Co-adaptive behavior of interacting populations in a habitat selection game significantly impacts ecosystem functions

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Abstract

Individuals of different interacting populations often adjust to prevailing conditions by changing their behavior simultaneously, with consequences for trophic relationships throughout the system. While we now have a good theoretical understanding of how individuals adjust their behavior, the population dynamical consequences of co-adaptive behaviors are rarely described. Further, mechanistic descriptions of ecosystem functions are based on population models that seldom take behavior into account. Here, we present a model that combines the population dynamics and adaptive behavior of organisms of two populations simultaneously. We explore how the Nash equilibrium of a system – i.e. the optimal behavior of its constituent organisms – can shape population dynamics, and conversely how population dynamics impact the Nash equilibrium of the system. We illustrate this for the case of diel vertical migration (DVM), the daily movement of marine organisms between food-depleted but safe dark depths and more risky nutrition-rich surface waters. DVM represents the archetypal example of populations choosing between a foraging arena (the upper sunlit ocean) and a refuge (the dark depths). We show that population sizes at equilibrium are significantly different if organisms can adapt their behavior, and that optimal DVM behaviors within the community vary significantly if population dynamics are considered. As a consequence, ecosystem function estimates such as trophic transfer efficiency and vertical carbon

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export differ greatly when fitness seeking behavior is included. Ignoring the role of behavior in multi-trophic population modeling can potentially lead to inaccurate predictions of population biomasses and ecosystem functions.

1   Introduction

A central challenge in mechanistic ecological modelling is to predict how the functioning of ecosystems will respond to global change (Steffen et al. 2018, Kiørboe et al. 2018). This requires a sound theoretical basis for not only how populations respond numerically to change, but also how they may adapt behaviorally (Schmitz et al. 2008, Sih et al. 2011). In essence, this calls for ecosystem models to simultaneously capture processes that take place at very different time scales: notably the time scale at which individual organisms behave, the time scale at which populations interact with each other and fluctuate in abundance, and the evolutionary time scale at which traits or species emerge or go extinct (Křivan and Cressman 2009). It is well known that the processes at one time scale can have phenomenological effects at other time scales (Pelletier et al. 2009, Schoener 2011). However, modelling these time scales conjointly proves difficult, especially if several interacting populations are involved, with the result that the implications of co-adaptive behavior on ecosystem function remains largely unexplored.

For a single species, the link between behavioral and population time scales is fairly well established, usually by allowing individuals to optimize a specific behavior (e.g. Lima 1985, Houston et al. 1993, Titelman and Fiksen 2004, Visser et al. 2012). Adaptive behavior can have various theoretical consequences such as reducing a food-chain length (Kondoh and Ninomiya 2009), promoting coexistence of prey (Křivan and Sikder 1999), altering the stability of a system (Abrams 2007, Křivan and Cressman 2009, Visser et al. 2012) or changing the amplitude of population cycles (Křivan 2007). Multiple interacting populations increases complexity as different populations can evolve simultaneously or adapt their behavior in response to the reciprocal responses adopted by other populations to which they are trophically linked. This mutual inter-dependence of individual responses is usually solved by finding the Nash equilibrium of the system (Iwasa 1982, Hugie and Dill 1994, Bouskila 2001). While Nash equilibria are Evolutionary Stable Strategy

(ESS) in single-species systems, for multiple-species systems the Nash equilibrium may not satisfy ESS stability criteria (Křivan et al. 2008). Therefore, we only refer to Nash equilibria in the following. Evolutionary game theory assesses how the frequency of traits (or strategies) in a population evolves, but rarely quantifies the consequences for emerging population dynamics which generally only receives a qualitative mention (Brown et al. 1999, Bouskila 2001, Pinti and Visser 2019). We therefore need a theoretical framework that is able to scale from the behavior of individuals from multiple trophic levels to the dynamics of multiple populations and ecosystems. This is different than adaptive dynamics (Metz 2012), as adaptive dynamics considers that population dynamics are at steady state and resolves evolution, while we instead assume that behavioral strategies evolve slowly and resolve the population dynamics.

Merging individual and population time scales (and to some extent evolutionary time scales) for a multi-species system leads to population game theory (Cressman et al. 2004). Specifically, at the fastest time scale, individuals behave adaptively to optimize their behavior in terms of Darwinian fitness. They do so in responses to both the abundance of conspecifics, predators and prey (density dependence) as well as the various strategies these players adopt (frequency dependence). The rationale here is that evolution has equipped individuals with rules that provide an optimal behavior in any given situation. Evolution shaped these optimal behaviors rather slowly, but individuals can react and adapt their behavior much faster than population evolves. The ensuing population dynamics then follow Lotka-Volterra dynamics. Most population game theory studies have focused on a predator and one or two prey in a two-patch environment, where prey and/or predators can adapt their behaviors (Křivan and Sikder 1999, Křivan and Schmitz 2003, Cressman et al. 2004, Křivan 2007, Křivan and Cressman 2009, Cressman and Křivan 2010). How behavior and population dynamics interact in realistic systems where both multiple trophic levels and multiple behavioral strategies are possible remains unresolved. Perhaps more critical and less well understood, are the controls these interactions have on emergent ecosystem functions.

In this work we explore how the Nash equilibrium of a system – i.e. the optimal behavior of its constituent organisms – can shape population dynamics, and conversely how population dynamics impact the Nash equilibrium of the system. We explore the systematic differences in ecosystem functions that are predicted by models depending on the aspects of behavior that are considered in the simulations. We illustrate the effect in a marine pelagic ecosystem, where Diel Vertical Migration (DVM) is a conspicuous behavior, played out across several trophic levels, that can be posited to have significant impact on key ecosystem

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functions of trophic transfer efficiency and carbon sequestration in the deep ocean. Specifically, DVM is a feature of marine and aquatic ecosystems, where significant fractions of various populations feed in surface waters at night, and retreat to depth during daylight hours (Mehner and Kasprzak 2011, Klevjer et al. 2016, Ohman and Romagnan 2016). The proximate rationale is a trade-off between predation risk and feeding opportunity, from which optimal migration pattern can be estimated (Giske and Aksnes 1992, Rosland and Giske 1994, Titelman and Fiksen 2004). However, one migrating population has knock-on effects on other populations with each seeking its own optimal DVM strategy. Placing the trade-offs into a game theoretic context provides estimates of the DVM patterns employed by multiple players as they jockey for advantage (Iwasa 1982, Hugie and Dill 1994, Sainmont et al. 2015, Thygesen and Patterson 2018, Pinti and Visser 2019, Pinti et al. 2019). The emerging inter-related behavioral network is characterised by a Nash equilibrium where the behavior of each individual is optimized, and where the default of any one player reduces its fitness.

We consider a tri-trophic food chain consisting of a phytoplankton resource, a zooplankton consumer and a visual predator, the last two playing against each other in a water column by adjusting their vertical position at day and at night. Using population game theory, we incorporate the plasticity of rational behaviors (i.e. each animal changes its migrating strategy to behave optimally at all times) in predator-prey dynamics, effectively reconciling the individual and population time scales for a game played out between two populations in multiple arenas. This allows us to compare population sizes with and without games, behavior of populations computed with or without population dynamics, and the resulting ecosystem function estimates. Our model is cast in terms of DVM between a zooplankton prey and a fish predator population, but we stress that given proper mechanistic descriptions, our method can be adapted to any multi-population multi-arena setting where all considered populations have varying behavior and population sizes.

2   Methods

We consider a tri-trophic chain (made of a resource (phytoplankton), a consumer (zooplankton), and a predator (fish)) and two time scales: the behavioral time scale, and the population time scale. We investigate three different models: model A considers only the behavioral time scale, model B considers only the population time scale, and model C considers both the behavioral and the population time scale.

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The organisms reside in a water column divided into M water layers. For models A and C, days are divided into two periods: daylight hours (a fraction σ of the time) and night ($1 - \sigma$ of the time). Phytoplankton cannot perform diel vertical migration, whereas zooplankton and visual predators can adapt their position at day and at night (DVM strategy) to maximise their fitness.

Model A derives the optimal behavior of zooplankton and fish by computing the Nash equilibrium of the system following Pinti and Visser (2019), with the exception that phytoplankton are an explicit resource grazed upon by zooplankton.

Model B is a simple 1D water column model of the population dynamics. In this model, we allow phytoplankton, zooplankton and fish to grow according to Lotka-Volterra equations. We do not consider population exchanges or diffusion between the different water layers, and phytoplankton grow following a chemostat. Their carrying capacity as well as their instantaneous growth rate are depth-dependent, to mimic the effects of light in the water column.

Model C combines models A and B: on a fast time scale, zooplankton and fish change their behavior as to always behave following their Nash equilibrium. On a slower time scale, population sizes vary similarly to model B, following Lotka-Volterra dynamics.

2.1 Model A

Model A refers to the model where organisms have an adaptive behavior, but where population sizes are fixed, similar to most game theoretic studies. Here, we fixed the consumer concentration to $N = 100\text{m}^{-3}$ and the predator concentration to $P = 1\text{m}^{-3}$. All parameters used are summarized in table 1. Most of the following equations are taken from Pinti and Visser (2019), and tailored to fit with our explicit description of the phytoplankton resources. For simplicity and readability, we drop the time dependencies of all variables, and i and j can either refer to a specific water bin (when used as an index) or to its corresponding depth (when used as a function variable).

We define the strategy matrices $\mathbf{n} = n_{ij}$ and $\mathbf{p} = p_{ij}$ as the frequency of the prey and predator population respectively, that follows strategy ij, i.e. being in layer j during day and i during night. By definition, we have:

$$\sum_{i=1}^{M}\sum_{j=1}^{M} n_{ij} = \sum_{i=1}^{M}\sum_{j=1}^{M} p_{ij} = 1, \tag{1}$$

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with M the number of layers in the water column. If N and P are the mean concentration of prey and predators in the water column (in m^{-3}), the prey concentration in layer j during daytime is:

$$N_{j,day} = MN \sum_{i=1}^{M} n_{ij}, \tag{2}$$

with similar expressions for predator and for nighttime concentrations. The clearance rate (i.e. the volume swept per unit of time when foraging) g of prey is constant as zooplankton are non-visual consumers, but the clearance rate b of visual predators varies with light levels, and thus with depth:

$$b(day, z) = \frac{L_{max} \exp(-\kappa z)}{L_0 + L_{max} \exp(-\kappa z)},$$
$$b(night, z) = \frac{\rho L_{max} \exp(-kz)}{L_0 + \rho L_{max} \exp(-\kappa z)}, \tag{3}$$

with L_{max} the daytime irradiance at the surface, κ the light attenuation coefficient of water, L_0 the half-saturation light intensity and ρ the attenuation coefficient between day and night. z represents depth, with $z = 0$ the surface and $z = z_{max}$ the maximum depth of the water column.

Fitness is defined as the difference between specific growth and potential mortality over a 24h cycle. The day-averaged growth rate of plankton is the integral of its growth rate, so the sum of its growth rate during daytime and during nighttime. For prey, growth is equal to:

$$G_{ij}^{N} = \varepsilon_N \frac{M_\varphi}{M_N} g \left[\sigma \varphi(j) + (1 - \sigma) \varphi(i) \right] - C(i, j), \tag{4}$$

with φ the resource concentration (varying with depth but not time in this model), $C(i, j)$ the migration cost between layer i and j, taken equal to $2c\Delta z|i - j|$, Δz the width of a bin and c the cost to migrate 1 m, ε_N the assimilation efficiency of zooplankton and $\frac{M_\varphi}{M_N}$ the weight ratio of phytoplankton and zooplankton organisms. For such strategy ij, the corresponding mortality risk is:

$$D_{ij}^{N} = MP \left[(1 - \sigma)b(night, i) \sum_{k=1}^{M} p_{ik} + \sigma b(day, j) \sum_{k=1}^{M} p_{kj} \right] - \mu, \tag{5}$$

with μ a background mortality rate. The mortality risk for prey is conversely a component of the predator's growth rate. For strategy ij, if we call η the conversion efficiency between prey and predator, the predator

growth rate is then:

$$G_{ij}^P = \eta MN \left[\sigma b(day, j) \sum_{k=1}^{M} n_{kj} + (1-\sigma) b(night, i) \sum_{k=1}^{M} n_{ik} \right] - C(i,j). \qquad (6)$$

The density-dependent mortality rate of predators reflects reduced fitness at high abundances to mimic possible interference with each other and attraction of top predators at high concentration (Hixon and Carr 1997, Pinti and Visser 2019), and is as follow:

$$D_{ij}^P = \mu_0 MP \left[\sigma \sum_{k=1}^{M} p_{kj} + (1-\sigma) \sum_{k=1}^{M} p_{ik} \right]. \qquad (7)$$

The fitness of prey is then $F_{ij}^N = G_{ij}^N - D_{ij}^N$, with a similar expression for the predator fitness F^P. The Nash equilibrium of the system is found using the replicator equation (Schuster and Siegmund 1983, Hofbauer and Sigmund 2003). In short, each strategy is allowed to grow proportionally to its fitness, before renormalization of the strategy matrices to ensure that condition 1 is satisfied.

$$\begin{cases} n'_{ij}(\tau + \Delta\tau) &= n_{ij}(\tau) \cdot (1 + \Delta\tau F_{ij}^N(\tau)), \\ p'_{ij}(\tau + \Delta\tau) &= p_{ij}(\tau) \cdot (1 + \Delta\tau F_{ij}^P(\tau)). \end{cases} \qquad (8)$$

$$\begin{cases} n_{ij}(\tau + \Delta\tau) = \dfrac{n'_{ij}(\tau + \Delta\tau)}{\sum_k \sum_l n'_{kl}(\tau + \Delta\tau)}, \\ p_{ij}(\tau + \Delta\tau) = \dfrac{p'_{ij}(\tau + \Delta\tau)}{\sum_k \sum_l p'_{kl}(\tau + \Delta\tau)}. \end{cases}$$

$\Delta\tau$ is a factor selected to keep the increase or decrease of strategy frequencies within reasonable limits at each iteration. It is chosen at each iteration according to:

$$\Delta\tau = \frac{\lambda}{\max(|F^N|, |F^P|)}. \qquad (9)$$

As a practical compromise, we chose $\lambda = 0.1$. For all simulations, equilibria were reached before $2 \cdot 10^6$ time steps. In general, the replicator equation can lead to several Nash equilibrium depending on initial conditions. We tested for this by using different initial conditions. This never led to different Nash equilibria, and the results presented here are independent of the initial conditions.

Model A has polymorphic-monomorphic equivalency (Broom and Rychtář 2014), meaning that the matri-

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ces **n** and **p** indicate the frequency distribution of strategies but not how these distributions arise: organisms could play a pure strategy (polymorphic population), or they could all play the same mixed strategy (monomorphic population), or any combination in between these two configurations – as long as the population-level strategy is equal to **n** and **p**. The proof of this equivalency provided by Pinti and Visser (2019) is valid in our case, as their model is similar to this one.

2.2 Model B

Model B refers to a simple 1D tri-trophic model, considering population dynamics but not the behavior of the different organisms. This model does not include light cycle nor organism migrations, so that the dynamics in all layers are essentially independent. The differential equations governing phytoplankton, zooplankton and fish dynamics are:

$$
\begin{aligned}
\frac{\partial \varphi}{\partial t} &= r(z) \left(1 - \frac{\varphi(z,t)}{K(z)} \right) \varphi(z,t) - \frac{M_\varphi}{M_N} g N(z,t) \varphi(z,t), \\
\frac{\partial N}{\partial t} &= \varepsilon_N \frac{M_\varphi}{M_N} g N(z,t) \varphi(z,t) - m_0(z) N(z,t) P(z,t) - \mu N(z,t), \\
\frac{\partial P}{\partial t} &= \varepsilon_P m_0(z) N(z,t) P(z,t) - \mu_0 P(z,t)^2 - \mu_1 P(z,t),
\end{aligned}
\tag{10}
$$

where r is the depth-dependent growth rate of phytoplankton, K its depth-dependent carrying capacity, g the clearance rate of zooplankton and m_0 the clearance rate of fish defined as $b_{max} \exp(-\kappa z)$. The quadratic mortality term for fish $-\mu_0 P(z,t)^2$ tends to stabilize oscillatory behaviors (Steele and Henderson 1992). To mimic the growth description of zooplankton in Pinti and Visser (2019), the carrying capacity of phytoplankton is set as:

$$
K(z) = \frac{K_0}{2} \left(1 - \tanh \left(\frac{z - z_0}{z_s} \right) \right),
\tag{11}
$$

with K_0 the surface carrying capacity, z_0 the depth of the mixed layer and z_s the thickness of the transition zone to a depleted layer. The growth rate $r(z)$ of phytoplankton depends on light:

$$
r(z) = r_0 \exp(-\kappa z),
\tag{12}
$$

with r_0 the surface growth rate.

The equilibrium distributions can then be derived analytically, and are at each level (if we omit for readabil-

187 ity the dependencies on time and depth)

$$\overline{N} = \frac{r\mu_0 \left(\varepsilon_N \frac{M_\varphi}{M_N} gK - \mu + m_0\mu_1/\mu_0\right)}{\varepsilon_P m_0^2 r + \varepsilon_N \frac{M_\varphi^2}{M_N^2} g^2 K \mu_0},$$

$$\overline{P} = \frac{\varepsilon_P m_0 \overline{N} - \mu_1}{\mu_0}, \tag{13}$$

$$\overline{\varphi} = \frac{m_0 \overline{P} + \mu}{\varepsilon_N \frac{M_\varphi}{M_N} g}$$

188 if all populations co-exist,

$$\overline{\varphi} = \frac{\mu}{\varepsilon_N \frac{M_\varphi}{M_N} g},$$

$$\overline{N} = \frac{r(1 - \overline{\varphi}/K)}{\frac{M_\varphi}{M_N} g} \tag{14}$$

189 if only phytoplankton and zooplankton are present, and

$$\overline{\varphi} = K \tag{15}$$

190 if only phytoplankton is present in the system.

191 In the particular case of an enrichment setting where the carrying capacity K of phytoplankton increases,

192 the system consecutively admits only phytoplankton, phytoplankton and zooplankton, and all three species.

193 The transition from one regime to the next can be derived analytically. Zooplankton appear at:

$$K_1 = \frac{\mu}{\varepsilon_N \frac{M_\varphi}{M_N} g}, \tag{16}$$

194 and visual predators at:

$$K_2 = \frac{\varepsilon_P \mu r m_0}{\varepsilon_N \frac{M_\varphi}{M_N} g \left[\varepsilon_P m_0 r - \mu_1 \frac{M_\varphi}{M_N} g\right]}. \tag{17}$$

195 The consecutive appearance of the three regimes depends on the set of parameters chosen, and happens

196 only if $0 < K_1 < K_2$. With our set of parameters, we have $K_1 = 30$ and $K_2 = 30.001$, making the second

197 regime indistinguishable in the figures.

2.3 Model C

199 Model C combines models A and B to consider both behavior and population dynamics. In essence, we

200 start by computing the Nash equilibrium in the strategy space as in model A, before updating the popula-

201 tion sizes as in model B. At the behavioral time scale, we assume that processes are going much faster than

202 at the population time scale, so the system should always be at equilibrium before any change at the pop-

203 ulation time scale takes place. The clearance rate of zooplankton on prey (i.e. the volume of water swept

204 by a foraging zooplankton per unit of time) is chosen such that the corresponding zooplankton growth rate

205 when the resource is at its carrying capacity K_0 is equal to the growth rate of zooplankton at the surface

206 in Pinti and Visser (2019). Zooplankton also suffer a low background mortality rate, to ensure that the

207 absence of food drives them to extinction even without predation. The details of the game dynamics and

208 the fitness definition are similar to model A. We call F^N (resp. F^P) the prey (resp. predator) fitness at the

209 Nash equilibrium. We can define one such value for all organisms as, by definition of the Nash equilibrium,

210 all organisms from the same population have the same fitness. Since phytoplankton have no behavior, their

211 fitness is of no interest other than in population dynamics.

212 At the population time scale, populations can grow and decay. Phytoplankton cannot change position, but

213 as they are grazed upon by zooplankton their population sizes can also change. For simplicity, we ignore

214 physical mixing between the different layers, and the concentration of phytoplankton in each layer is inde-

215 pendent from the other layers and follows a chemostat. The population sizes are updated following func-

216 tional responses type I:

$$
\begin{aligned}
\frac{\partial}{\partial t}\varphi(z,t) &= \varphi(z,t)\left(r(z)\left(1 - \frac{\varphi(z,t)}{K(z)}\right) - \sigma\frac{M_\varphi}{M_N}gN_{day}(z) - (1-\sigma)\frac{M_\varphi}{M_N}gN_{night}(z)\right) \\
\frac{d}{dt}N(t) &= N(t)F^N \\
\frac{d}{dt}P(t) &= P(t)F^P,
\end{aligned}
\tag{18}
$$

217 with r and K defined as in model B. Thereafter, the behavioral and population dynamic processes are

218 looped until steady state is reached, for both population sizes and migration strategies.

Table 1: Glossary of parameters.

Parameter	Description	Value	Unit
t	Time	-	day
z	Depth	-	m
M	Number of water layers	30	-
Δz	Thickness of depth bins	10	m
z_{max}	Total depth of the water column	$M \cdot \Delta z = 300$	m
σ	Fraction of daylight hours per day	0.65	-
$N_{day/night}(z,t)$	Concentration of prey during day (night) at depth z	eq. 2	m^{-3}
$P_{day/night}(z,t)$	Concentration of predator during day (night) at depth z	eq. 2	m^{-3}
$\varphi(z,t)$	Concentration of resources at depth z	eq. 18	m^{-3}
$N(t)$	Mean prey concentration in the water column	eq. 18	m^{-3}
$P(t)$	Mean predator concentration in the water column	eq. 18	m^{-3}
$\overline{\varphi}, \overline{N}, \overline{P}$	Equilibrium concentrations	eq. 13, 14, 15	m^{-3}
$K(z)$	Carrying capacity for phytoplankton	eq. 11	m^{-3}
K_0	Surface carrying capacity for phytoplankton	10^4	m^{-3}
z_0	Mixed layer depth	50	m
z_s	Sharpness of the transition zone	10	m
$r(z)$	Growth rate of phytoplankton	eq. 12	day^{-1}
κ	Light attenuation coefficient of water	0.07	m^{-1}
r_0	Maximum growth rate of phytoplankton	1	day^{-1}
$F_N(t)$	Fitness of the prey population at time t	-	day^{-1}
$F_P(t)$	Fitness of the predator population at time t	-	day^{-1}
$F_{ij}^N(t)$	Fitness of prey following strategy ij at time t	-	day^{-1}
$F_{ij}^P(t)$	Fitness of predator following strategy ij at time t	-	day^{-1}
g	Clearance rate of zooplankton	10^{-1}	$m^3 day^{-1}$
$\frac{M_\varphi}{M_N}$	Weight ratio between phytoplankton and zooplankton	0.01	-
δt	Time step	0.01	day

Table 1 – continued from previous page

Parameter	Description	Value	Unit
$\mathbf{n} = n_{ij}$, $\mathbf{p} = p_{ij}$	Frequency matrix of prey (predator) strategies	-	-
$\tau, \Delta\tau$	Time and time steps of the replicator dynamics	-	-
λ	Factor for the increase rate of the replicator equation	0.1	-
b	Predator clearance rate	eq. 3	$\mathrm{m^3 day^{-1}}$
L_{max}	Surface irradiance during daytime	100	$\mathrm{W\,m^{-2}}$
L_0	Half-saturation light intensity for visual predators	1	$\mathrm{W\,m^{-2}}$
ρ	Fractional difference between day and night light levels	10^{-3}	-
G_{ij}^N, G_{ij}^P	Growth rate of prey (predators)	eq. 4 and 6	$\mathrm{day^{-1}}$
D_{ij}^N, D_{ij}^P	Mortality rate of prey (predators)	eq. 5 and 7	$\mathrm{day^{-1}}$
$C(i,j)$	Migration cost for strategy ij	$2c\Delta z|i-j|$	$\mathrm{day^{-1}}$
c	Cost to migrate 1m	10^{-5}	$\mathrm{m^{-1} day^{-1}}$
μ	Background mortality rate of prey	0.01	$\mathrm{day^{-1}}$
μ_0	Density-dependent mortality rate of predators	10^{-3}	$\mathrm{m^3 day^{-1}}$
μ_1	Mortality rate of predators	10^{-3}	$\mathrm{day^{-1}}$
ε_N	Zooplankton assimilation efficiency	$1/3$	-
ε_P	Fish assimilation efficiency	$1/3$	-
η	Predator growth efficiency	10^{-2}	-
m_0	Clearance rate of fish for zooplankton	$b_{max}\exp(-\kappa z)$	$\mathrm{m^3 day^{-1}}$
b_{max}	Clearance rate of fish at the surface	-	$\mathrm{m^3 day^{-1}}$
TTE	Trophic transfer efficiency	eq. S1	-
C_{exp}^X	Active carbon export mediated by X	eq. S2	$\mathrm{gC\,m^{-2} day^{-1}}$
X_{migr}	Fraction of DVM migrants between the epipelagic and the depths	eq. S3	-
ε_D	Fraction of ingested food egested	$1/3$	-
τ_D	Fraction of food ingested at the surface egested at depth	$1/2$	-
$m_{c,\varphi}$	Carbon weight of a resource	10^{-8}	gC
$m_{c,N}$	Carbon weight of a consumer	10^{-5}	gC

Table 1 – continued from previous page

Parameter	Description	Value	Unit
$I_X(z,t)$	Ingestion rate of an individual X	-	day^{-1}

2.4   Simulations

We recreate an enrichment experiment Oksanen et al. (1981), where we increase the resource carrying ca-
pacity. This simulation recreates a wide variety of environmental conditions, from oligotrophic to more
productive regions. We explore the response of the three models in terms of individual behaviors, popula-
tion dynamics and ecosystem functions (carbon export and trophic transfer efficiency). In addition, we also
discuss the behavior of the models when varying the predator clearance rate, to understand the counter-
intuitive patterns observed by Pinti and Visser (2019) at high clearance rates in a setting similar to model
A.

Definitions of the ecosystem functions used in the models are given in SI1.

The MATLAB code necessary to run these models is available on the following repository: `https://`
`gitlab.gbar.dtu.dk/jppi/Frequency-dependent_behavior_of_interacting_`
`populations_significantly_impacts_ecosystem_function.`

3   Results

We compare three models: adaptive behavior with fixed population sizes (model A), population dynamics
with fixed behavior (model B), and both behavior and population dynamics (model C). We explore the in-
fluence of the phytoplankton carrying capacity on the system. These three models are compared in terms of
two predicted ecosystem functions: trophic transfer efficiency and active carbon export flux.

3.1   Games with and without population dynamics

With fixed population sizes (model A), three migration regimes emerge (figure 1 a-b and figure S1 a-b-c-
d). At low resource carrying capacity, prey remain at depth at all times and predator are scattered through
the water column (figure S1 b-d). At intermediate values of the two parameters, prey exhibit DVM patterns

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and predators are scattered throughout the water column. Finally, at high resource carrying capacity, fish and zooplankton reside close to the surface with a high spatial overlap (figure 1 b). These results are dependent on the choice of population sizes. For example, a much higher predator population would create a higher pressure on prey that may consequently remain at depths for a much wider range of carrying capacities. The fixed population values ($N = 100$ m^{-3} and $P = 1$ m^{-3}) were chosen as to be in the range of population variations in model C.

The vertical distribution in model C allows only two regimes (figure 2). Counter to a model with fixed population sizes (model A, Pinti and Visser 2019), there is no complete depth residency, as organisms go extinct without feeding. In addition, population dynamics drives the emergence of prey DVM across most of their existence range (figure 2 and figure S1 a-c). Predators, in contrast, are scattered throughout the water column during the day and gather only during nighttime at the surface (figure 2 and figure S1 b-d). The fact that predators are scattered in the water column even where prey are absent (figure 2) is a consequence of the game theoretical approach. Predators all have the same fitness, whether they are scattered in the water column or at depth where prey are present during the day. Potential feeding benefits during daytime are too low compared to the density-dependent mortality that a gathering at depth would incur, hence organisms spread in the water column during daytime and focus on eating during nighttime at the surface, where their clearance rate is higher.

3.2   Population dynamics with and without games

Population sizes at equilibrium are considerably different when adaptive behavior is included or not (model B and C, figure 1 c-d-e). An adaptive behavior (model C) allows a wider range of coexistence for all three populations. Varying the phytoplankton carrying capacity (figure 1) exhibits an enrichment ladder, where successively higher trophic levels are admitted as productivity surpasses certain levels (Oksanen et al. 1981). Adaptive behaviors reduce the productivity levels necessary for the emergence of consumers and predators. The equilibrium population sizes at high carrying capacity are also different when considering adaptive behaviors: the resource biomass does not grow exponentially but saturates, causing the saturation of the zooplankton and fish biomass as well.
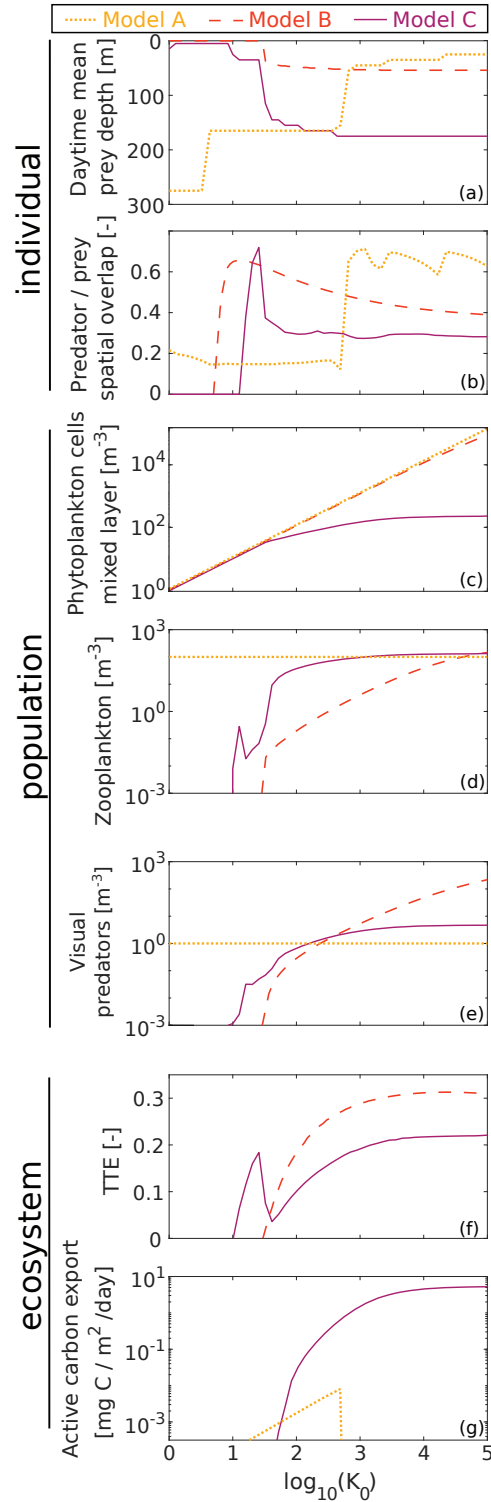
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Figure 1: (a) Day mean prey position, (b) Spatial overlap between predator and prey, (c) phytoplankton concentration in the mixed layer, (d) mean zooplankton concentration in the water column, (e) mean fish concentration, (f) trophic transfer efficiency and (g) active carbon export as a function of the phytoplankton carrying capacity. Yellow dotted lines for the model with only behavior (model A), red dashed lines for the model with no behavior considerations (model B) and plain purple lines are for the model where both behavior and population dynamics are considered (model C). For model A, population sizes are fixed at $N = 100 \text{ m}^{-3}$ and $P = 1 \text{ m}^{-3}$.
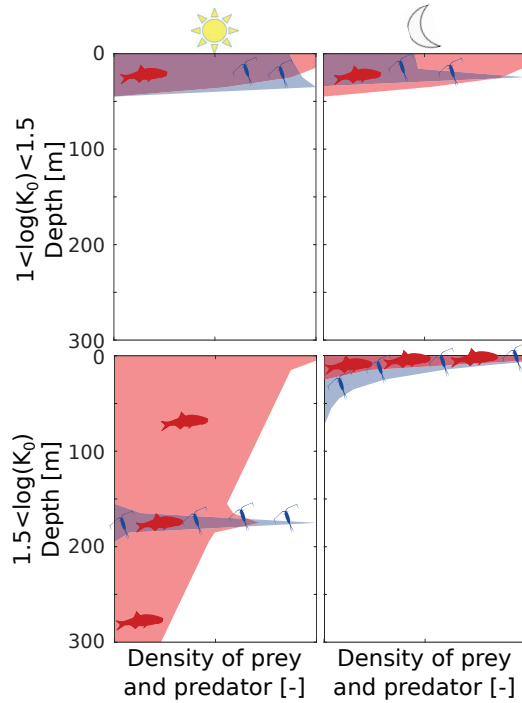
Figure 2: Two examples of typical vertical distribution of organisms during day and night for model C. Top panels: predation pressure is very low (beginning of the existence range of predators). Bottom panels: after $\log_{10}(K_0) = 1.5$, predation pressure is higher and prey perform DVM.

3.3 Trophic transfer efficiency

The trophic transfer efficiency (TTE) is very low when predator start to emerge (figure 1 f), but when considering behavior the TTE increases at first, falls down (when prey start to perform DVM, see figure 1 a) and then increases again as the the population sizes increase, to saturate around 0.22. The TTE of model B increases much slower, as the predator population needs a higher resource carrying capacity to establish. But the TTE saturates around 0.3, higher than for model C. This is because all energy is transferred to the higher trophic level (except for a small background mortality term), as zooplankton cannot defend themselves against predation by migrating deeper during daytime.

3.4 Carbon Export

As for TTE, the different models yield very different active carbon export estimates. Except when the predator starts to emerge, the active carbon export in model C (with population dynamics, figure 1 g) is higher than in model A (no population dynamics), because predators are more abundant (figure 1 e) and

because a more important fraction of the population performs DVM (figure S1).

At low phytoplankton carrying capacity (and high carrying capacity for the model A without population dynamics), the active export is null, either because the populations went extinct, or because they do not migrate and remain at depth or at the surface at all times.

4   Discussion

Our method successfully couples the effects of the behavioral and the population time scales on two populations. By considering the individual and population time scales, our model unravels effects at both time scales simultaneously. The results when considering both time scales are different than when a single time scale is considered, whether it be the individual or the population time scale. Crucially, our simulations demonstrate that an adaptive behavior alters ecosystem functions, something already proven experimentally in grassland meadows (Ovadia and Schmitz 2002). The trophic transfer efficiency (TTE) is lowered when adaptive behavior is considered, especially at high resource carrying capacity. This is because zooplankton mortality risk directly depends on the behavior adopted. The general top-down control of consumers, especially in productive areas (Hairston et al. 1960, Oksanen et al. 1981) seem to indicate that TTE would typically be reduced when consumer adopt an adaptive behavior as the incurred energy cost is lost for the next trophic level.

More generally, behavior can affect multiple ecosystem functions (trophic transfer, nutrient cycling and carbon export), and a failure to identify and consider possible adaptive behaviors may lead to severely biased estimates. Population games are an efficient way to couple behavior and population dynamics, and the method can be used to compute meticulously emergent ecosystem functions.

We framed our study as a game played out between predator and prey in a diel vertical migration context, but we stress that provided with adequate description of the population interactions our method can be tailored to reproduce other systems where the behavior and population dynamics of several populations are worth considering simultaneously – such as the adaptive behavior and trophic cascades in pond invertebrates (Start 2020), the succession of color morphs in a lizard species (Sinervo and Lively 1996), or the competition between owls and snakes preying on rodents (Bouskila 2001). More generally, previous studies pointed the importance of considering risk consequences in predator prey interactions (Lima and

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Bednekoff 1999, Lima 2002), and a more systematic inclusion of behavior in population dynamics and ecosystem functions studies would probably be beneficial to the mechanistic understanding of the systems in focus.

It is not straightforward to anticipate what happens at a time scale different from the ones resolved by the model, e.g. what behavior would emerge in the population from models without behavior implemented, or what happens at the population level from static games. A high or low fitness does not necessarily mean that a population will grow or go extinct, as behaviors can change and individuals can adapt to new constraints through density and frequency dependent effects with repercussions for the fitness of all other players in the system. For example, considering the behavior of individuals from a single population can have a range of consequences, such as relaxing the predation pressure on some species (Holt and Lawton 1994) or stabilizing the food-web structure (Kondoh and Ninomiya 2009). Non-consumptive effects of predation can also lead to physiological changes such as modified assimilation efficiency (Trussell et al. 2006, Thaler et al. 2012). In addition, a more realistic description of ecosystem processes would consider real time dynamics. Our study only considered population dynamics when the equilibrium was reached, but population sizes vary with seasonal cycles in nature. Implementing this game to describe real time dynamics requires considering these natural variations, but also reproductive output as well as life history strategies of the considered organisms.

Moreover, the evolutionary time scale (not explicitly considered in this work), would also be relevant for the system (Mitchell 2000), especially as predators can have important evolutionary roles in shaping up ecosystems despite having a marginal ecological importance (Brown and Vincent 1992). If we consider the evolution of the predator clearance rate as a trait (for example, through improved eye performances or increased swimming speed), because of frequency-dependent effects, the predator surprisingly does worse as it becomes more efficient – in the dynamic models (B and C) the population size decreases (figures S3 and S4). For an individual, it would always be beneficial to increase clearance rate providing a competitive edge over conspecifics, and as such, all individuals should evolve following red queen dynamics toward better performances (Dieckmann et al. 1995). In this light, the population will then drive itself to extinction, being, "too accomplished for their own good" (Pinti and Visser 2019). However, there are always constraints (Rosenzweig et al. 1987), and there is invariably some trade-off to balance (Stearns 1989). An increased eye capacity or swimming ability would, for example, come at the cost of an increased metabolic

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rate for predatory fish. As a consequence, there may be an optimum trait value for the clearance rate, which would ultimately control the state of our system.

There is also the real possibility that this trait optimization could lead to speciation. Conceivably, different subgroups of a polymorphic population (i.e. a population where different individuals can have different strategies) may diverge. In our illustrative example, for instance, polymorphism could lead to the emergence of two predator types, such as high light - low light specialists. Such considerations would provide insight into the types of traits and behavioral strategies expressed in a given community, with cascading consequences for biodiversity and ecosystem function estimates.

5   Conclusion

In addition to the abundance and diversity of its constituent species, the functioning of an ecosystem also depends on how its indigenous organisms behave. Particularly with regards to trophic interactions, behavioral strategies form an inter-connected network, predicated by game-theory and honed by evolution – the etho-web – where a small change in conditions can trigger a restructuring of behavioral strategies across large sectors of the ecosystem, precipitating a significant change in ecosystem function. We have demonstrated this for the pelagic ecosystem where daily cycles of risk and opportunity drive a rich mosaic of populations and behavioral strategies, and where predicted ecosystem functions show significant density and frequency dependence. For the case of the pelagic ocean, these dependencies impact directly on two of the most important ecosystem services of the global ocean, namely fisheries production and carbon sequestration. How such abundance-frequency dependencies play out in other ecosystems remains an open question, but we contend that trophic relationships almost invariably have co-evolved with behavioral strategies that mitigate risk and maximize opportunity for all individuals in their concurrent roles as competitors, predators and prey.

Conflict of interest

None to declare.

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