growth potential of the prey at different depths. It would be possible to calibrate the model against acoustic surveys of prey biomass, and against the vertical movements of the predators as observed with electronic tags including depth measurements.

5 Conclusion

We have proposed a generic game between predators and prey where the key ingredients are the way the prey growth rate depends on depth, as well as how the clearance volume of the predators depends on time and depth. The optimal strategies, identified as the Nash equilibrium, feature distinct deep scattering layers which perform diel vertical migrations. With little calibration, the model reproduces striking observed patterns, and it thus provides a mechanistic explanation for these remarkable phenomena, even if formulated generically. The model makes further predictions which match observed patterns in the global oceans, such as the diel fluctuations in trophic encounter rates. The model can be used to examine how the total growth rate and mortality of predators and prey depend on system parameters, and we have shown that in some situations, increasing the predator abundance results in a decreased mortality experienced by the prey.

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