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Preface

This thesis has been prepared at the Department of Applied Mathematics and Computer Science, Technical University of Denmark in fulfilment of the requirements for acquiring the degree of Doctor of Philosophy.

The dissertation summarizes the work carried out by the author during his Ph.D. project. It started on 1st July 2019 and was completed on 30th September 2022. The Ph.D. project has been funded by the internal DTU Compute scholarship and the Centre for Ocean Life at DTU Aqua.

The thesis is composed of 4 chapters which summarize the three attached scientific papers, 1 of which have been peer-reviewed and published, 1 of which has been submitted to a peer-reviewed journal and 1 of which is in preparation.

30th of September, 2022

M. Maz

Maksim Mazuryn

Summary (English)

Diel vertical migration (DVM) is a daily migration between the depths and the surface of the sea on various scales in marine communities ranging from zooplankton to marine mammals. In DVM marine animals remain in deep, dark layers of a water column during daytime period to avoid encountering visual predators and migrate to shallow nutrient-rich regions at dusk to feed.

It is usually assumed that animals optimize some fitness functional and, thus, the interactions between the organisms should be modelled and understood using the game theoretical toolbox. For diel vertical migration the migrational patterns can be thought as strategies the animals select trying to optimize their biological fitness over lifetime period.

This PhD thesis develops a mean field game theoretical framework for expressing diel vertical migration as a vertical differential game the marine animals play against each other. Understanding these ecological games is of great importance to theoretical ecology, which helps predicting responses of the marine ecosystem to various changes in the ecological environment like climate change.

Summary (Danish)

Den daglige vertikal migration (DVM) er en migration mellem det dybe hav og havoverfladen, af marine grupper på tværs af hele størrelselspektret, fra zooplankton til havpattedyr. I den daglige vertikale migration forbliver de fleste dyr i de dybe mørke dele af vandsøjlen om dagen for at undgå visuel prædation, og om ved skumring migrerer de op til de næringsholdige dele af vandsøjlen nær overfladen.

Det er almindeligt at antage at dyr optimerer et funktionale der beskriver deres vækst, og derfor bør interaktionerne mellem dem forstås ved at benytte sig af værktøjskassen fra spilteori. I den daglige vertikale migration så kan bevægelsels mønstrene i migrationen forstås som strategier dyrene vælger for at optimere deres biologiske fitness over hele deres levetid.

Denne PhD afhandling udvikler en spilteoretisk tilgang der kan benyttes til at beskrive den daglige vertikal migration som et differntialspil som dyr i havet spiller mod hinanden. At forstår disse spil i økosystemer er af stor betydning for teoretisk økologi, da de kan benyttes til at forudsige effekten af diverse ændringer i miljøet så som klimaforandringer på økosystemer.

Acknowledgements

I would like to express my gratitude to my main PhD advisor, Uffe Høgsbro Thygesen, his guidance during the all PhD years, our inspiring discussions, his passion for research and genuine academic curiosity. I really appreciated provided academic freedom to explore tangent ideas while working on the PhD project, but also providing valuable and insightful feedback. I also want to thank my co-supervisors, Mirza Karamehmedović from DTU Compute and Andre Visser from DTU Aqua, for many interesting discussions during the 3 year period.

I would like to thank all my DTU colleagues, especially Mathias Blicher Bjerregård, Niclas Brok, Vladimir Dvorkin, Emil Friis Frølich, Rune Grønborg Junker, Adam Mielke, Nicolai Siim Larsen, Amos Schledorn and Justinas Smertinas for all of the great scientific (and not only) discussions over the PhD years.

Last but not least, I would like to thank my parents and my sister. I am so grateful for their unconditional support and encouragement during all the years.

Contents

Part I

Summary Report

CHAPTER 1

Introduction

1.1 Context and motivation

Two of the main objectives in theoretical ecology and the Centre for Ocean Life in particular are to develop a fundamental understanding of marine ecosystems and build predictive ecosystem models, that e.g. can predict how the marine ecosystems respond to increased fishing pressure or change of temperature due to climate change. Thus, one needs to know how population dynamics of marine organisms respond to these changes in the environment.

To make these concepts more specific, this PhD thesis focuses on diel vertical migration (DVM), a pronounced phenomenon constituting the largest daily movement of organisms on the planet Hays (2003) which is ubiquitous on various scales in marine communities from plankton to marine mammals Brierley (2014). DVM is a migration pattern when marine organisms remain in deep, dark layers of a water column during daylight hours to reduce encounter rate with visual predators and migrate to shallow depths with higher concentration of nutrients at dusk to feed. In this PhD dissertation only this form of diel vertical migration is modelled, though a so-called reverse DVM (dusk descent - dawn ascend) exists Sims et al. (2005). An example of the daily migration is shown in 4 echograms from different oceans in Figure 1.1.

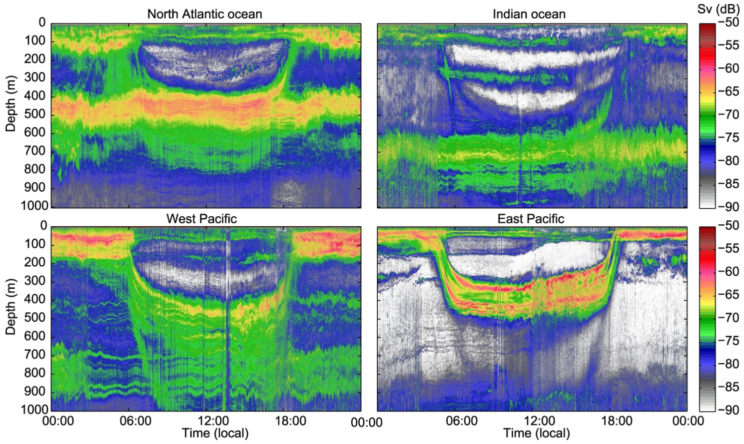

Figure 1.1: Echograms of a water column from different geographic regions spanning 24 hour period. Warmer colours indicate a higher concentration of biomass. The image has been taken from Klevjer et al. (2016).

Analysis of diel vertical migration in the thesis starts on the individual level, since the population dynamic is determined by the behavior of individuals in the populations. In theoretical ecology it is usually assumed that the individuals are fitness optimizing, which must be understood in game theoretic sense. Hence, the game theoretical toolbox is widely applied in ecological context and important biological phenomena like the evolution of cooperative behaviour among animals Maynard Smith (1982) have been explained using game theoretical analysis.

Game theory deals with interacting individuals in a conflict situation where each agent has a number of available choices and the final outcome or the received reward of the game depends upon the choices of all other players. Thus, every agent has an impact on the result of the interaction and the reward that she receives. By resolving ecological games like diel vertical migration one can determine emergent population dynamics, and predict responses to various changes in the ecological environment at ecosystem level.

Each marine organism performing diel vertical migration faces a trade-off between staying in a foraging arena with higher concentration of nutrients and avoiding predation risk at dark depths. The migration patterns can be rationalized as strategies, where each animal is considered as a player who tries to optimize its biological fitness over lifetime period subject to natural constraints like cost of locomotion between different depth levels in the water column. The marine ecosystems involve a large number of interacting agents, thus the area of mean field game theory is the central topic of the PhD dissertation.

Mean field game theory (MFG), originally outlined by Lasry and Lions around 2006-2007 in papers Lasry and Lions (2006a,b, 2007), generalizes traditional mean field theory from statistical physics which studies models from a "continuum limit" – by letting the number of particles go to infinity. In contrast to statistical physics studying particle ensembles, mean field game theory grants the individual particles choice and considers them as rational players. Each individual player maximizes some optimization criterion and the MFG theory studies large populations of interacting agents, potentially in the limit as the number of players goes to infinity $n \to +\infty$, and the structure of equilibria in these games.

Usually equilibrium behavior of a large number of particles is untraceable analytically. Thus, mean field game theory assumes that all the players are identical, meaning that they have the same state dynamics, share the same set of admissible strategies and have identical structure of the objective function. Every agent has access to the information about the structure of the population through, for example, empirical measure and has to make decisions based on statistical information about the surrounding environment as shown in Figure 1.2. In turn, decisions of each agent together influence the macroscopic properties of the whole population. These symmetry assumptions simplify analysis of the behaviour of a large population of rational agents in a equilibrium, a Nash equilibrium in particular for competing agents. Mean field game theory has a number of applications in economic theory and financial engineering modelling from financial market stability to the dynamics of the income distribution Carmona and Delarue (2018a,b), behaviour of crowds Carmona and Delarue (2018a) and emission control with carbon regulation design Carmona (2016).

The first work on game-theoretical modelling of diel vertical migration has been done in Iwasa (1982) where a habitat-selection matrix game model of DVM has been derived. The established results have been pushed further either by constructing games with more features Sainmont et al. (2013); Pinti and Visser (2019) or utilizing dynamic programming approach Mangel and Clark (1986); Fiksen and Giske (1995); Sainmont et al. (2015); Thygesen and Patterson (2019). But most of these models have discrete space or time domains, thus unable to provide high resolutions of the players' behaviour at dawn and dusk, when the migration between depth layers happens. The paper Thygesen and Patterson (2019) was a starting point of the PhD project and considers diel vertical migration in both continuous space and time, but ignoring the cost of motion.

Understanding the dynamics driving this large scale movement is important for modelling vertical transport of carbon from upper to deeper layers in a water

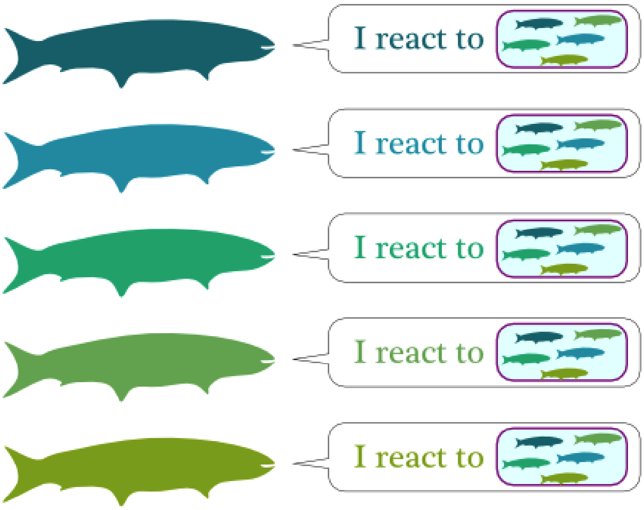

Figure 1.2: The mean field game theoretical type of interaction between agents in a population when each player sees aggregated statistical information (empirical measure, for example) about the whole population. Credit: `https://www.science4all.org`.

column, the so-called biological carbon pump phenomenon. Marine organisms moving vertically in a water column transport carbon between water layers, which has implications for the global carbon cycle and a better understanding of global climate Pinti et al. (2021); Hansen and Visser (2016). As the vertical migration influences the encounter rates between animals, DVM is also important for understanding fluxes through the food networks Thygesen and Patterson (2019).

Also, there is an emergent paradigm in theoretical ecology, namely that predictive ecosystem models should derived by assuming that individuals behave optimally. This PhD thesis explores the feasibility of this paradigm by considering the specific case of diel vertical migrations in the ocean.

1.2 Thesis outline

Chapter 2 presents the necessary theoretical scope for subsequent chapters to make the presentation self-contained. Five sections introduce the necessary overview of main theoretical results from game theory, calculus of variations, control theory, mean field game theory, numerical methods and provide main references for further details.

Chapter 3 summarizes the peer-reviewed scientific output of the three PhD subprojects. The first part of the chapter formulates diel vertical migration as a vertical differential game on the individual level for a so-called representative player. Subsequent chapters derive mean field systems for finding optimal vertical distribution in a water column as a Nash equilibrium.

Chapter 4 summarizes the main results of the PhD dissertation, discusses arised issues with the derived models and outlines perspective directions for future research.

CHAPTER 2

Preliminaries

This chapter covers the background material for presented papers in the next chapters of the PhD thesis to make the presentation self-sufficient. Overview of the main topics is presented and used references are provided.

2.1 Game theory

Classical game theory studies situations with interacting decision making agents who simultaneously maximize their own utility functions. A utility function, which is also called a pay-off, payment or gain function, is usually a real-valued function which reflects how “good” or “bad” is an outcome of the game for an agent. More formally, a utility function for a n-player game can be defined in the following way:

DEFINITION 2.1 In a game with n interacting players, each with a corresponding finite set $\mathcal{A}_i$ of admissible strategies, a utility function u_i is a mapping between the set of all n-tuples of admissible strategies into real numbers:

$$\begin{aligned} u_i : \mathcal{A}_1 \times \mathcal{A}_2 \times \ldots \times \mathcal{A}_n &\to \mathbb{R}, \\ (\alpha_1, \alpha_2, \ldots, \alpha_n) &\mapsto u_i(\alpha_1, \alpha_2, \ldots, \alpha_n). \end{aligned} \tag{2.1}$$

The utility function (2.1) can be external to the player as a reward for winning in a game, financial gain or probability of survival during a day; or it can be internal as the agent's own preference or satisfaction of an outcome of a game.

Game theory models and analyses the behavior between interacting decision makers. Each player in the game has its own goals as well as trade-offs, which can be conflicting with other players' objectives, and the decision of each agent affects the total outcome for all the interacting agents. This is the main feature which distinguishes game theory from classical optimization theory.

The interaction structure between the agents divides game theory into two major subfields: *cooperative* games, where the players can agree on coordinated actions to achieve their goals, and *noncooperative* games with the agents play independently of each other. The main focus of this thesis is to model diel vertical migration of marine organisms as a noncooperative game in the limit when the number of players $n \to +\infty$ with infinitely many feasible strategies.

2.1.1 Nash equilibrium

Game theory considers players as a group of rational interacting agents who individually try to find an advantageous strategy in the game. The concept of an advantageous strategy profile, n-tuples of individual strategies, can have several interpretations and the choice of an appropriate definition is the key to the analysis of any game.

An intuitive approach is to consider strategy profiles where no individual player wants to deviate from her strategy if other players stick to the planned actions. This reasoning gives rise to a notion of a Nash equilibirum.

More formally, by a n-tuple $\alpha^* = (\alpha_1^*, \alpha_2^*, \dots, \alpha_n^*)$ is denoted a strategy profile where the i-th player chooses her admissible strategy $\alpha_i^* \in \mathcal{A}_i$. Then let $\alpha_{-i}^* = (\alpha_1^*, \dots, \alpha_{i-1}^*, \alpha_{i+1}^*, \dots, \alpha_n^*)$ be a strategy vector of all the players not including the player i.

Definition 2.2 A strategy α_i^* is a best reply (best response) of i-th player to the strategy profile α_{-i}^* if:

$$u(\alpha_i^*, \alpha_{-i}^*) = \max_{\alpha_i \in \mathcal{A}_i} u(\alpha_i, \alpha_{-i}^*) \tag{2.2}$$

Definition 2.3 A strategy profile $\alpha^* = (\alpha_1^*, \alpha_2^*, \dots, \alpha_n^*)$ is a Nash equilibrium if and only if for every player $1 \le i \le n$ the following inequality holds:

$$u(\alpha_i^*, \alpha_{-i}^*) \ge u(\alpha_i, \alpha_{-i}^*) \quad \text{for} \quad \forall \alpha_i \in \mathcal{A}_i \tag{2.3}$$

In simple terms, the definition 2.3 says that in a Nash equilibrium no single player benefits by deviating from the equilibrium if other decision makers stick to their choice. Or, using the definition 2.2 and comparing expressions (2.2) and (2.3), one can say that a Nash equilibrium is a best response to itself.

The definition 2.3 raises the following questions: Does a Nash equilibrium exist in every game? Is it unique? Next three examples of two-player games shed some light on the matter. The strategies are shown in blue and red for player 1 and 2, respectively, with the corresponding utilities on intersections of selected strategies.

Example 2.1 *Let's consider a game with two competing fishing boats trawling the same fish-stock in a sea. There are four possible outcomes: both parties stay without any profit if no one fishes from the stock. If only one player uses the fishing resource, then she gains a share of market and the other fisherman does not receives anything. If both of them fish, then all players receive some positive income. The pay-off matrix for this set-up is shown in Table 2.1.*

	B_1 (not fish)	B_2 (fish)
A_1 (not fish)	0 / 0	0 / 2
A_2 (fish)	2 / 0	1 / 1

Table 2.1: *Pay-offs in the Game 1.*

This game has only one Nash equilibrium profile – (fish, fish) strategy. Both parties should fish in the sea.

Example 2.2 *Here is a more realistic modification of the Game 1: if both player fish, then they overfish the stock and it goes extinct. The modified pay-off matrix is presented in Table 2.2.*

	B_1 (not fish)	B_2 (fish)
A_1 (not fish)	0 / 0	0 / 2
A_2 (fish)	2 / 0	-1 / -1

Table 2.2: *Pay-offs in the Game 2.*

The Game 2 has two Nash equilibria - (fish, not fish) and (not fish, fish) strategies. In ecological literature, this situation is referred as survival of the first.

Example 2.3 *Third example is a well-known game of Rock Paper Scissors. Pay-off matrix of the game is presented in Table 2.3.*

This game has no Nash equilibrium.

	B_1 (rock)	B_2 (paper)	B_3 (scissors)
A_1 (rock)	0 / 0	-1 / +1	+1 / -1
A_2 (paper)	+1 / -1	0 / 0	-1 / +1
A_3 (scissors)	-1 / +1	+1 / -1	0 / 0

Table 2.3: *Pay-offs in the Game 3.*

These examples illustrate that situations with no, one or many Nash equilibria are equally possible. One of the main results in game theory in Von Neumann and Morgenstern (2007) which has been further extended by Nash in Nash (1951) says that if randomness in strategy selection is allowed, so-called mixed strategy profiles, then any finite player game has a Nash equilibrium.

Definition 2.4 A mixed strategy σ of a player is a probability distribution over her set of admissible strategies $\mathcal{A}$ where $|\mathcal{A}| = k$ i.e.

$$\sigma = \left(p^{(1)}, p^{(2)}, \ldots, p^{(k)}\right), \tag{2.4}$$

where $p^{(j)}$ is a probability to choose the jth strategy $\alpha_j \in \mathcal{A}$ and $p^{(1)} + p^{(2)} + \ldots + p^{(k)} = 1$.

In simple terms, a mixed strategy (2.4) is a probability distribution which specifies frequencies at which the admissible pure strategies are selected assuming that each player makes her choice independently. It should be noted that a pure strategy α_j is a mixed strategy with the probability 1 one j-th place. Then the utility function for mixed strategies profile $(\sigma_1, \sigma_2, \ldots, \sigma_n)$ is the expected value of the corresponding random variable:

$$u(\sigma_1, \sigma_2, \ldots, \sigma_n) = \sum_{(\alpha_{j_1}, \ldots, \alpha_{j_n}) \in \mathcal{A}_1 \times \ldots \times \mathcal{A}_n} u(\alpha_{j_1}, \alpha_{j_2}, \ldots, \alpha_{j_n}) p_1^{(j_1)} p_2^{(j_2)} \ldots p_n^{(j_n)} \tag{2.5}$$

Theorem 2.5 *Nash (1951) Every game with a finite number of players and in which every player has a finite number of strategies, has a Nash equilibrium in mixed strategies.*

Returning back to the presented above examples, as has been shown already in the example 2.3, the Game 2.3 doesn't have a Nash equilibrium in pure strategies. But this game, according to the Nash theorem 2.5, should have a Nash equilibrium in mixed strategies – a strategy profile where both players equally likely choose rock, paper or scissors, i.e. the mixed strategy $\sigma = (1/3, 1/3, 1/3)$.

One more thing to note: the Nash theorem 2.5 only establishes the existence of a Nash equilibrium, but nothing about the uniqueness. The Game 2.2 is an example of a game with several Nash equilibria.

2.1.2 Evolutionary stable strategy

In contrast to classical game theory, the main assumption about rationality of the interacting agents in biology is omitted because it's unreasonable to expect rational game-theoretical reasoning from a fish or a zooplankton. This assumption is replaced by evolutionary selection with the following line of reasoning: animals might not behave rationally, but if players' strategies are replicated in future generations, agents who do not play a beneficial strategy will be replaced by players with a better strategy profile and it should propagate in future generations. Thus, evolutionary selection of advantageous strategies is a good substitute for the rationality assumption.

As has been discussed above, a Nash equilibrium is a best response strategy to itself. However, in ecology, a strategy being a best reply to itself does not always prevent invasion of animals adopting a more beneficial strategy. Thus, a more refined notion of a Nash equilibrium is needed to deal with this case.

Now a large population of animals is considered and by $u(\alpha^*, \alpha^{**})$ is denoted the expected utility of an animal playing the strategy (potentially a mixed one) α^* in the population where all other players adopt the mixed strategy α^{**}, which represents the frequencies of strategies in the population.

Let's consider a population with the vast majority of individuals following a strategy α^*, while a fraction ε of the population (mutants, invaders) adopts another strategy α^{**}. Then the strategy profile of the whole population is denoted by $(1-\varepsilon)\delta_{\alpha^*} + \varepsilon\delta_{\alpha^{**}}$.

Definition 2.6 A strategy α^* is said to be evolutionarily stable against another strategy α^{**} if there exists an ε^* such that:

$$u(\alpha^*, (1-\varepsilon)\delta_{\alpha^*} + \varepsilon\delta_{\alpha^{**}}) > u(\alpha^{**}, (1-\varepsilon)\delta_{\alpha^*} + \varepsilon\delta_{\alpha^{**}}) \quad \text{for} \quad 0 < \varepsilon \leq \varepsilon^*. \tag{2.6}$$

The strategy α^* is an Evolutionarily Stable Strategy (ESS) if it is evolutionarily stable against α^{**} for every other strategy $\alpha^* \neq \alpha^{**}$.

The ESS definition (2.6) in this manuscript is adopted from Broom and Rychtár (2013).

In other terms, the inequality (2.6) means that any invasive strategy α^{**} must do worse than the initial strategy for small enough number of invaders. ESS is a strategy such that if all animals in a population adopt it, then no mutant strategy can invade the population under the influence of natural selection.

Comparing the definitions of a Nash equilibrium and an ESS one can see that a Nash equilibrium is a strategy profile, where actions of all players matter, while an ESS is a population strategy and actions of a single player in the population don't matter. And if a strategy is evolutionarily stable, then it is a Nash equilibrium. But the other direction does not hold.

Example 2.4 *In this game two hunters decide if they are going to hunt on a stag or a hare. The pay-off matrix is presented in Table 2.4.*

	B_1 (hunt stag)	B_2 (hunt hare)
A_1 (hunt stag)	2 / 2	0 / 2
A_2 (hunt hare)	2 / 0	1 / 1

Table 2.4: *Pay-offs in the Game 4.*

The Game 4 has two Nash equilibria - (hunt stag, hunt stag) and (hunt hare, hunt hare) strategies. But there is only one evolutionary stable strategy.

For the strategy hunt stag we have:

$$u(A_1, (1-\varepsilon)B_1 + \varepsilon B_2) = 2 - 2\varepsilon < 2 - \varepsilon = u(A_2, (1-\varepsilon)B_1 + \varepsilon B_2)$$

which indicates that hunt stag is not an ESS.

For the strategy hunt hare we have:

$$u(A_2, (1-\varepsilon)B_2 + \varepsilon B_1) = 1 - \varepsilon \geq 2\varepsilon = u(A_1, (1-\varepsilon)B_2 + \varepsilon B_1),$$

i.e. hunt hare is an ESS if less than $\varepsilon^* = 1/3$ *of the population adopt the invasive strategy strategy hunt stag.*

The Nash theorem 2.5 guarantees the existence of a Nash equilibrium and the same question arises about ESS: does an evolutionarily stable strategy always exist? The answer is negative.

Example 2.5 *Maynard Smith (1982) This game is a modification of the Rock Paper Scissors game from the example 2.3. Updated pay-off matrix is presented in Table 2.5.*

	B_1	B_2	B_3
A_1	2/3 / 2/3	0 / 1	1 / 0
A_2	1 / 0	2/3 / 2/3	0 / 1
A_3	0 / 1	1 / 0	2/3 / 2/3

Table 2.5: *Pay-offs in the without ESS.*

This game has one Nash equilibrium in mixed strategies $\sigma = (1/3, 1/3, 1/3)$ *for both players. To see if it's an evolutionary stable strategy, the inequality from the definition 2.6 has to be verified. For example, the mutants adopt the strategy* $x = (1, 0, 0)$ *always playing* A_1 *yield pay-offs:*

$$u(\sigma, (1-\varepsilon)\delta_\sigma + \varepsilon\delta_x) = 5/9 < 5/9 + 3\varepsilon = u(x, (1-\varepsilon)\delta_\sigma + \varepsilon\delta_x),$$

for any $\varepsilon > 0$. *Then the Nash equilibrium strategy* σ *is not an ESS.*

2.1.3 References

The foundation of game theory for games with a finite number of players has been established in the book Von Neumann and Morgenstern (2007) by the mathematician John von Neumann and the economist Oskar Morgenstern with the first edition published in 1944. Later the established theory has been pushed further and extended by a series of papers regarding equilibrium strategy profiles by the mathematician John Forbes Nash in Nash Jr (1950a,b); Nash (1951) from 1950s. The book Maschler et al. (2020) provides a comprehensive introduction to various topics in classical and modern game theory. The book Broom and Rychtár (2013) introduces game-theoretical concepts like evolutionarily stable strategy from the point of view of applications in biology. The book Maynard Smith (1982) provides an excellent reference on evolutionary game theory.

2.2 Calculus of variations

Calculus of variations generalizes a notion of a constrained optimization problem to functional spaces. Now the set of all admissible points is a functional set and the objective function has a form of mapping between the function space and real numbers, a functional. The standard formulation of a calculus of variations problem can be stated in the following way:

Among all admissible real-valued functions $f \in \mathcal{A}$, $f : [a,b] \to \mathbb{R}$ satisfying boundary conditions:

$$y(a) = y_0 \qquad y(b) = y_1,$$

find a maximizer of the cost functional:

$$J(y) = \int_a^b L(y(t), y'(t), t)\,\mathrm{d}t. \tag{2.7}$$

Usually one is interested in the admissible set $\mathcal{A}$ being a space of smooth functions. For example, a standard option is $\mathcal{A} = C^d([a,b])$ – a set of d times differentiable functions on the interval $[a,b]$.

Considering small perturbations in the function y in the set of admissible functions and resulting changes in the functional (2.7), writing down its first-order Taylor expansion, one can arrive to the following theorem:

Theorem 2.7 *A function f is a stationary point of the optimization problem* (2.7) *if and only if*

$$\frac{\partial L}{\partial y} = \frac{\partial}{\partial t}\left(\frac{\partial L}{\partial y'}\right), \tag{2.8}$$

where the derivatives with respect to y and y' should be understood in the classical sense, treating the functions as independent variables.

The equation (2.8) is called Euler-Lagrange equation. This is a (system) of second-order ordinary differential equations which provides the first-order necessary condition for optimality.

2.2.1 References

The main used reference is Liberzon (2011) with detailed introduction to calculus of variations, historical remarks of the theory and connections between optimal control theory and calculus of variations.

2.3 Control theory

Optimal control theory, or which is sometimes called dynamic optimization, deals with situations where the behaviour of a dynamical system is controlled through an input function from a given set of admissible controls. Then, for a given performance measure, one can assign a value to the system's behaviour and the ultimate goal is to find an input function which yields the optimal behaviour of the controlled system on a specified time interval of interest. In this thesis only optimal control problems with finite time horizon will be considered, i.e. problems on the time interval $[0, T]$, where $T < +\infty$. An example of a dynamic optimization problem is an animal who tries to optimize its total harvested energy over the time interval $[0, T]$ including a cost of migration in a water column. For example, the paper Thygesen et al. (2016) explores dynamic optimization model of Bigeye tuna maximizing its energy harvest rate.

Informally, an optimal control problem consists of two main components which are described below. The first main component of an optimal control problem is a dynamical (controlled) system which is governed by a (system) of ordinary differential equations:

$$\dot{x}_t = f(x_t, \alpha_t, t), \quad x(0) = x_0, \tag{2.9}$$

where f is a given deterministic function, x_0 is the initial state of the controlled dynamical system and $\alpha_t \in \mathcal{A}$ in an input (control) function from the admissible set $\mathcal{A}$. It is assumed that the problem (2.9) is well-posed: the solution x_t exists and unique on the time interval $[0, T]$.

In the equation (2.9) by x_t is denoted the state of the controlled system. It can be, for example, a vertical position of a fish in a water column or gut fullness of a marine animal. Then α_t is the fish's vertical speed at time t or a strategy of the animal to eat or escape the feeding arena.

The second basic component is the cost functional $J(\alpha)$, which serves as a measure of system's performance for the selected control function α_t. For each admissible control the cost functional assigns a real value. In this thesis, the cost functional will be of the form:

$$J(\alpha) = \int_0^T L(x_s, \alpha_s, s)\,\mathrm{d}s + K(x_T, T), \tag{2.10}$$

where L is the running cost, and K is the terminal cost, which are given functions and T is the final (terminal) time. The functional (2.10) can be, for example, the amount of harvested energy by the fish over the time interval $[0, T]$.

Then the ultimate goal of the optimal control problem (2.9) - (2.10) is to find an optimal control α^* among admissible controls in $\mathcal{A}$ which maximizes (or minimizes) the functional $J(\alpha)$.

2.3.1 The Hamilton-Jacobi-Bellman equation

One of the approaches to solve an optimal control problem is via the dynamic programming approach utilizing the principle of optimality. This principle will be stated precisely later, but verbally it can be formulated in the following way:

DEFINITION 2.8 (Optimality principle) Bellman (1966) An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision.

Then the idea is to start with the terminal cost $K(x_T, T)$ and iteratively move backwards and solve a family of sub-problems.

To start with, an auxiliary function $J(x, \alpha, t)$ is introduced:

$$J(x, \alpha, t) = \int_t^T L(x_s, \alpha_s, s)\,\mathrm{d}s + K(x_T, T), \tag{2.11}$$

which is a cost function of an optimal control sub-problem of the original control problem (2.9) - (2.10) starting at time t.

The following function, so-called value function, is defined as:

$$u(x, t) = \sup_{\alpha} J(x, \alpha, t) \tag{2.12}$$

In simple terms, the value function (2.12) tells how “good” is the position x of the dynamical system at time t (assuming that the optimal control α is applied). Then the principle of optimality from the definition 2.8 can be formulated as:

$$u(x, t) = \sup_{\alpha_{[t, t+\Delta t]}} \left\{ \int_t^{t+\Delta t} L(x_s, \alpha_s, s)\,\mathrm{d}s + u\left(x(t + \Delta t), t + \Delta t\right) \right\} \tag{2.13}$$

Applying the Taylor expansion to the formulation of the principle of optimality (2.13) we arrive to the so-called Hamilton–Jacobi–Bellman equation:

$$\frac{\partial u}{\partial t} + \sup_{\alpha} \left(\frac{\partial u}{\partial x} f(x, \alpha, t) + L(x, \alpha, t) \right) = 0, \quad u(x, T) = K(x_T, T). \tag{2.14}$$

The Hamilton–Jacobi–Bellman equation (2.14) is a non-linear partial differential equation, which is usually impossible to solve analytically with a couple of simple cases when the functions f and L are "good enough". But this PDE allows to quantify the value function u and, if the solution is sufficiently smooth, infer the optimal control α^* which yields the optimal behaviour of the dynamical system (2.9). The following theorem provides more details on this matter.

Theorem 2.9 *Liberzon (2011) Let a C^1 function u^* satisfies the Hamilton-Jacobi-Bellman equation* (2.14) *and suppose that a control α^* is where the supremum is attained. Then u^* is the optimal cost and α^* is an optimal control.*

The theorem guarantees that if a sufficiently smooth solution exists and an control where the supremum is attained is found, then it's optimal. But it doesn't say anything about uniqueness of the optimal control, there might be several input functions which yield the same value of the cost functional.

2.3.2 Stochastic case

For the sake of completeness, the case of stochastic optimal control problems is presented here. Now the dynamics of the controlled system is governed by a (system) of stochastic differential equations:

$$\mathrm{d}X_t = f(X_t, \alpha_t, t)\,\mathrm{d}t + \sigma(X_t, \alpha_t, t)\,\mathrm{d}B_t, \quad X_0 = x_0, \tag{2.15}$$

where B_t is standard Brownian motion. It is again assumed that the problem (2.15) is well-posed: the solution exists and unique on the time interval $[0, T]$.

Since trajectories of the dynamical system (2.15) are subject to random fluctuations, the functional (2.10) is adjusted make sense in the stochastic case:

$$J(\alpha) = \mathbb{E}\left[\int_0^T L(X_s, \alpha_s, s)\,\mathrm{d}s + K(X_T, T)\right] \tag{2.16}$$

The value function is defined in a similar way as in the deterministic case:

$$u(x,t) = \sup_\alpha J(x, \alpha, t) \tag{2.17}$$

The Hamilton-Jacobi-Bellman equation in the stochastic case has a slightly different form compared with the deterministic one:

$$\frac{\partial u}{\partial t} + \sup_\alpha \left(\frac{\partial u}{\partial x} f(x,\alpha,t) + \frac{\sigma^2(x,\alpha,t)}{2}\frac{\partial^2 u}{\partial x^2} + L(x,\alpha,t)\right) = 0, \quad u(x,T) = K(x_T, T), \tag{2.18}$$

i.e. now the partial differential equation includes a second derivative of the value function.

The stochastic analog to the verification theorem is stated below:

THEOREM 2.10 *Oksendal (2013) Let a C^2 function u^* satisfies the Hamilton-Jacobi-Bellman equation* (2.18) *and suppose that a control α^* is where the supremum is attained. Then u^* is the optimal cost and α^* is an optimal control.*

It also should be noted that in many cases, both for deterministic and stochastic controlled systems, the value function u is a not smooth function. Hence, there is the need for a weaker notion of a solution to the Hamilton-Jacobi-Bellman equation. One development in this direction is a notion of a viscosity solutions Evans (2010), but it will not be considered in this manuscript.

2.3.3 Feynman–Kac formula

For the sake of completeness, here is presented the Feynman–Kac formula which establishes the connection between theory of partial differential equation and probability theory. This formula has been used further in the thesis to derive the mean field systems of partial differential equations.

THEOREM 2.11 *Carmona (2016) Let u solves the partial differential equation:*

$$\frac{\partial u}{\partial t} + f(x,t)\frac{\partial u}{\partial x} + \frac{\sigma^2(x,t)}{2}\frac{\partial^2 u}{\partial x^2} - c(x,t)u + d(x,t) = 0, \quad u(x,T) = g(x), \tag{2.19}$$

then the solution u has the following representation:

$$\begin{aligned} u(x,t) = \mathbb{E}\Bigg[\int_t^T d(X_s,s)\exp\left(-\int_t^s c(X_r,t)\,\mathrm{d}r\right)\mathrm{d}s \\ +g(X_T,T)\exp\left(-\int_t^T c(X_r,r)\,\mathrm{d}r\right)\Bigg] \end{aligned} \tag{2.20}$$

if f, σ, c, d are continuous functions and d has quadratic growth on x.

Sometimes (2.20) is called the Feynman-Kac representation formula.

The important aspect of the Feynman-Kac formula is that it allows exponential discounting inside the integral (2.20), which is used in the PhD manuscript to take into account the probability of death of a player in differential games, i.e., the exponential integral is the probability of survival during a specified time interval.

2.3.4 References

The main used reference is the book Liberzon (2011) which provides a good introduction to main concepts and results of deterministic optimal control theory. A more detailed discussion on the Hamilton-Jacobi-Bellman equation together with some extensions to non-classical solutions, viscosity solutions as one example, is presented in the book Evans (2010). The book Oksendal (2013) provides an excellent introduction to theory of stochastic differential equations and stochastic optimal control. First chapters of the book Carmona (2016) serve as a good introduction to stochastic optimal control and connections with mean field game theory.

2.4 Mean field game theory

Mean field game theory studies systems of n interacting Ito processes and their individual state dynamics is governed by a system of coupled stochastic differential equations:

$$\mathrm{d}X_t^i = f(X_t^i, \alpha_t^i, \widehat{\mu}_t)\,\mathrm{d}t + \sigma(X_t^i, \alpha_t^i, \widehat{\mu}_t)\,\mathrm{d}B_t^i, \tag{2.21}$$

where $\widehat{\mu}_t$ is the empirical measure of the particle system:

$$\widehat{\mu}_t = \frac{1}{n}\sum_{j=1}^{n} \delta_{X_t^j}, \tag{2.22}$$

The empirical measure $\widehat{\mu}$ from (2.21) is the only source of interaction between the agents and shows that each player can see only aggregated statistical information about the behaviour of the total population.

The drift f and diffusion σ coefficients in the system (2.21) are the same for each particle and any two particles have independent driving Brownian motions. These assumptions postulate that the particle system is symmetric, meaning that any permutation of the Ito processes X_t^i results in exactly the same system.

Each agent i in the population of agents tries to maximize some objective criterion of the form:

$$J_i(\alpha_1, \alpha_2, \ldots, \alpha_N) = \mathbb{E}\left[\int_0^T L(X_s^i, \alpha_{i,s}, \widehat{\mu}_s)\,\mathrm{d}s + K(X_T^i, \widehat{\mu}_T)\right], \tag{2.23}$$

where $T > 0$ is a finite time horizon of the optimization problem and each particle i can select an admissible control process $\alpha_{i,t}$. Again, by the symmetry assumption, the running cost L and the terminal cost K are required to be the same for each player. The optimization problem (2.23) faced by each particle in the system are interdependent due to the coupling term through the empirical measure $\widehat{\mu}$.

Passing the number of players n to the limit $n \to +\infty$, the interaction between the agents through the empirical measure becomes weaker. At some point, when n is big enough, contribution of each particle in (2.22) becomes negligible and can be disregarded. Then all the particles should be identically independently distributed (i.i.d.), because all have the same drift, noise level and independent trajectories of Brownian motion.

Keeping the above mentioned assumptions about the symmetry between agents in mean field games, identical objective function and the limit, the idea is to consider a so-called representative player from the population and solve the corresponding control problem. Then, the results of the control problem can be extrapolated to all other agents invoking the symmetry.

Mean field theory studies systems of partial differential equations in the form:

$$\left\{\begin{array}{l} \frac{\partial u}{\partial t} + \sup_\alpha \left(\frac{\partial u}{\partial x} f + \frac{\sigma^2}{2}\Delta u + L\right) = 0 \\ \frac{\partial \mu}{\partial t} - \frac{\sigma^2}{2}\Delta\mu + \nabla.\,(f\mu) = 0, \end{array}\right. \tag{2.24}$$

which is essentially is a system of the Hamilton-Jacobi-Bellman and the Fokker-Planck equations together. This coupling is illustrated in Figure 2.1.

Solving such a system analytically or numerically is a very non-trivial task. Moreover, very little known about existence and uniqueness of solutions to the systems of partial differential equations in the form (2.24) with a few very technical results are available, for example, Lasry and Lions (2007).

The main objective of this PhD thesis is modelling and analysis of the behaviour of the system of marine animals in an equilibrium. It is assumed that the players in this vertical differential game don't cooperate in optimizing their own objective functions. Thus, this dissertation focuses on the behavior of the particle system in a Nash equilibrium.

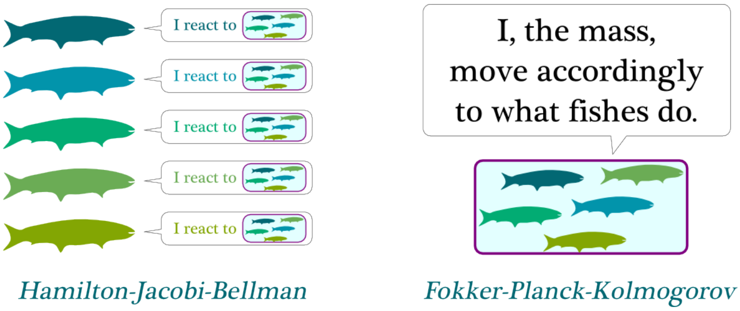

Figure 2.1: Visual representation of the coupling (2.24). The Hamilton-Jacobi-Bellman equation describes how agents react to the interaction and optimize (left panel). The Fokker-Planck defines the movement of the whole population (right panel). Credit: `https://www.science4all.org`.

2.4.1 References

A two-volume standard reference for mean field game theory is Carmona and Delarue (2018a,b), which provides a detailed introduction to the theory with applications in finance, economics and social science. The book Carmona (2016) is an excelled supplementary material with a focus on applications in finance. Two other references Lacker (2015, 2018) are less-structured, but can serve as supplementary reading to the main textbooks.

2.5 Numerical methods

The remaining part of this introductory chapter will be dedicated to presenting a short overview of the spectral element methods, which have been extensively applied to approximate solutions to the mean field systems of partial differential equations in the PhD sub-projects.

The idea of the spectral methods is to look for the unknown solution to a partial differential equation in a “good enough” functional space. For technical reasons, which are discussed below, the most suitable space, so-called approximation space, is a space equipped with weighted inner product and a norm. One of the most popular choices is a Hilbert space $L^2_w(a,b)$. The weighted Hilbert space

$L^2_w(a,b)$ defined as:

$$L^2_w(a,b) = \left\{ f : [a,b] \to \mathbb{R}, \quad \int_a^b |f(x)|^2 w(x)\,\mathrm{d}x < \infty \right\}, \tag{2.25}$$

with the inner product associated with this space is:

$$(f,g)_{L^2_w(a,b)} = \int_a^b f(x)g(x)w(x)\,\mathrm{d}x, \tag{2.26}$$

for any two function $f, g \in L^2_w(a,b)$.

Since $L^2_w(a,b)$ has a basis, then the unknown function can be expanded in the form:

$$u(x) = \sum_{j=0}^{+\infty} \widehat{u}_j p_j(x), \tag{2.27}$$

where $\widehat{u}_j$ are unknown coefficients. These are the coefficients of the projection of the unknown function u on the basis, usually orthonormal, p_j in the approximation space L^2_w and the goal of the spectral methods is estimate the coefficients $\widehat{u}_j$. The approximation (2.27) is a modal expansion with coefficients $\widehat{u}_j$.

To make use of the basis expansion for computational applications, the infinite series (2.27) has to be truncated and replaced by a finite series up to some pre-defined order N:

$$u_N(x) = \sum_{j=0}^{N} \widehat{u}_j p_j(x), \tag{2.28}$$

Then the error of the truncation of the infinite series is equal:

$$\tau(x) = \sum_{j=N+1}^{+\infty} \widehat{u}_j p_j(x). \tag{2.29}$$

Thus, the true solution is composed of two parts:

$$u(x) = u_N(x) + \tau(x), \tag{2.30}$$

and to estimate the accuracy of the approximation, norm of the truncation error of the approximate series (2.28), from the Parseval's identity, is given by:

$$\|\tau\| = \sum_{j=N+1}^{+\infty} |\widehat{u}_j|^2 \|p_j\|^2, \tag{2.31}$$

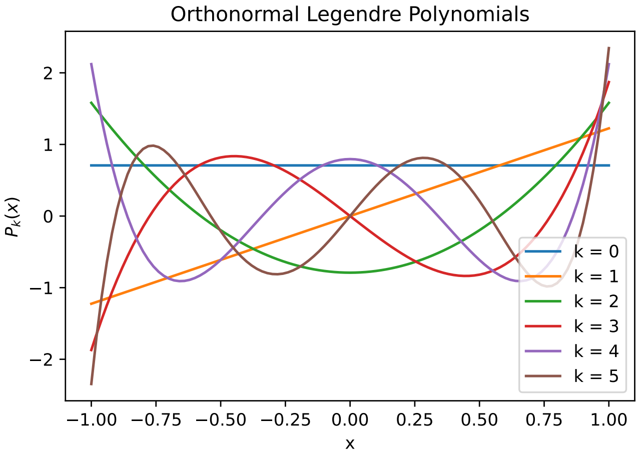

Figure 2.2: First polynomials of order ≤ 5 from the orthonormal Legendre basis system in $L^2(-1, 1)$ with $w(x) = 1$.

i.e. the norm of the error depends on the decay of the coefficients $\widehat{u}_j$. For orthonormal basis the norm $\|p_j\|^2 = 1$. Although the approximation theory for general basis choice is rather technical, the main result says that the decay rate of the modes depends on smoothness of the function u and can be exponential for infinitely smooth functions Kopriva (2009). This result implies that for smooth functions, to achieve the same order of accuracy compared with low-order numerical methods for solving differential equations like finite difference schemes, less basis functions is needed, and, thus, less computational effort. This results in faster numerical routines.

A defining character of any spectral method is the choice of orthogonal basis functions used to approximate the solution with. Suitable choice of a functional basis might be beneficial and can help satisfy boundary conditions. For example, Fourier basis with the complex exponentials $\exp(ikx)$ is a standard choice for periodic problems. In other cases the Jacobi polynomials $P_k^{(\alpha,\beta)}(x)$, with Legendre polynomials as a particular class of Jacobi polynomials with $\alpha = \beta = 0$, is a standard basis selection. First orthonormal Legendre polynomials are shown in Figure 2.2.

Another advantage of the spectral methods over finite difference schemes is geometrical flexibility. To handle complex geometries or make a trade-off between approximating the unknown function on the whole domain with more basis functions or approximating on subdomains with less basis functions, one can reduce the approximation of the unknown function on the whole domain to

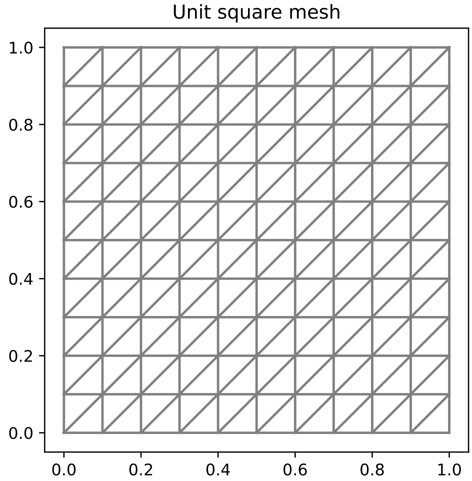

Figure 2.3: Triangulation of the unit square domain. The square is split into a set of smaller triangular domains and the unknown solution is approximated over each triangle.

approximation on subdomains.

For example, the computational domain of a unit square can be split into triangular subdomains by the triangulation procedure as shown in Figure 2.3, but other shapes like rectangles in 2D or tetrahedra hexahedra in 3D. Then the unknown solution is approximated on each subdomain and approximations on the subdomains are gethered together to restore the whole solution.

2.5.1 References

The main reference for spectral element methods is the book Kopriva (2009) which provides introduction to the theory and detailed explanation of implementation of the numerical methods. The books Canuto et al. (2007b,a); Hesthaven and Warburton (2007) focus more on theoretical foundations of the spectral element methods.

CHAPTER 3

Vertical Mean Field Games

This chapter is dedicated to summarizing the key findings of the 3 papers on modelling diel vertical migration as a mean field game the animals play against each other.

3.1 Individual-level dynamics

To start with, the usual mathematical set-up is a water column of depth H which is represented as an interval $x \in [0, H]$ and time $t \in [0, +\infty)$.

Modelling diel vertical migration as an optimal control problem starts with defining the individual level dynamics of a representative agent from the population. Then, as discussed above, the standard approach is to consider the dynamics of the representative player to infer the information about temporal evolution of the players' distribution on the population level.

By X_t is denoted the vertical position of an animal in the water column at time t and it is assumed that all agents in the population are identical, i.e. the standard symmetry assumption in mean field game theory. The vertical state of the representative agent in the water column is driven by the stochastic differential equation:

$$\mathrm{d}X_t = f(X_t, V_t, t)\,\mathrm{d}t + \sigma(X_t, V_t, t)\,\mathrm{d}B_t, \tag{3.1}$$

where V_t is the vertical speed which the representative player can control. The drift f and the diffusion σ functions are predefined in the model and B_t as standard Brownian motion. The reflective boundary condition is imposed for the equation (3.1) on the surface and the bottom of the water column meaning that no new agents can appear through the boundary. It should also be noted that the state equation (3.1) does not include coupling terms with the population.

For diel vertical migration model in the thesis the drift is chosen to be equal to the player's control:

$$f(X_t, V_t, t) = V_t, \tag{3.2}$$

meaning that each player in the population can control its drift coefficient. The noise level is assumed to be a constant:

$$\sigma(X_t, V_t, t) = C, \tag{3.3}$$

which means that the vertical positions in the water column is subject to random fluctuations due to, for example, local turbulence. The noise level is independent of the player's state X_t and its vertical speed V_t.

The equation (3.1) on the individual level is consistent the Fokker-Planck or the forward Kolmogorov equation on the population level. Temporal evolution of vertical distribution of the population follows:

$$\frac{\partial N}{\partial t} = -\frac{\partial (NV)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}, \tag{3.4}$$

where N describes vertical distribution function of the population in the water column and is the velocity field. The velocity field V is a Markovian control, i.e. $V = V(X_t, t)$ which assigns the vertical velocity to an agent at the position X_t at time t.

The objective function the representative player from the population is trying to optimize has the form:

$$J(V) = \int_0^{\tau} L(X_s, V_s, s)\,\mathrm{d}s, \tag{3.5}$$

where τ is a Markovian random time of death. For the representative player to be dead means that the state process follows (3.1) for $t < \tau$ and, after the death $t \geq \tau$ the Ito process enters a special "coffin" state $X_t = \partial$ and stays there Oksendal (2013). The death or killing rate of the stochastic process X_t is defined as:

$$\mu(x,t) = \lim_{s \to 0} \frac{1}{s} \mathbb{P}\left[X_{t+s} = \partial \mid X_t = x,\ x \neq \partial\right]. \tag{3.6}$$

The particular form of the mortality rate extensively used in this thesis is:

$$\mu(x,t) = \mu_0 + \mu_1 N(x,t), \tag{3.7}$$

which a sum of the encounter rate due to high abundance of light in the water column through μ_0 and the density dependent term $\mu_1 N$, which describes the encounter risk for prey in big groups.

In this PhD thesis the running cost has the form:

$$L(x,v,t) = g(x,t) - \frac{\nu|v|^2}{2}. \tag{3.8}$$

This form of the running cost emphasizes the trade-off each representative player faces between staying closer to the water surface in regions with high nutrient concentration and forage through the term g or reducing the encounter rate with predators through the mortality rate μ subject to the cost of motion at a rate $\nu|v|^2/2$. Squared cost of motion is selected to illustrate the model and other power laws are possible when modelling diel vertical migration of large animals.

The reason to consider energy gain (3.5) as the optimization criterion for the representative player is the following: what each animal is really optimizing is the number of descendants, according to Darwin's theory of evolution by natural selection. And one can use as a proxy the net energy gain during the lifetime with the reasoning: the individual is limited by how much energy is put into reproduction.

The ultimate goal of the PhD sub-projects presented in subsequent sections of this chapter is to model diel vertical migration as a mean field game and find the equilibrium behaviour of the population of animals, in a Nash equilibrium to be more precise, since no cooperation between the animals is assumed.

3.2 Mean field game without diffusion

Paper A considers the deterministic case when the representative player controls its vertical speed in the water column and no diffusion influences its vertical state, i.e. the governing equation is:

$$\mathrm{d}X_t = V_t \,\mathrm{d}t \tag{3.9}$$

Several assumptions are made to simplify analysis of the final model. First, it's assumed that the animals live in a periodic environment, i.e. that all days are identical and seasonal fluctuations in the environment are disregarded. Which means that only periodic pairs of the solutions (N, V) are of interest.

Second, only long-lived animals, compared to one day time, are modelled. With these assumptions the expression for the objective function (3.5) changes to:

$$J(V) = \int_0^T L(X_s, V_s, s)\,\mathrm{d}s, \tag{3.10}$$

where $T = 24$ hours. Then the running cost L from (3.8) has the form:

$$L(x, v, t) = g(x, t) - F\mu(x, t) - \frac{\nu|v|^2}{2}. \tag{3.11}$$

Here the parameter F is the expected harvested energy until the animal dies:

$$F(x,t) = \int_t^\infty \left[g(X_s, s) - \frac{1}{2}\nu|V_s|^2 \right] \exp\left(\int_t^s \mu(X_\xi, \xi)\,\mathrm{d}\xi \right) \mathrm{d}s \tag{3.12}$$

The discounting exponent inside the integral (3.12) is the survival probability of the representative player over the interval $[t, s]$. With the assumption about the long-lived animals, fluctuations in the expected fitness F over time can be discarded and the parameter becomes a constant. This is a so-called quasi-static approximation.

Also, due to short time period of the control problem, fluctuations in the population size N can be disregarded and the population dynamics can be neglected.

Then it is possible to consider the optimization problem (3.10) as a problem from calculus of variations and invoke the Euler–Lagrange equation (2.8) for finding the optimal velocity field V. Substituting all the form of the running cost, adding the transport equation to the system one arrives to:

$$\begin{aligned} \frac{\partial N}{\partial t} + \frac{\partial (NV)}{\partial x} &= 0 \\ \nu\left(\frac{\partial V}{\partial t} + \frac{1}{2}\frac{\partial (V^2)}{\partial x} \right) + \frac{\partial g}{\partial x} - F\left(\frac{\partial \mu_0}{\partial x} + \frac{\partial (N\mu_1)}{\partial x} \right) &= 0 \end{aligned} \tag{3.13}$$

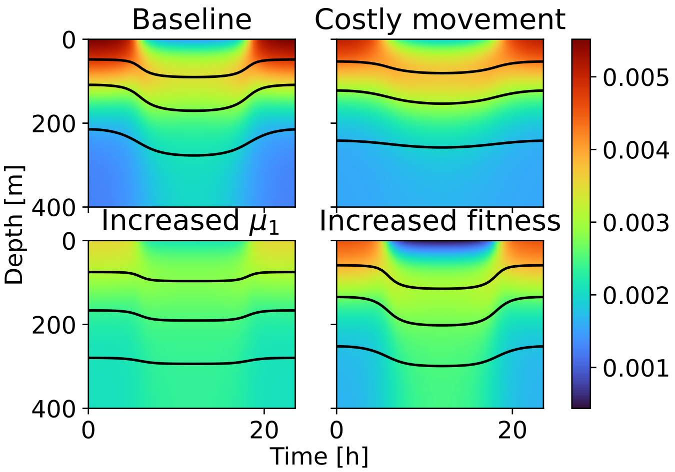

Figure 3.1: Solutions to the PDE system (3.13) for several modelling scenarios are shown. Dark lines correspond to trajectories of individual animals. Picture is taken from A.

The system of PDEs (3.13) defines the optimal distribution of the animals N in the water column and the corresponding optimal vertical speed profile V for the population.

It is very important to emphasize that this equation must only hold where animals are found, i.e. in regions of the water column where the distribution $N > 0$, since in parts where $N = 0$, i.e. vacuum regions, the vertical velocity V is not defined.

Solutions to several modelling scenarios for varying the modelling parameters in the system (3.13) are shown in Figure 3.1. It should be noted, as discussed above, that all the modelling cases have positive distribution of the animals in the water columns at any point of time, i.e. so-called “shallow water case”. And this is the main limitation of the established model, that the domain should be selected to keep the distribution N positive everywhere, otherwise standard numerical schemes become unstable.

To overcome the numerical instabilities while solving the system (3.13), a tailored computational scheme has been developed to resolve these equations. The idea is to iteratively solve a sequence of parameterized sub-problems (3.14), where ε is a parameter. The solution for the case $\varepsilon = 0$ is known and, using the solution to previous iteration as an initial guess in the next one, varying the parameter $\varepsilon \to 1$, one can find a numerical approximation to the solution to the original system (3.13). It is an adaptation of the homotopy method Alexander and Yorke (1978).

$$\begin{aligned} \frac{\partial N}{\partial t} + \frac{\partial (NV)}{\partial x} &= 0 \\ \nu \left(\frac{\partial V}{\partial t} + \frac{1}{2} \frac{\partial (V^2)}{\partial x} \right) + \varepsilon \frac{\partial g}{\partial x} - F \left(\varepsilon \frac{\partial \mu_0}{\partial x} + \frac{\partial (N \mu_1)}{\partial x} \right) &= 0 \end{aligned} \tag{3.14}$$

The main contribution of Paper A is establishing a framework for formulating the vertical game as a mean field system of partial differential equations governing the optimal behaviour of the animals in the water column. But the main limitation of the model is the requirement of positive distribution everywhere in the water column, i.e. the so-called "shallow-water case".

3.3 Mean field game with diffusion

To overcome the complications with the domain selection, Paper B adds random noise to the vertical state of the representative player, i.e. the position of the agent in the water column is governed by the stochastic differential equation:

$$\mathrm{d}X_t = V_t \, \mathrm{d}t + \sigma \, \mathrm{d}B_t \tag{3.15}$$

With added noise to the state, the representative animal has a non-zero probability to be at any point of the water column and the distribution is positive everywhere for any water column of arbitrary depth.

Also, the assumption about the negligible fluctuations in the fitness function F is omitted and now the objective functional (3.5) in its initial form with the random death time τ is considered. The following function is introduced:

$$u(x,t) = \sup_V \mathbb{E}^{X_t = x} \left[\int_t^{+\infty} \left(g(X_s, s) - \frac{\nu}{2} V^2(X_s, s) \right) \exp\left(- \int_t^s \mu(X_\xi, \xi) \, \mathrm{d}\xi \right) \mathrm{d}s \mid x \neq \partial \right], \tag{3.16}$$

which is the expected fitness of the representative player who starts in $X_t = x_0$ at time t. The exponent in the expression is the conditional probability of the player surviving the $[t,s]$ time interval.

Invoking the Feynman–Kac representation formula, it turns out that the function u solves the partial differential equation:

$$\frac{\partial u}{\partial t} + \sup_v \left(Lu + g - \frac{\nu v^2}{2} \right) = 0, \tag{3.17}$$

where the the differential operator L is defined as:

$$Lu = v\frac{\partial u}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 u}{\partial x^2} - \mu u. \tag{3.18}$$

Gathering all the pieces together, the mean field system for finding the Nash equilibrium for the stochastic case has the following form:

$$\begin{cases} \frac{\partial N}{\partial t} = -\frac{\partial (NV)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2} & (x,t) \in (0,H) \times (0,T) \\ \frac{\partial u}{\partial t} + \frac{1}{2\nu}\left(\frac{\partial u}{\partial x}\right)^2 + \frac{\sigma^2}{2}\frac{\partial^2 u}{\partial x^2} + g - u(\mu_0 + \mu_1 N) = 0 & (x,t) \in (0,H) \times (0,T) \\ \int_0^H N(y,t)\,\mathrm{d}y = 1 & t \in [0,T] \\ u(x,0) = u(x,T) & x \in [0,H] \\ N(x,0) = N(x,T) & x \in [0,H] \\ (NV - \frac{\sigma^2}{2}\frac{\partial N}{\partial x})(x,t) = 0 & x \in \{0,H\} \\ \frac{\partial u}{\partial x}(x,t) = 0 & x \in \{0,H\} \\ V = \frac{1}{\nu}\frac{\partial u}{\partial x} \end{cases} \tag{3.19}$$

Varying the model parameters in the system (3.19) yields the solutions as presented in Figure 3.2. As can be seen in the right panel of the plot, the fitness function u is allowed to fluctuate compared with the previous model, where the quasi-static approximation has been imposed.

The main contribution of Paper B is extending the mean field framework to a broader range of depths by including the diffusivity to the vertical state. The Hamilton-Jacobi-Bellman formalism allows to define what is the optimal vertical speed in void regions where there are no animals, i.e. the speed of an agent which happens to be there. It also allows to cover cases with fluctuating environment without assuming the constant fitness, in contrast to Paper A with the quasi-static approximation.

3.4 Multispecies mean field game

Paper C extends the established mean field game theoretical framework and the results from Paper B to a multispecies set-up. Papers A, B included predators

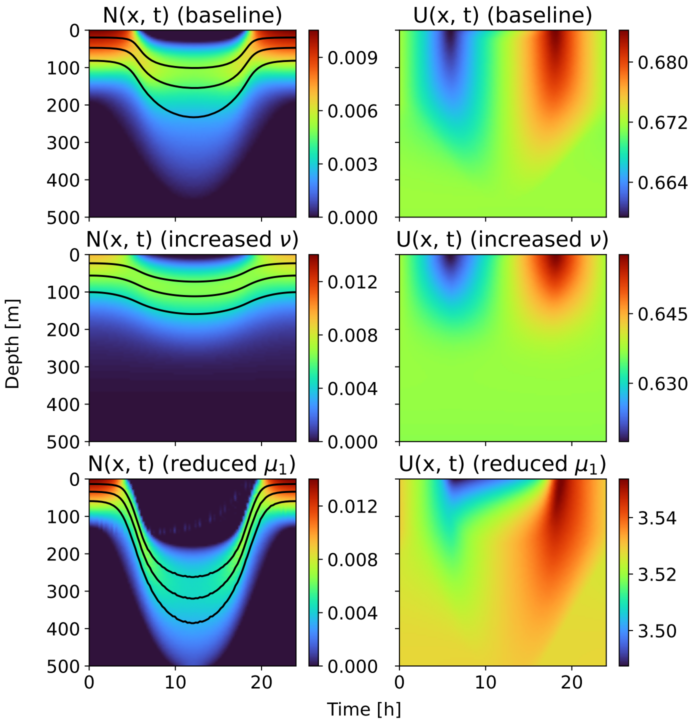

Figure 3.2: Solutions to the mean field system (3.19). Dark lines correspond to trajectories of individual animals. Picture is taken from B.

implicitly through the predation risk terms. Now the aim is to resolve the vertical dynamics with explicit presence of predators.

As usual, the mean field game formulation starts with deriving the state dynamics and the objective functional for a representative agent. In this case, with two explicitly interacting populations, the representative animal from each population is considered to derive the mean field system.

State dynamics of the representative prey in the water column is driven by the stochastic differential equation:

$$\mathrm{d}X_t^{\mathrm{prey}} = V_t^{\mathrm{prey}}\,\mathrm{d}t + \sigma^{\mathrm{prey}}\,\mathrm{d}B_t, \tag{3.20}$$

where the player controls the drift part of the state equation and the diffusion coefficient σ^{prey} is a constant parameter in the model.

The prey player optimizes her objective functional in the form:

$$J^{\text{prey}}(V^{\text{prey}}) = \mathbb{E}\left[\int_0^{\tau^{\text{prey}}} g - \frac{\nu^{\text{prey}}(V_s^{\text{prey}})^2}{2}\,\mathrm{d}s\right], \tag{3.21}$$

where g corresponds to energy harvest rate and τ^{prey} is a Markovian death time for the prey defined in terms of the mortality rate:

$$\mu^{\text{prey}}(x,t) = \mu^{\text{light}}(x,t)C^{\text{pred}}N^{\text{pred}}(x,t) + \mu_1 C^{\text{prey}}N^{\text{prey}}(x,t). \tag{3.22}$$

The risk rate (3.22) for the prey representative player is composed of two parts: the first term in the expression is the mortality rate due to visual predation, which depends on the light abundance μ^{light} and local predator concentration $C^{\text{pred}}N^{\text{pred}}$. The second term in the sum is the risk rate due to interactions with other prey.

Then the mean field system for prey is given by:

$$\begin{cases} \frac{\partial N^{\text{prey}}}{\partial t} = -\frac{\partial(N^{\text{prey}}V^{\text{prey}})}{\partial x} + \frac{(\sigma^{\text{prey}})^2}{2}\frac{\partial^2 N^{\text{prey}}}{\partial x^2} \\ \frac{\partial U^{\text{prey}}}{\partial t} + \frac{1}{2\nu^{\text{prey}}}\left(\frac{\partial U^{\text{prey}}}{\partial x}\right)^2 + \frac{(\sigma^{\text{prey}})^2}{2}\frac{\partial^2 U^{\text{prey}}}{\partial x^2} + g - U^{\text{prey}}\mu^{\text{prey}} = 0 \end{cases} \tag{3.23}$$

Individual dynamics of the representative predator in the water column is driven by the stochastic differential equation:

$$\mathrm{d}X_t^{\text{pred}} = V_t^{\text{pred}}\,\mathrm{d}t + \sigma^{\text{pred}}\,\mathrm{d}B_t, \tag{3.24}$$

i.e. the predator controls its vertical speed and the state is subject to random fluctuations.

The fitness of the predator over its lifetime period:

$$J^{\text{pred}}(V^{\text{pred}}) = \mathbb{E}\left[\int_0^{\tau^{\text{pred}}} \varepsilon C^{\text{prey}}\mu^{\text{light}}N^{\text{prey}} - \frac{\nu^{\text{pred}}(V_s^{\text{pred}})^2}{2}\,\mathrm{d}s\right], \tag{3.25}$$

where the predator can feed on prey through the term $\varepsilon C^{\text{prey}}\mu^{\text{light}}N^{\text{prey}}$ and the random death time τ^{pred} is defined in terms of the mortaliy rate, as for the prey:

$$\mu^{\text{pred}}(x,t) = \mu_2.$$

For the sake of simplicity, the model considers the case of constant predator mortality.

Utilizing the mean field limit, gathering all pieces together from the predators individual dynamics, one arrives to the mean field system of partial differential equations:

$$\begin{cases} \dfrac{\partial N^{\text{pred}}}{\partial t} = -\dfrac{\partial (N^{\text{pred}} V^{\text{pred}})}{\partial x} + \dfrac{(\sigma^{\text{pred}})^2}{2} \dfrac{\partial^2 N^{\text{pred}}}{\partial x^2} \\ \dfrac{\partial U^{\text{pred}}}{\partial t} + \dfrac{1}{2\nu^{\text{pred}}} \left(\dfrac{\partial U^{\text{pred}}}{\partial x} \right)^2 + \dfrac{(\sigma^{\text{pred}})^2}{2} \dfrac{\partial^2 U^{\text{pred}}}{\partial x^2} + \varepsilon C^{\text{prey}} \beta N^{\text{prey}} - U^{\text{pred}} \mu^{\text{pred}} = 0 \end{cases} \tag{3.26}$$

The final mean field system describing the optimal distribution of prey and predators in the water column over one day time period is composed of two sub-systems (3.23) and (3.26). Numerical solution to the system of partial differential equations is shown in Figure 3.3.

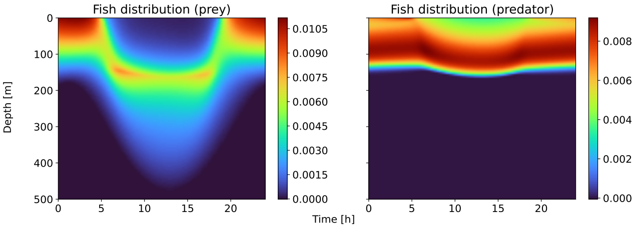

Figure 3.3: Time evolution of vertical distributions of prey and predator populations in the Nash equilibrium over one day given by (3.23), (3.26). Picture is taken from Paper C.

The main contribution of Paper C is formulation of the mean field system for several interacting populations, two player set-up in this case. Now the source of the interaction between the prey and predators is in the growth and mortality terms in the system (3.23), (3.26). This allows to explicitly resolve the vertical migration patterns of two interacting populations of the predators and the prey in the water column during the one day time period.

Chapter 4

Conclusions and Perspectives

This thesis contributes by advancing modelling diel vertical migration with mean field game theoretical framework. In this chapter the main results are summarized and possible directions for future research are outlined.

4.1 Overview of contributions

The main focus of this dissertation has been centered around formulating the mean field game theoretical framework for expressing diel vertical migration as a differential game.

Paper A established the ground for deriving the mean field system for the deterministic case, without noise in the state equation. Solutions to the derived system of partial differential equations reproduced the diel vertical migration pattern in the water column over one day time period. For the derived system the tailored numerical scheme has been proposed, but the system of PDEs has to be solved only for the “shallow water” set-up.

Paper B expanded the derived mean field game theoretical model from Paper

A to the stochastic case, i.e. the vertical state of the agents in the water column is subject to random fluctuations. This technical extension has resolved the so-called "deep water problem". Deriving the governing system of partial differential equations for finding the Nash equilibrium has been done via utilizing the The Feynman–Kac formula, a different approach compared with the Hamilton-Jacobi-Bellman formalism.

Paper C has pushed the results from Paper B further and extended the mean field system of partial differential equations to the multi-player set-up with several interacting populations, a predator-prey system with two explicitly coupled populations of players for the case of Paper C.

The main conclusion and result of the PhD thesis that mean field game theory present a huge opportunity to model interaction of large populations of agents with diel vertical migration as a particular case of this manuscript.

Although the optimal behaviour paradigm in theoretical ecology is conceptually appealing, it remains a technical challenge to actually identify these optimal behaviors of the animals. The thesis has contributed to making this paradigm operational by explicitly resolving such a game in a particular case of diel vertical migration.

4.2 Future research

The main results of this dissertation and arised issues while working on the papers motivate several future research directions which will be presented in the remaining part of the chapter.

4.2.1 Numerical methods

Solving the derived mean field systems numerically constituted a large part of the PhD projects and has been a source of many issues with calculated approximations to the unknown solution to the systems of partial differential equations.

To solve these mean field systems of partial differential equation, the family of spectral element methods (see Sec. 2.5) for discretizing the differential equations has been selected and applied. In particular, the continuous Galerkin (CG) methods subset of the spectral method toolbox. The distinguishing feature of the CG methods is the requirement that the numerical approximations over each subdomain (element) should coincide on the elements' boundary, i.e. the continuity requirement on the boundaries. One of the two mains reasons for selecting the CG is good convergence properties of these methods for smooth functions compared with compared with finite difference schemes and, thus, smaller required grid size to achieve the same level of numerical accuracy. Another advantage of the CG methods is the geometrical flexibility which allows to handle complex computational domains by constructing suitable mesh. Moreover, the basis selection flexibility of the CG numerical methods can help to choose a suitable basis set and satisfy the boundary conditions for the differential equations in the model.

But while solving the analytical models, the numerical routines diverged sometimes, which required increased grid size and reduced step size in the Newton stepping method part of the numerical procedure. In the end, these changes resulted in longer computational times for some model scenarios.

Two two main reasons were identified as a potential source of issues for this divergent behaviour. First, the structural properties of the unknown solution to the mean field systems. The solution can have shocks or kinks, which reduces exponential convergence of the CG methods and makes them less suitable for the problem, reducing their overall performance. One way to get around this issue to apply the discontinuous Galerkin (DG) spectral element methods Hesthaven and Warburton (2007); Kopriva (2009). These methods omit the continuity requirement on the subdomains' boundaries as shown in Figure 4.1. This can be advantageous for approximating discontinuous functions or functions with jumps or shocks, since a carefully constructed mesh coincides or approximates the jumps in the function. Plus, the DG methods are highly parallelizable which can further reduce computational time compared with the continuous Galerkin methods.

Another explanation for the divergent behaviour is analytical properties, yet unknown and unexplored, of the solutions to the mean field systems which should be taken into account when choosing a suitable numerical toolbox. Further analytical investigation of the model equations is required and constitute an interesting mathematical direction for future research.

4.2.2 Reinforcement learning approach

Reinforcement learning Sutton and Barto (2018) in another computational paradigm for solving control problems. This is an agent-based approach, where an agent learns how to behave optimally in the problem through repetitive interaction with the surrounding environment. For each selected action the agent receives

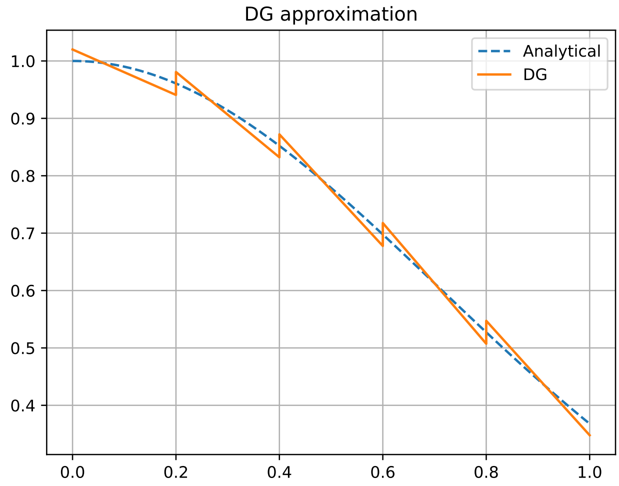

Figure 4.1: Discontinuous Galerkin approximation of a function where approximation on the subdomains have discontinuous jumps on the boundaries.

a reward (internal or external), updates current information about the environment and repeats this loop. The learning process is outlined in Figure 4.2.

The reinforcement learning paradigm can be applied to model diel vertical migration in a water column. The agents not necessarily need to know any prior model of the surrounding environment and should learn the optimal policy through repetitive interaction with the environment in the water column and the other agents in the water column. The results should coincide with the numerical solutions to the mean field systems. But the advantage of the reinforcement approach is the absence of any differential equations, which are usually very hard to analyse analytically and solve numerically. The disadvantage of this approach is slow convergence rate of the state-of-the-art reinforcement learning algorithms, when many iterations are required for the algorithms to converge to a good approximation of the optimal behaviour.

One interesting case to investigate further diel vertical migration models with reinforcement learning is the questions about how quick can one expect to see behavioral adaption to a new environment when the surrounding environment changes? It is fair to assume that organisms have been exposed to fluctuating environments over evolutionary timescales, and therefore animals have evolved strategies to respond to such fluctuations. However, how large fluctuations can

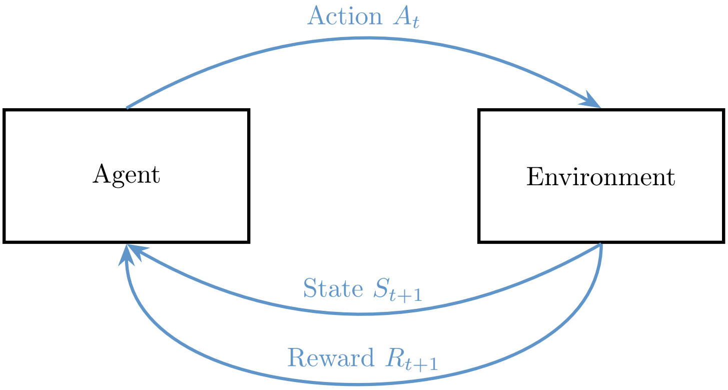

Figure 4.2: Reinforcement interaction loop where the agent selects an action A_t at time step t. Then the system's state is updated to S_{t+1} and the agent receives a reward R_{t+1}. The quantities S_{t+1} and R_{t+1} are then used to update the agent's current knowledge of the surrounding environment and the whole loop repeats.

they handle, and which information do they use to learn that the environment has changed? Because the derived mean field game models assume perfect information about the environment. This is where reinforcement learning could be applied.

4.2.3 Model improvements

In this thesis the game theoretical framework has been proposed under certain simplifications to illustrate the theoretical framework. Here several improvements of the final models are suggested to make the established modelling toolbox more realistic.

One possible direction for future improvement is to omit the assumed time-scale separation between the behaviour in the form of a vertical game (fast time scale) and population dynamics (slow time scale). When deriving the mean field system it is assumed that the population dynamics can be ignored when studying a single day time frame. Thus, the population size is assumed to be a fixed quantity since the one-day time is shorter than the life time of an animal. Without this assumption analysis of the model will include the slow-fast coupling between the behavioral level with diel vertical migration and the original mean field system and the population level with changing population's size through the Lotka–Volterra model, for example. Expanding the time horizon of the optimal control problem will ultimately include growth and mortality terms in the Fokker-Planck equation which will require some notion of quasi-periodicity of the solutions. Another addition when studying diel vertical migration on the extended time period is seasonal migration of animals in the ocean to make the model more realistic. Including possibility of horizontal dynamics and examining sensitivity of the solution to the mean field system with seasonal migration of the animals would be interesting to pursue.

Another improvement of the governing equations is to consider more sophisticated functional responses in the models. For now the nutrient consumption, for example, has linear form. A more realistic case is to include functional responses, where a predator has saturation in growth term. The prey can locally saturate the predators, so this would lead to "positive" density dependence in the mortality term which would make beneficial aggregation in a group, ultimately leading to schooling type phenomena. This is an interesting and rich improvement of the mean field model.

One more possible improvement of the derived models is by including other forms of the cost of movement. Current models include quadratic cost in the speed, which describes the energy spent on locomotion for small animals. For larger animals, the flow around the swimming animal is not viscous/creeping, so the quadratic scaling does not apply. For very large animals, one could use the high-Reynolds number limit, which would be a cubic scaling. Other forms of penalty is time spent on migration (assuming that the animal cannot feed and migrate simultaneously) and increased exposure to predators.

Independence of white noise realizations is a very important technical assumption in the models, but a more realistic scenario is a form of correlation of disturbance in the vertical position for neighboring animals, with turbulence in the water column as an example. In contrast to (2.21), the state of a representative player in common noise models is governed by a stochastic differential equation:

$$\mathrm{d}X_t^i = f(X_t^i, \alpha_t^i, \widehat{\mu}_t)\,\mathrm{d}t + \sigma(X_t^i, \alpha_t^i, \widehat{\mu}_t)\,\mathrm{d}B_t^i + \sigma_0(X_t^i, \alpha_t^i, \widehat{\mu}_t)\,\mathrm{d}W_t,$$

adding one more independent Brownian motion W_t for all the players.

This gives a rise to cases with correlated noise, common noise or shocks Carmona and Delarue (2018a,b) with systems of stochastic partial differential equations. These models will have increased analytical and numerical complexity and serve as an interesting mathematical challenge for future research.

Another possible topic of future research is the situation where animals of the same species are not completely identical, but differ e.g. in size. This would presumably lead to a structured distribution, where animals of different size employ different strategies and therefore end up occupying different niches in a water column.

4.3 Final conclusion

The derived mean field systems of partial differential equations in the thesis gradually expand previous models on modelling diel vertical migration phenomenon. The PhD sub-projects pushed the mean field game theoretical framework by combining diffusion in the vertical state of a representative agent in the water column, taking into account a cost of motion between water layers and resolve the vertical differential game in continuous space and time domains.

Overall, the PhD dissertation contains the methodologies required to derive the mean field systems, reproduce the migration phenomenon and compare the results with the real-world data. The equations can be used to predict changes in the marine ecosystems, in particular the responses to natural and anthropogenic forcing, by including the behavior of individuals when deriving the equilibrium behaviour of animal populations.

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Part II

Publications

Paper A

Ideal Free Flows of Optimal Foragers: Vertical Migrations in the Ocean

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ORIGINAL ARTICLE

Ideal free flows of optimal foragers: Vertical migrations in the ocean

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Abstract

We consider the collective motion of animals in time-varying environments, using as a case the diel vertical migration of marine copepods. The animals are distributed in space such that each animal moves optimally, seeking regions which offer high growth rates and low mortalities, subject to costs on excessive movements as well as being in regions with high densities of conspecifics. The model applies to repeated scenarios such as diel or seasonal patterns, where the animals are aware of both current and future environmental conditions. We show that this problem can be viewed as a differential game of mean field type, and that the evolutionary stable solution, i.e., the Nash equilibrium, is characterized by partial differential equations, which govern the distributions and migration velocities of animals. These equations have similarities to equations that appear in the fluid dynamics, specifically the Euler equations for compressible inviscid fluids. If the environment is constant, the ideal free distribution emerges as an equilibrium. We illustrate the theory with a numerical example of vertical migrations of oceanic copepods, where animals are attracted to nutrient-rich surface waters while repulsed from light during daytime due to the presence of visual predators, aiming to reduce both proximity to conspecifics and swimming efforts. For this case, we show that optimal movements are diel vertical migrations in qualitative agreement with observations of copepods.

Keywords Vertical migration · Optimal behavior · Evolutionary games · Habitat selection

Introduction

Animals move in space in order to forage, avoid predators, or seek mates, and the resulting movements impact the dynamics of ecosystems (Nathan et al. 2008). The spatial distributions of populations, which emerge from the movements of individuals, govern the rate with which predators meet prey, and therefore how biomass is transported from lower trophic levels to higher trophic levels, as well as the growth rate and mortality of the various populations. In turn, the movements of individual animals are motivated by the spatial structure of their habitat.

A noteworthy example of animal movement is vertical migrations in the ocean, which are ubiquitous (Brierley 2014) and believed to constitute the largest movement of biomass on the planet. Even phytoplankton display vertical migration (Wirtz and Smith 2020), while diel migrations of zooplankton and forage fish give rise to the dynamics of the deep scattering layer (Cisewski et al. 2010). Top predators generally track the movements of their prey, but take into account the limits imposed by physiological constraints such as light, oxygen, and temperature (Thygesen et al. 2016). These migrations that occur across trophic levels have implications not just for the animals that perform them, their prey and predators, but also for ecosystem functioning such as the vertical transport of carbon, a mechanism known as the biological carbon pump (Longhurst and Harrison 1989). Vertical distributions also affect measurements taken from the system and their interpretation, such as trawl surveys or acoustic surveys targeting forage fish or zooplankton (Gauthier and Rose 2005).

It is generally agreed that prey descend at day into the dark deep to avoid visual predation (Bollens and Frost 1989) and that predators follow their prey (Josse et al. 1998). Optimization arguments have been used to explain both the behavior of planktonic prey and planktivorous predators (Mangel and Clark 1988). While these motions seem to have "bottom-up" dynamics, in that the prey initiate the

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movement and the predators follow, they must be understood in a game-theoretic setting, since they involve the simultaneous decisions of several agents which each pursue their own interests. One phenomenon which adds credibility to the game-theoretic understanding is that the migrations can drive reverse migrations by even lower trophic levels (Ohman et al. 1983): Here, as predatory copepods descend at dawn to avoid visual predation from forage fish, their smaller planktonic prey ascend to spend the day near the surface, where the absence of predatory copepods implies relative safety.

To understand and explain these diel vertical migrations using the notions of game theory, Iwasa (1982) was seminal in modeling the phenomenon as a matrix game. This framework was pursued further by several authors including Sainmont et al. (2013) and Pinti and Visser (2019), with increasing fidelity as well as complexity, both in terms of modeling and computations. Thygesen and Patterson (2018) modeled the phenomenon in continuous space and time, using differential equations. This leads to higher fidelity and in particular resolves the narrow windows of opportunity and risk that arise at dawn and dusk, and also allows a more direct comparison to data. However, the modeling framework is more technically challenging, and to make progress, Thygesen and Patterson (2018) ignored the costs and constraints of locomotion. While this may be reasonable for larger animals, such as tunas, smaller animals such as copepods or larvae are constrained by their maximum swimming speed, and the cost of locomotion can be expected to be a significant part of their energy budgets (Sprung 1984).

Therefore, this study aims to improve on the modeling framework developed by Thygesen and Patterson (2018) by including the cost of locomotion. Thus, we formulate a game, where each player is an animal which chooses a trajectory in space such as to maximize its fitness in a Darwinian sense. We assume that there are effectively infinitely many players, so that model is a differential mean field game in the sense of Lasry and Lions (2007). To achieve a simple and tractable model structure, we focus on the single-species case, where individuals of the same species play against each other. A model with some structural similarity has recently been posed for the collective motion of human pedestrians (Achdou and Lasry 2019).

We apply calculus of variations (Liberzon 2011) to reach a characterization of the Nash equilibrium in terms of partial differential equations, which turn out to have similarities to—but also notable differences from—the governing equations of fluid mechanics. Similar observations have been made in the field of differential mean field games (Lasry and Lions 2007). A seminal mean field game in spatial ecology is that which leads to the ideal free distribution (Fretwell and Lucas 1969), and we show that our model can be viewed as a dynamic extension of this paradigm.

Models based on partial differential equations are common in spatial ecology (Okubo and Levin 2001), many of these models being advection–diffusion equations. Most basically, such models assume the movement strategies of animals and determine the resulting distributions. In contrast, we seek the optimal strategies as well as the resulting distributions, across all conceivable movement strategies, but assuming that animals are rational decision-makers that have perfect global information about their current and future environment. Thus, our motivation is similar to that of Cosner (2005) and Cantrell and Cosner (2018), who identified dispersal strategies that resulted in the ideal free distribution: Starting from the axiom that each individual acts in its own interest, but do so in environments shaped by the actions of other animals, we seek equations that describe the dynamics at population level.

To be more specific, we demonstrate the approach using a test case which mimics diel vertical migrations of marine copepods. The animals are attracted to feeding opportunities near the surface, but repulsed from daylight due to the presence of visual predators; they also aim to avoid movements and being too close to conspecifics. This is an archetypal situation where animals have an incentive to migrate in response to persistent fluctuations in their environment. Our ambition is to verify that diel vertical migrations are the optimal behavioral response to this scenario, and to examine the shape of these migrations as we vary key parameters in the model. Relative to the study of Thygesen and Patterson (2018), our method offers the advantage of including cost of motion. Relative to the methodology employed by Pinti and Visser (2019), which was to formulate the problem as a matrix game and solve it using the replicator equation, our method has the advantage of representing time and space and time continuously and in particular resolve dawn and dusk. Moreover, the partial differential equations in our model lend themselves to efficient methods for analysis, including numerical analysis.

Indeed, an important element of our contribution is numerical analysis of the resulting equations. The structural similarity between the dynamics of fluids and those of optimal foragers suggests that inspiration can be found in well-established methods for computational fluid dynamics. However, these methods cannot be used off the shelf, since we pursue periodic solutions which turn out to be unstable, and therefore we establish numerical methods tailored for the specific problem.

Although our study focuses on the case of diel vertical migration in the plankton, we believe that differentiable mean field games are a natural framework in ecology that has wider applicability. The models we pursue here can cover also other cases of predictable migrations, such as seasonal migrations across latitudes. Further, the framework can be modified to cover dynamics of other state variables than position, such as individual body size. Our ambition for the study is to build a case for the general applicability of the approach, by demonstrating it on a fairly specific example. In the discussion we shall return to these perspectives.

Migrations as a dynamic game between individuals of the same species

Consider a population of animals distributed in a spatial domain $\mathbf{X} \subset \mathbf{R}^d$; the dimension d of the space may be one, two or three. We are interested in how the spatial density of animals varies over time, i.e., the function $N(t, x)$, $t \in \mathbf{R}$, $x \in \mathbf{X}$. Animals at position (t, x) move vertically with velocity $V(t, x)$. Our current aim is to pose equations that govern N and V. We are interested in phenomena which take place on a shorter timescale than the life span of an individual, so we ignore population dynamics and require that the continuity equation

$$\dot{N} + \nabla \cdot (NV) = 0 \tag{1}$$

holds. Here, $\dot{N} = \partial N/\partial t$ is time derivative while $\nabla\cdot$ is the divergence, $\sum_i \partial/\partial x_i$. Our interest is in a bounded domain with no-flux boundary conditions, which express that no animals leave or enter the domain across the boundary:

$$(NV)(t,x) \perp n(x) \text{ for all } t \in \mathbf{R}, x \in \partial\mathbf{X} \tag{2}$$

where $n(x)$ is normal to the boundary of $\mathbf{X}$ at x. Together, the continuity Eq. (1) and the no-flux boundary Eq. (2) express that a constant number of animals redistribute themselves in space by moving according to the velocity field V. This field V arises from decisions by the animals and thus derives from fitness optimization, as detailed in the following.

An animal at time t, position x and moving with velocity v is able to harvest energy at a rate $g(t, x)$ but spends energy on locomotion at a rate $\frac{1}{2}\nu|v|^2$. At the same time, it is subjected to a density-dependent mortality

$$\mu(t,x) = \mu_0(t,x) + \mu_1 N(t,x) \tag{3}$$

which is large enough to affect the decisions of the animals yet small enough that the resulting population dynamics can be ignored. For simplicity we let the density-dependent mortality be governed by a coefficient $\mu_1 > 0$ which is constant in space and time. Our interest is the situation of diel migrations where g and μ_0 are periodic in time with period $T = 1$ day.

The animal aims to maximize its net energy gain while minimizing its mortality and therefore has an incentive to seek out regions in space where the harvest rate $g(x, t)$ is high and the mortality $\mu(t,x)$ is low, but it must do so without excessive movements. According to unified foraging theory (Mangel and Clark 1986), these conflicting objectives are traded off against each other by combining them into a net gain rate

$$r(t,x,v) = g(t,x) - \frac{1}{2}\nu|v|^2 - F\mu(t,x), \tag{4}$$

which includes harvest, cost of locomotion, and mortality. Here the parameter F converts mortality to energy and is the expected harvest of energy until the animal dies, so that probability of dying $\mu\, dt$ in a small time interval dt is energetically equivalent to a loss of energy $F\mu\, dt$. We describe F as the "fitness" of the animal, since the energy harvested could be channeled into reproduction; this term should not be understood too literally.

For complete consistency, the fitness F would depend on time and space and would be obtained as the expected future energy harvest, i.e.,

$$F(t,x) = \int_t^\infty \left[g(X_s,s) - \frac{1}{2}\nu|V_s|^2\right] S_s\, ds \tag{5}$$

where (X_s, V_s) is the position and velocity of an animal which is alive at time t and at position $X_t = x$, and which behaves optimally thereafter. S_s is the probability that this animal is alive at time $s > t$, i.e., $S_s = \exp(-\int_t^s \mu(u, X_u)\, du)$. However, we once again assume that our model covers a small time span relative to the lifespan of the individual, so that temporal fluctuations in fitness can be ignored, and therefore we can consider F constant in time. Moreover, we aim to establish a game between the animals and pursue the Nash equilibrium of this game; at this equilibrium, all animals have the same fitness, so that F does not vary with space. Finally, by focusing on a single day and realizing that the environmental conditions may vary during the remaining lifetime of the animal, F cannot be computed solely from present-day conditions. In summary, we consider F constant and a free parameter.

If an animal chooses a trajectory $\{X_t : t \in [0,T]\}$ with corresponding velocity $\{U_t = dX_t/dt = V(t, X_t)\}$, then its change in fitness over one period [0, T] is

$$\int_0^T r(t, X_t, U_t)\, dt \quad . \tag{6}$$

Our fundamental assumption is that each animal behaves optimally in the sense of choosing a periodic trajectory $\{(X_t, U_t) : 0 \le t \le T\}$ such as to maximize this integral, for a given density function $N : (t,x) \mapsto N(t,x)$, i.e., the solution (N, V) must have the property that if all animals are distributed in space according to $N(t, x)$, then no single animal can benefit by deviating from the strategy $U_t = V(t, X_t)$. From a game-theoretic perspective, this is the definition of a Nash equilibrium in the mean field game, where each individual plays against the continuum of the remaining population (Lasry and Lions 2007). Mathematically, it can also be interpreted as a symmetric Nash equilibrium in mixed strategies in a two-player game, where $N(t,x)$ represents the probability density function of the opponent. From the point of view of evolution and adaptive dynamics (Geritz et al. 1998), the model is related to the strategy $U_t = V(t,X_t)$ being evolutionary singular: If the resident follows this strategy, then no rare mutant can obtain a higher invasion fitness. Note, however, that our model does not include population dynamics and therefore we do not follow the entire program of adaptive dynamics, where the hypothetical invader meets a resident population in ecological equilibrium.

From this fundamental assumption, we can derive the variational principle that the change in fitness (6) over one period must be insensitive to perturbations δX_t of the trajectory, i.e., the first variation vanishes. As is standard in calculus of variations (Liberzon 2011), we reach the Euler–Lagrange equations, which are d coupled ordinary differential equations governing X_t and U_t:

$$\frac{\partial r}{\partial x}(t,X_t,U_t) - \frac{d}{dt}\left[\frac{\partial r}{\partial v}(t,X_t,U_t)\right] dt = 0 \quad .$$

Inserting the specific forms for r, we find

$$\nabla(g - F\mu_0) - \mu_1 F\nabla N + v\frac{d}{dt}U_t = 0$$

Here, we omit the arguments (t,X_t) for notational clarity. If an animal has velocity $U_t = V(t,X_t)$, then its acceleration is $\frac{d}{dt}U_t = \nabla V(t,X_t)V(t,X_t) + \dot{V}(t,X_t)$, where ∇V is a matrix field with elements $\partial V_i/\partial x_j$. We obtain:

$$v\left[\dot{V} + (\nabla V)V\right] + \nabla(g - F\mu_0) - \mu_1 F\nabla N = 0 \quad . \tag{7}$$

Importantly, this equation must only hold where animals are found, i.e., at points (t,x) such that $N(t,x) > 0$. In places (t,x) where $N(t,x) = 0$, we do not define the velocity. Any trajectory that spends time in a region with $N = 0$ must lead to an increase in fitness over a period which is no greater than what is obtained by the animals that follow optimal trajectories. In this study we disregard this side condition, as our numerical case has $N(t,x) > 0$ everywhere, but we shall return to it in the discussion.

It is instructive to notice the structural similarity between this Eq. (7) and the one describing conservation of momentum in the flow of a compressible inviscid fluids, i.e., the Euler equation (Batchelor 1967, p. 164). See also the discussion in (Lasry and Lions 2007). With our notation, conservation of momentum in a fluid would imply

$$\dot{V} + (\nabla V)V + \nabla u + \frac{1}{N}\nabla p = 0$$

where (N, V) would be fluid density and velocity, u would be an external mass-specific potential acting on the fluid, and p would be pressure. We see that in this analogy, the habitat quality $(g - \mu_0 F)/v$ corresponds to the potential u driving the motion. Notice that the resulting "force" on the individual animal is in the direction of *decreased* quality $g - \mu_0 F$. This sign may seem counter-intuitive, but is consistent with the single-animal problem (Thygesen, in prep). Apart from the sign, it is an expected analogy that the external environment—specifically, spatial fluctuations in growth and mortality—drive the motion of animals. The term $\mu_1 F\nabla N$ in (7) indicate how animals should respond to the density of conspecifics. This corresponds to the pressure term in fluid dynamics, if we define the "pressure" as $p(t,x) = -N^2(t,x)\mu_1 F/v$. Note the sign and that the force on the individual animal, arising from the pressure gradient, is toward *increased* densities, which also may seem counter-intuitive but follows the same logic as the external forces. In summary, optimal foragers satisfy equations that are reminiscent of those governing fluid flows, although the signs and forces and the functional form of pressure could probably not have been guessed. The underlying reason for this similarity is the principle of least action (Goldstein et al. 2002). This principle, which permeates physics, states that molecules in a fluid follow trajectories which render the so-called action integral stationary, in the same way optimal foragers follow trajectories which render the fitness integral stationary.

Steady state and the ideal free distribution

Our principal interest is on the dynamics, but it is useful to also consider steady states. This, of course, assumes that the harvest rate g and the mortality μ do not vary with time. In one spatial dimension ($d = 1$), we seek solutions where $\partial N/\partial t = 0$ and $V \equiv 0$, i.e., each animal has chosen a fixed spatial location. Then, (7) simplifies to

$$\frac{\partial g}{\partial x} - F\frac{\partial \mu_0}{\partial x} - \mu_1 F\frac{\partial N}{\partial x} = 0 \quad .$$

By integration, we find $g - F\mu_0 - \mu_1 FN = c$ where c is an integration constant. This is the celebrated ideal free distribution (Fretwell and Lucas 1969): In that terminology, $g(x) - F\mu_0(x) - \mu_1 FN(x)$ is the *suitability* of the habitat at x, which in our case decreases linearly with the density N. In the ideal free distribution, the animals distribute themselves according to $N(x)$ such that no animal can benefit from relocating; a consequence is that all animals experience the same suitability c. The side condition then states that all void habitats ($N(x) = 0$) have a smaller *basic suitability* $g(x) - F\mu_0(x)$, implying that no animal can benefit from moving into a void habitat.

We can therefore view our model as an extension of the ideal free distribution to dynamic situations and taking into account cost of locomotion. This explains that we characterize the general solution as an ideal free flow of optimal foragers.

In a true steady state, consistency requires that the fitness F can be found from the integral (5) and thus satisfies

$$F = \frac{g(x)}{\mu_0(x) + \mu_1(x)N(x)},$$

for all x. Thus the integration constant vanishes ($c = 0$), and we reach

$$g(x) - \mu_0(x)F - \mu_1 FN(x) = 0 \quad ,$$

or, isolating the density $N(x)$:

$$N(x) = \frac{g(x) - F\mu_0(x)}{F\mu_1} \quad \text{whenever } N(x) > 0.$$

If the total abundance, i.e., the integral $\int N(x)\,dx$, is known, then this allows us to determine F and subsequently the distribution $N(x)$. Alternatively, if we assume steady-state also for population dynamics, then the fitness F can in principle be determined as the energetic cost to produce an offspring, and this allows us to determine the distribution $N(x)$ and the total abundance $\int N(x)\,dx$.

This establishes an equilibrium solution to the governing Eqs. (1) and (7) for the case where the parameters g and μ are constant in time. This equilibrium is typically hyperbolic, i.e., there exist stable and unstable manifolds consisting of solutions that converge to, or diverge from, the equilibrium. These stable solutions come into play when the environment is stationary, but the population is initially out of steady state and therefore has to redistribute to reach the ideal free distribution. Similarly, a terminal reward can be added to the model so that the population will eventually depart from the ideal free distribution along the unstable manifold to pursue the terminal reward. This hyperbolic structure is a general feature of dynamic optimization problems (Liberzon 2011). An important consequence of this, for the case of time-varying parameters, is that one should not attempt to solve the governing equations as initial value problems: Such solutions will quickly diverge along the unstable manifolds, which renders the solutions useless.

A numerical example

In this section we discuss a particular case of diel vertical migration in the ocean. The model is chosen to illustrate the mathematical framework as simply as possible, rather than to mimic a specific system. We envision a species of zooplankton, e.g., copepods, that are small enough that their movements are constrained by viscous drag and hence the power required is quadratic in the speed, in agreement with (7). We consider a relatively shallow habitat such as a continental shelf sea (alternatively, a deep lake), so that it is plausible that the simplifying condition $N(t, x) > 0$ holds everywhere. The copepods are subject to predation by planktivorous fish, which rely on visual detection, so that the instantaneous mortality depends on local light levels. The copepods themselves, in turn, rely on mechanosensing, so that their feeding rates do not depend on light levels but only on the abundance of prey, which varies with depth but not with time.

Model specification

We now detail the model, i.e., the functional forms of energy harvest rates and mortalities. Specific parameters in the model are given in Table 1 and argued for at the end of this section.

Mortality

The density-independent mortality μ_0 stems from visual predators. We take the resulting mortality to derive directly from the local light intensity, which governs the distance at which a predator can detect its prey. Our starting point is therefore the surface irradiance, which varies with the time of day according to the periodic function

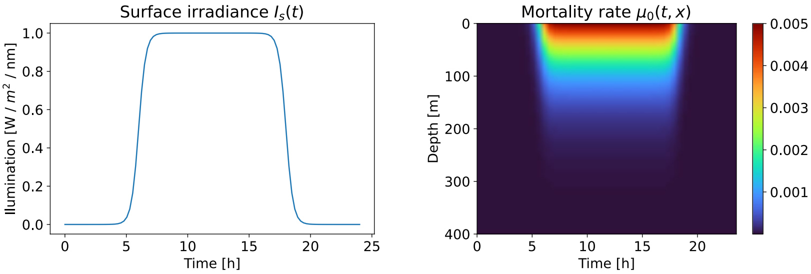
$$I_s(t) = \frac{I_0}{1 + \exp\left(A\cos(2\pi t/T)\right)} \quad . \tag{8}$$

The resulting irradiance is seen in Fig. 1 (left panel). Note that Thygesen and Patterson (2018) take into account astronomy and atmosphere optics; such an effort would hardly be worthwhile in the present more idealized context. Below the water surface, light decays exponentially with absorption

Table 1 Parameters in the model

Symbol	Parameter	Value	Units
H	Depth	400	m
T	Period	24	hour
A	Amplitude of light fluctuations	13	-
γ	Maximum detection distance	0.02	m
ν	Drag	10^{-6}	Jh/m^2
μ_1	Density-dependent mortality	1	1/hour
F	Fitness	2	J
k_1	Absorption coefficient	0.02	1/m
g_0	Maximum food availability	10^{-2}	J/hour
k_2	Harvest decay rate	0.02	1/m
x_{clin}	Mixed layer depth	100	m
m	Mortality scaling	25	m^{-2}hour^{-1}
I_0	Maximum irradiance	1	W m^{-2}nm^{-1}
K	Saturating light level	1	W m^{-2}nm^{-1}

Fig. 1 Model components. *Left panel:* Surface irradiance $I_s(t)$ during a day. *Right panel:* The density-independent mortality rate $\mu_0(t,x)$ (in per hour) as a function of depth and time of day



coefficient k_1. Then the light intensity $I(t, x)$ at depth x is given by

$$I(t,x) = I_s(t)\exp(-k_1x) \quad . \tag{9}$$

We next introduce the local detection radius $r(t, x)$, which is defined as the distance at which a predator can detect a prey at depth x and time t. We follow the reasoning of Aksnes and Utne (1997) and take as detection criterion that enough scattered photons from a prey arrive on the predator's retina and trigger a neural response in the predator. Aksnes and Utne (1997) take into account the spherical spread of light between prey and predator, the exponential decay of light along this line due to absorption, and saturation in the neural response, to arrive at the transcendental equation

$$r^2\exp(k_1r) = \gamma^2\frac{I(t,x)}{K + I(t,x)}. \tag{10}$$

Here I is the light level from (9) and K is a saturation parameter reflecting the transformation of the light energy to neural activity. γ is a compound parameter which combines the optical properties of the prey with the sensitivity of the predator, and which can be characterized as the detection distance in clear water ($k_1 = 0$) when light is abundant ($I \to \infty$). Once the detection distance r has been found, we posit that the predation mortality scales quadratically with the detection distance:

$$\mu_0(t,x) = mr^2 \quad . \tag{11}$$

Here, m is a free parameter which combines the speed, abundance and attacking success of predators. The justification is that predators cruise through the water with a speed that exceeds those of the zooplankton, effectively clearing cylindrical volumes (Kiørboe 2008a) in which the radius is r. This implicitly assumes that the density of predators is constant; a simplification that could be bypassed by explicitly modeling the distribution and movements of predators. The resulting mortality is depicted in Fig. 1, right panel.

The density-dependent mortality, in turn, is considered constant and fixed (Table 1). This is a coarse simplification of how densities of conspecifics affect the vital rates of an organism, and its justification is solely mathematical simplicity. We return to this in the discussion.

Energy harvest rate

We assume that the energy harvest rate is greatest near the surface and decreases with depth. Since we do not wish to include an explicit model of the distribution of the phytoplankton or microzooplankton that are the food source of our focal organism, we simply assume that harvest rate $g(t, x)$ depends logistically on depth:

$$g(t,x) = \frac{g_0}{1 + \exp(k_2(x - x_{\text{clin}}))} \quad . \tag{12}$$

Note that we take the harvest rate to be constant in time. This is consistent with copepods detecting prey using mechanical cues and assumes that behavior and prey density is constant during the day, which appears to be a reasonable approximation.

Model parametrization

The numerical values for parameters, as given in Table 1, are fixed mainly for illustrative purposes, but mimicking a case of an oceanic copepod of length 1 mm.

The maximum light level $I_0 = 1\ \text{Wm}^{-2}\text{mm}^{-1}$ just below the surface corresponds to blue light on a typical clear day (Wozniak and Dera 2007, p. 4), and the light amplitude $A = 13$ implies that the light levels at midnight are reduced with a factor $\exp(13) \approx 4.4 \cdot 10^5$ corresponding to a full moon (Bond 1861). The day is roughly as long as the night, meaning that the scene is low latitudes and/or around equinox. The absorption coefficient $k_1 = 0.02$ per meter corresponds to blue light in fairly clear ocean water (Wozniak and Dera 2007, p. 6). A saturation constant of $K = 1\ \text{Wm}^{-2}\text{mm}^{-1}$ in the vision of the predatory fish implies that they are generally not limited by light saturation, except partly at noon and at the surface. For the upper limit on detection distance we take $\gamma = 2$ cm in coarse agreement with (Munk and Kiørboe 1985). With these parameters, it is the spherical spread of light between prey and predator, rather than absorption, that determines the detection probability, as detection distances are short compared to the length scale of absorption.

The drag coefficient of $2 \cdot 10^{-6}$ Jh/m^2 corresponds to a spherical body of diameter 1 mm and a viscosity of 1 mPa s (Sharqawy et al. 2010, Fig. 8). Here we have used Stokes' law $F = 6\pi r \eta v$ for the viscous drag, the well-known relationship between force, velocity, and power, a muscular efficiency of 26 % and a hydrodynamic efficiency of 1 % (Kiørboe 2008b), and we have converted time from seconds to hours.

For the maximum rate of energy uptake, Kiørboe et al. (2014) reports a daily egg production under ideal conditions of 65 % of the body mass, with a 36 % efficiency from intake to eggs, and a body dry weight of 13 μg. We assume that the dry weight of the eggs is all protein and therefore has energy density 16 kJ/g. This gives an energy uptake of 15 mJ/hour. To reflect that uptake in the field is likely lower than under ideal laboratory conditions, we round this down and use a maximum uptake of $g_0 = 10$ mJ/hour. For the vertical profile, we take a fairly gradual transition with a cline at $x_{\text{clin}} = 100$ m and a $1/k_2 = 50$ m transition zone, noting that the vertical structure of the oceans display considerable variation (de Boyer et al. 2004).

The mortality parameter m is fixed so that the maximum predation mortality is $m\gamma^2 = 0.01$ pr. hour, and the fitness F corresponds to the energy harvested over a time span of 200 hours. These mortalities and life spans are within the range reported by Hirst and Kiørboe (2002). Note that we study a single day during the yearly cycle, and that constant uptakes and mortalities can be added to the model without changing the optimal migrations, so that fitness does not need to balance growth and mortality exactly.

Realizing that many of these parameters are very coarsely estimated, we use these parameters as a baseline and investigate also alternative scenarios, where selected key parameters are modified. We return to the issue of parameters in the discussion.

Computational scheme

We determine the periodic-in-time solution to the Eqs. (1) and (7) with no-flux boundary conditions (2) numerically by discretizing time and space and solving the resulting system of algebraic equations using a Newton method. To ensure convergence of the Newton method, we apply a homotopy perturbation method (Alexander and Yorke 1978; He 1999). Specifically, we include a homotopy perturbation parameter ϵ which modifies the original Eqs. (1) and (7) to the following system

$$\frac{\partial N}{\partial t} + \frac{\partial (NV)}{\partial x} = 0$$

$$v\left(\frac{\partial V}{\partial t} + \frac{1}{2}\frac{\partial (V^2)}{\partial x}\right) + \epsilon\frac{\partial g}{\partial x} - F\left(\epsilon\frac{\partial \mu_0}{\partial x} + \frac{\partial (N\mu_1)}{\partial x}\right) = 0 \tag{13}$$

Following the homotopy perturbation principle, the case $\epsilon = 1$ recovers the original system of equations, while for $\epsilon = 0$ we know an analytical solution: $N(t, x)$ is constant in space and time, and $V(t, x) \equiv 0$. Increasing the parameter ϵ from 0 to 1, we track the solution, until the solution to the original system is obtained with $\epsilon = 1$.

For a given value of $\epsilon \in (0, 1]$, we find the solution using an iterative Newton method. At each iteration, we linearize the equations around the previous guess and solve the resulting linearized PDE system. Our experience with the numerics is that these systems are all well posed so that the good initial guess from the previous value of ϵ ensures that the Newton method converges swiftly. We have not pursued the theoretical question if these systems of equations are well posed.

We discretize both time and space using the spectral collocation method. As functional basis we choose the Fourier basis with equidistant quadrature nodes for time, since we pursue periodic-in-time solutions, while for space we use a Legendre basis with Gauss–Lobatto quadrature nodes, respectively (Kopriva 2009). The computations are performed in `Python`.

Results

Figure 2 displays the density $N(t, x)$ corresponding to the baseline parameters in Table 1 (top left panel). During the daytime, the animals move to deeper waters to avoid visual

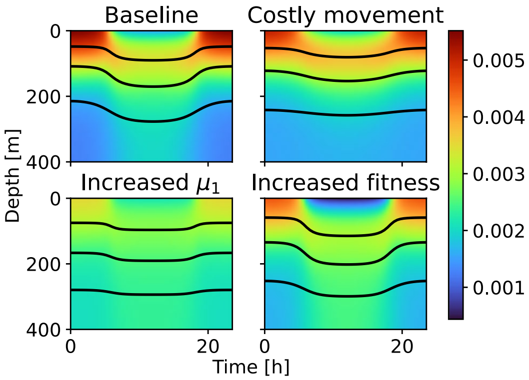


Fig. 2 Different simulated scenarios. Dark lines correspond to trajectories of an animal. Top left: Parameters from Table 1. Top right: Increased cost of motion v (×10). Bottom left: Increased density-dependent mortality μ_1 (×3). Bottom right: Increased fitness F (×1.5)

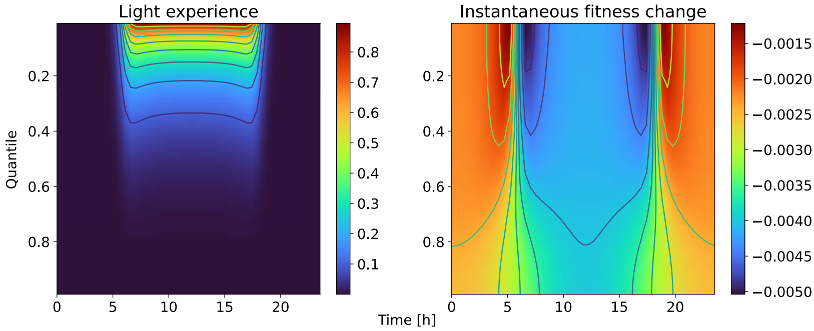


Fig. 3 The environment that an animal experience during a day. In both panels, the horizontal axis gives the time during the day (in hours) while the vertical axis gives the quantile of the animal in question; 0 being the animal nearest the surface and 1 being the animal nearest the bottom. *Left panel:* The light level experienced by the animal (in $\mathrm{W/m^2/nm}$). *Right panel:* The instantaneous rate of change in the fitness of the animal. Both panels are for the reference parameters in Table 1

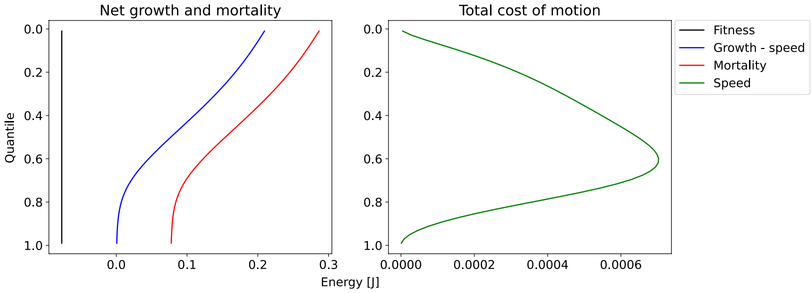
predation, while at dusk they return to upper levels to benefit from better feeding conditions during the night. The panel also displays the trajectories of 3 individual animals, chosen at the 25, 50, and 75 percentile of the distribution, respectively.

The figure also displays the results of modifying the underlying parameters. In the top right panel, the cost of motion has been increased by multiplying the parameter ν with a factor 10. As expected, the effect of this is that the animals perform migrations with narrower range. In the bottom left panel, the parameter μ_1 describing density-dependent mortality has been increased with a factor 3, resulting in a less concentrated distribution of animals. In the bottom right panel, the fitness F has been increased with a factor 1.5, corresponding to a situation where conditions are expected to improve, or where an extra constant source of food is available. The effect of this is that the trade-off between energy harvest and mortality is altered, so that the animals pursue more cautious strategies, i.e., follow deeper trajectories.

Figure 3 shows the environment that a single animal experiences during the course of a day. The quantile in these plots refer to the vertical distribution of animals, so that an animal with quantile 0 is always the closest animal to the surface while an animal with quantile 0.5 always has 50% of the animal population above it. Note that the model assumes that animals maintain their quantiles during the day, i.e., they do not pass each other, as this would be suboptimal. In the left panel, we see the light experienced by the animals. We see that animals, despite migration downward at dawn, experience much higher light levels during the day, although the light levels gradually decreases around noon, as the animals continue their migration. In the right panel, we see the instantaneous rate of change of fitness, i.e., the integrand r in (6) given by (4). We see that animals closer to the surface experience greater daily fluctuations, where the nighttime provide positive change due to feeding opportunities under relative safety, while the daytime poses threats of mortality that outweigh feeding opportunities. For the deeper animals, the pattern is qualitatively identical but less pronounced, as these animals experience less fluctuating environments.

Figure 4 shows the contributions to the change in fitness, integrated over the single day, for different animals given in terms of their quantiles. The left panel shows the net growth (uptake minus cost of motion) as well as loss of fitness due to mortality, while the right panel focuses on cost of transport. Note the different scales on the two horizontal axes; the cost of motion is orders of magnitude lower than

Fig. 4 The components in the daily change in fitness. In both panels, the horizontal axis gives the change in fitness (in joules) while vertical axis gives the quantile of the animal in question, as in Fig. 3. *Left panel:* Net growth (uptake minus cost of motion) (blue), loss of fitness due to mortality (red), and total gain of fitness (black) . *Right panel:* Total cost of motion (green)



the other fitness components. In the left panel, we see that all animals have the same loss of fitness of approximately 0.07 J during the day, which follows from the construction of a Nash equilibrium between the animals. However, the different animals reach this total in very different ways: The deepest animals have hardly any growth and low mortality, corresponding to an expected life time of approximately 25 days, while the animals closest to the surface only have an expected lifetime of about 7 days, but compensate with significant growth. In the right panel, we see that the cost of motion is generally low in comparison to the other components, but also that the animals in the middle spend the most energy on migrating.

Discussion

We have considered a population distributed in space, where each individual moves to maximize its fitness, and shown that the governing equations for the bulk movement of the population coincides with those that describe an inviscid compressible fluid.

Our case study concerns diel vertical migrations of a single species in the aquatic regime, but the problem and the approach has wider applicability in ecology. Most directly, it could be adapted to seasonal migrations, taking into account both costs of migrations and density dependence. In the aquatic regime, seasonal migrations driven by fluctuations in food availability and predation risks are common among the fishes and have been investigated with optimization models, for example roaches migrating between lakes and streams (Brönmark et al. 2008). We speculate that the approach could be applied to seasonal migrations of birds, insects, and terrestrial herbivores. Each of these applications possesses features that would require adaptation of the framework, such as intermittent migration of herbivores (Owen-Smith et al. 2010) and the effects of wind on long-range migration of insects (Chapman et al. 2015). Since the analysis provides both spatial distributions and trajectories of individual animals, data both at individual and population level can be used to inform, parametrize, and validate the models. The outcome of such modeling studies could be to predict changes in distributions and migratory behavior as results of changing environmental conditions.

At a higher level of abstraction, the approach can be generalized from movements in physical space to describe also changes in other state variables of the animal, such as body size. This would make the approach applicable to size-structured communities (Andersen 2019), where organisms face a growth/mortality trade-off which is influenced by the size composition in their community. In a broader sense, our study was motivated by the quest for mathematical techniques to support the trait-based approach to ecology (Kiørboe et al. 2018). Here, we believe that a natural and promising starting point is mean-field games, where individuals aim to maximize fitness in environments that are shaped by the behavior of other animals.

Many of these potential applications involve multiple interacting species, so a topic of future studies is to include predator–prey interactions or competition between multiple species. While this is straightforward, in principle, the modeling efforts will grow with the complexity of the system, as will the computational challenges, so case studies must be designed carefully. A first step could be to apply the present modeling framework to the system of Thygesen and Patterson (2018).

When parameters are constant in time, the ideal free distribution emerges as a special solution, and thus our model is a dynamic generalization of the ideal free distribution. There are several alternative approaches to such dynamic ideal free distributions: Cosner (2005) posed a partial differential equation, the equilibrium solution of which is the ideal free distribution. Cantrell et al. (2021) used the framework of adaptive dynamics to derive an evolutionarily stable dispersal strategy, and recently, Cantrell et al. (2010) extended the framework to path-dependent fitness in time-periodic environments. A key distinguishing element between models is the assumed information available to the animals. In standard chemotaxis models (Okubo and Levin 2001), animals infer on local conditions from sensory inputs, and Cantrell and Cosner (2018) showed that local information could yield the ideal free distribution in a stationary environment, but not in a time-periodic one. Here, we have made the idealization that animals are perfectly aware of both current and future conditions in the entire domain. Thus, our model can explain motion in response to periodic fluctuations in conditions, which have remained stable over evolutionary timescales. Diel and seasonal migrations are the most immediate examples of such motion.

We have not addressed if and how actual animals can follow the optimal trajectories that we have identified. In our case study, the solutions resemble qualitatively the widely documented diel vertical migrations of zooplankton (Klevjer et al. 2016), but we have refrained from a more quantitative comparison at a specific time, place, and for a given species. It is plausible that similar motions can be implemented with simple behavioral rules, for example, pursuing a constant light intensity while avoiding high densities of conspecifics as and excessive movements. The rationale behind the current study is that evolution has established some mechanism which yields patterns that resemble optimal ones. An interesting avenue of future research would be to extend the sensitivity study lying under Fig. 2 to examine also to which degrees such different trajectories can be obtained by simple behavioral rules. Such a study would arguably be more worthwhile in a more specific setting, parameterized for a particular species and system, as opposed to the idealized and generic settings of the current study.

In the periodic solutions we establish, all animals obtain by definition the same increase in fitness over the day, even if this increase may be distributed over the period differently for different animals. However, the animals closer to the surface obtain this increase by aggressively pursuing high growth rates, thus also enduring high mortalities. In contrast, the deeper animals have slower growth and lower mortality; also, different animals incur very different costs of locomotion. Thus, the population spans a niche in which different zones call for different specialized adaptations, and it is plausible that there are limits to how wide this niche can be while still remain in the scope of the species. These considerations are beyond the present modeling study, but would be interesting to pursue.

At a technical level, we established the governing equations using calculus of variations. The most common approach in studies of mean field games is to include diffusion and pose a Hamilton–Jacobi–Bellman equation, which would govern the optimization problem of the individual animal, in which the density of conspecifics enter as data. Here, without diffusive motion in the model, calculus of variations seems more direct and also yields the similarity with the Euler equations of fluid dynamics. However, the model can yield regions that are completely void of animals due to disadvantageous conditions at a given point in time, in the same way the ideal free distribution may predict void regions. Voids are numerically challenging, so we chose parameters for our numerical case study to avoid such regions. It would be interesting to investigate if such void regions can be resolved numerically using techniques from free surface flows, but pragmatically they can also be avoided by including a small diffusivity as a regularization parameter. With diffusion, the Hamilton–Jacobi–Bellman approach appears stronger. We intend to pursue more efficient numerical methods in future studies, so that wider regions in parameter space can be explored, and so that regions void or almost-void of animals can be investigated.

Computational practicalities aside, ecological reasoning would justify the inclusion of diffusion in the model of motion (Okubo and Levin 2001): The small aquatic animals we have in mind generally move unpredictably, which can be modeled as biased random walks and represented with diffusion terms in the governing equations, and are subject to turbulence which can also be represented by diffusion. In the interest of sparsity we have omitted diffusion from the model, noting that the main effect of diffusivity—to make animals spread out—is found in the model thanks to the density dependence of fitness, which gives the animals an incentive to disperse.

Our numerical analysis has employed spectral methods, while the common choice in numerical analysis of mean field games is finite difference methods (Achdou and Capuzzo-Dolcetta 2010; Achdou and Lasry 2019). The time periodicity of the domain, and the expected smoothness of the solution, motivated our choice. While spectral methods in this case give relatively high fidelity with relatively few basis functions, it is more difficult to establish properties of the discretized operators which guarantee convergence of the iterative solvers. Although the homotopy principle performed well, we believe that this issue underlies the numerical problems we encountered when pushing the limits of parameters space, in particular, as regions in space become almost-void of animals. We aim to investigate this further in future studies.

Our model is built using simplified functional forms, which could be expanded in future studies. First, our cost of movement is quadratic in the speed. This describes the energy spent on propulsion in creeping flow, which is justifiable for small animals. Other forms could include inviscid flows, which would lead to a cubic relationship between speed and cost, lost opportunity as described, e.g., by Thygesen et al. (2016), or increased conspicuousness to predators (Kiørboe et al. 1985). A second simplification is that the cost depends linearly on the density of conspecifics. A mechanistically based density dependence is not trivial to include in the model, as it could involve both interference in the foraging of conspecifics and attraction of predators to patches of conspecifics. Both of these extensions point in the direction of two-species models, or more generally multi-species models, which we aim to address in future studies. In the present study, the role of density dependent is to avoid singular distributions, i.e., all animals following the same trajectory, whereas the specifics of the density-dependent term is rather arbitrary. Another simplification is the form of the nutrient uptake, i.e., the term g in (4). It simple to extend this uptake to reflect a specific habitat with higher fidelity, but a more substantial extension, which would require quite different techniques for analysis, would be to include the dynamics and constraints of stomach fullness.

In our case study, the parameters have been chosen with a view toward oceanic copepods, but without being explicit about the system and the species. The justification for this is that the case is primarily motivated to illustrate the theoretical framework, and it must be acknowledged that several key parameters are not well known; in particular, the density dependence and the fitness. Therefore, sensitivity studies remain an important element of any study.

Our model is based on a time scale separation, where we argue that population dynamics can be ignored when studying a single day, even if mortality is high enough that animals take it into account when choosing diel strategies. The copepods in our case have a life time of weeks, which is arguably around the lower limit for the time scale separation to be justifiable. It would be easy to include mortality in the conservation equation, and correspondingly make the fitness a function of time, but we would then pursue quasi-periodic solutions rather than strictly periodic ones, and the benefit of including mortality explicitly would be questionable. Reproduction would be more difficult to include, as such a model would probably also have to include seasonal fluctuations in conditions, the stage structure of the populations in question, and the life history of the individual. Extending the model in these directions would perhaps be simple from a conceptual perspective, but tedious in terms of modeling and computations, and we believe that such an effort would not result in increased clarity compared to our approach of investigating a fast periodic pattern during which life history can be neglected.

We have emphasized the analogy between our governing equations and the Euler equations of fluid dynamics which describe compressible inviscid fluids. In this analogy, the density-independent terms in growth and mortality serve as an exogenous potential that varies in time and space and which drives the motion, while the density-dependent terms correspond to the thermodynamic concept of pressure. This analogy gives conceptual insight which may appeal in particular to ocean ecologists, as fluid flows already play a fundamental role in shaping oceanic habitats as well as the vital rates of animals that move and forage in these habitats. The analogy also gives access to a rich toolbox for analysis, including established numerical methods.

Nevertheless, there are important differences between the motion of animals and those of fluid particles, even within the model. First, while the potential in a physical model corresponds to net growth in a behavioral optimization model, we expect a compressible fluid to concentrate where the potential is lowest, while we expect animals to aggregate where the net growth rate is highest. Similarly, it may seem disturbing that the “pressure” of animals is negative and decreases with the density. These observations are related to the solutions of interest: While focus of fluid mechanics is, generally, on (Lyapunov) stable solutions or attractors, the solutions of interest for the motion of animals are intrinsically unstable when viewed as initial value problems.

This also contrasts our model to the typical advection–diffusion equations in spatial ecology: In our case, the solutions are stabilized by the animals looking ahead in time when taking decisions and responding to anticipated events such as sunrise, so information travels backward while densities evolve forwards. This is the situation for optimal control problems (Liberzon 2011) as well as for mean-field differential games (Lasry and Lions 2007; Achdou and Capuzzo-Dolcetta 2010). For numerical analysis, one can therefore not rely on time stepping (neither forward nor backward), which is the reason we in this paper have focused on time-periodic solutions, as was also done by Achdou and Capuzzo-Dolcetta (2010). Alternatively, one may consider mixed initial/terminal value problems, as was done by Achdou and Lasry (2019) for human pedestrians.

In conclusion, we have established a framework consisting of partial differential equations governing the optimal motion of individual members of a population in response to periodically fluctuating environmental conditions. The equations are similar to those governing fluid flows, so that their solutions describe ideal free flows of optimal foragers. We have investigated a particular case, in an idealized setting, of planktonic copepods performing diel vertical migrations in the water column in response to sunrise and sunset, and shown that the model predicts patterns which are similar to those empirically observed. In general, we believe that the framework of differential mean field games has wide applications in ecology. More specifically, we believe that viewing migrating animals as elements in ideal free flows can illuminate animal migration and offers rich opportunities for further development, both in terms of theoretical analysis and specific case studies.

Author contributions UHT conceived the study and the analysis. MM detailed the analysis and the numerical implementation. UHT drafted the initial manuscript and both authors completed the manuscript.

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Code availability The code used to perform the calculations and generate the figures will be placed in a publicly accessible GitHub repository after acceptance of the manuscript.

Declarations

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Paper B

Mean Field Games for Diel Vertical Migration with Diffusion

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Mean field games for diel vertical migration with diffusion

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Abstract

We present a theoretical framework, based on differential mean field games, for expressing diel vertical migration in the ocean as a game with a continuum of players. In such a game each agent partially controls its own state by adjusting its vertical velocity but the vertical position in a water column also subject to random fluctuations. A representative player has to make decisions based on aggregated information about the states of the other players. For this vertical differential game we derive a mean field system of partial differential equations for finding a Nash equilibrium for the whole population. It turns out that finding Nash equilibria in the game is equivalent to solving a PDE-constrained optimization problem, which we derive under constant approximation of the expected fitness of the representative player and solve both formulations numerically. We illustrate the results on simple numerical examples and construct several test cases to compare the two analytical approaches.

Keywords: Vertical migration, Optimal behavior, Mean field games, Habitat selection

MSC Classification: 91A16 , 92D50 , 49N80 , 49N20

1 Introduction

Mean field game theory, introduced by Lasry and Lions in Lasry and Lions (2007), models games with a large number of interacting agents in the limit as the number of players goes to infinity $N \to +\infty$. To make the limiting case traceable it is usually assumed that all the players are equivalent, meaning that they share the same set of admissible strategies and have identical structure of the utility function, but see for example Carmona and Zhu (2016); Bensoussan et al (2018) for games with relaxed assumption on the symmetry between the players. Every agent has access to aggregated information about the organization of the population and has to make decisions based on the mean field structure of the available information about the surrounding environment. In turn, individual decisions of each agent change the macroscopic organization of the whole population. Mean field game theory has a number of applications in economic theory and financial engineering Carmona (2020); Gomes et al (2015); Bertucci et al (2020), behaviour of crowds Carmona and Delarue (2018a) and policy design Carmona (2016).

Another domain with large populations of interacting agents is ecology, where animals may interact through predation and compete for limited resources. One example of a game with a vast number of players is diel vertical migration in aquatic systems, which is believed to constitute the largest movement of biomass on the planet and is ubiquitous in the ocean Brierley (2014). In the migration process animals remain in deep water layers during daylight hours to avoid visual predators and migrate to upper levels in a water column at dusk to feed.

This manuscript contributes to a series of papers to understand and model diel vertical migration using a game theoretical framework. The first work to our knowledge is Iwasa (1982) where the author constructed a matrix game model of the phenomenon. Established results were pushed further by several authors, for example: the work Sainmont et al (2013) divided the water column in two layers – namely, surface and depth. However, these solutions are not evolutionarily stable due to absence of self-interaction Gabriel and Thomas (1988). The paper Pinti and Visser (2019) increased the spatial resolution but kept the time resolution in two states – day and night time periods. These models use coarse resolution in either space or time (or both), thus giving a very crude approximation of the positions and strategies of the players at transition time period – at dawn and dusk. The work Thygesen and Patterson (2019) modeled vertical migrations in continuous space and time, using control theory tools Liberzon (2011) for finding optimal strategies of the animals. It allows to resolve the narrow time frame at dawn and dusk and a more direct comparison to data. However, the resulting modeling framework is more technical and the paper Thygesen and Patterson (2019) ignored the costs and constraints of locomotion. The model from Thygesen and Mazuryn (2022) resolves the dynamics in continuous space and time taking into account the cost of motion, but the equations are limited to the shallow water case, where the optimal density of the players is strictly positive at each point of a water column. The aim of this manuscript is to extend our previous modelling framework from Thygesen and Mazuryn (2022) with added random fluctuations in the vertical position of the agents to cover all depth ranges. In contrast to the previous paper, we utilize the Feynman-Kac formula Kac (1949) to derive the resulting mean field system with the previous model being a special case of the new one.

Here, we model diel vertical migration as a mean field game with a continuum of individuals and apply the mean field game theoretical framework to describe Nash equilibrium in terms of partial differential equations. We add random fluctuations to the state of each agent which might be due to incomplete perception of the surrounding environment or random forces acting on the individual, e.g. from turbulence. It is important to stress that any two agents have independent trajectories of the white noise realizations. The case with correlated noise, common noise or shocks Carmona and Delarue (2018a,b) will not be considered in this manuscript.

An important contribution of this work is establishing two equivalent formulations of the problem: as a system of partial differential equations via mean field limit or, under quasi-static approximation, as a PDE-constrained optimization problem. This equivalence allows access to a wide range of analytical tools to study the problem analytically and numerically.

2 Method

2.1 The vertical game formulation

We consider a population of generic species distributed in a water column $[0, H]$ of maximum depth H with $X_t^{(i)}$ as the vertical position of i-th player at time t. Our model includes only vertical migration of the agents and disregards horizontal dynamics. We model diel vertical migration of marine organisms as a game with infinitely many players where each animal plays against others, seeking regions with high concentration of food and low mortality subject to cost of motion. The vertical speed $V_t^{(i)}$ can be considered as a strategy the i-th player can choose to play against other agents. Sometimes we will utilize control theory terminology and refer to $X_t^{(i)}$ and $V_t^{(i)}$ as a state of the individual and its control, respectively.

It is assumed that all the players are identical and the information an agent has access to is a mean field type, i.e. each player can only see aggregated information about the population. Due to the symmetry between the players we choose a representative player to model the behaviour of the whole population. To highlight indistinguishability of the agents in the game we omit upper indexes in the state X_t and the control V_t variables and consider them as vertical coordinate and speed of the representative player, respectively.

The position dynamics of the representative agent in the water column is driven by the stochastic differential equation:

$$\mathrm{d}X_t = V_t \,\mathrm{d}t + \sigma \,\mathrm{d}B_t, \tag{1}$$

with B_t as standard Brownian motion scaled with constant noise level σ and each player in the population has an independent realization of the Brownian motion. The scaling factor σ is the same for all the players.

The equation (1) describes vertical motion of the representative player who can control its vertical speed V_t at each moment of time subject to uncontrolled external random fluctuations $\sigma\,\mathrm{d}B_t$ of its vertical position. We impose reflective boundary condition on the surface and the bottom of the water column $[0, H]$ assuming that no new agents can appear through the boundary.

Each player in this vertical game optimizes the fitness functional over its lifetime period:

$$J(V) = \mathbb{E}^{X_0=x}\left[\int_0^\tau g(X_s, s) - \frac{\nu}{2}V^2(X_s, s)\,\mathrm{d}s\right], \tag{2}$$

where τ is a random time of death of the representative player. For the process X_t to be alive means that for $t < \tau$ it follows the equation (1), while for time $t \geq \tau$ after the "death" we assume that the process enters a special "coffin" state $X_t = \partial$ and stays there for $t \geq \tau$ Oksendal (2013). The killing rate is defined as:

$$\mu(x, t) = \lim_{s\to 0}\frac{1}{s}\mathbb{P}^{X_t=x}\left[X_{t+s} = \partial\right], \quad x \neq \partial$$

Further in the text we use terms killing rate and risk rate interchangeably.

The functional (2) represents the fitness of the representative player defined as expected accumulated energy of the player over the lifetime period following the trajectory X_t and the vertical speed V_t, which are coupled by the stochastic differential equation (1). Expression of the functional favours regions of high food concentration with the energy harvest rate g and avoids visiting regions with high mortality rate μ, which is implicitly present through the death time τ of the agent. The functional takes into account the cost of locomotion by penalizing quick changes in the vertical position of the player. We assume that our animals are small enough, for example copepods or other zooplankton, to keep the cost of motion proportional to squared vertical speed with drag coefficient ν.

The risk rate μ is defined as:

$$\mu(x, t) = \mu_0(x, t) + \mu_1 N(x, t). \tag{3}$$

The risk rate is composed of density independent mortality rate μ_0, which represents the risk of encounter of a single agent with visual predators and defined as a function of light abundance, and the density dependent mortality term $\mu_1 N$ which penalizes aggregation of the players. The latter term in (3) is a mean field component of the model which describes the interaction between the representative player and the whole population.

We fix the time period $T = 24$ hours and assume that both harvest g and density independent mortality μ_0 rates are periodic functions with a period T, i.e. all days are identical and seasonal fluctuations are disregarded. The selected time period is small enough to neglect population dynamics and fluctuations in the population size. We fix the total biomass in the water column and normalize it to 1. Now the optimal density N can be considered as a probability distribution of finding a player in a specified depth range at a fixed point of time.

Utilizing the above mentioned symmetry assumption we are looking for the vertical speed as a Markovian closed loop control in the form $V = V(X_t, t)$, i.e. the optimal strategy for the representative player is a function of its state X_t at time t. With periodic mortality μ_0 and harvest g terms we are looking for a time-periodic solution pair (N, V) to the differential game.

2.2 Mean field system

The outlined formulation of the game as a control problem with the state (1) and the objective functional (2) can be transformed into a system of partial differential equations via the mean-field limit. The idea is to utilize the postulated symmetry of the information and the fact that the game has infinite number of players. It allows to zoom out from the individual-level dynamics of the representative player descried by the stochastic differential equation (1) and consider the time evolution of the population density.

The stochastic differential equation (1), which governs evolution of the vertical position of the representative player, is consistent with the forward Kolmogorov or Fokker-Plank equation:

$$\frac{\partial N}{\partial t} = -\frac{\partial (NV)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}. \tag{4}$$

We omit mortality and source terms in the forward Kolmogorov equation from the random death time τ because we are solving the vertical game in a short time period, relative to the lifetime of the players, where the population dynamics can be disregarded.

The no-flux condition on the boundary $x = \{0, H\}$ of the water column is expressed as:

$$NV - \frac{\sigma^2}{2}\frac{\partial N}{\partial x} = 0. \tag{5}$$

The normalization condition for the total biomass is written as:

$$\int_0^H N(y,t)\,\mathrm{d}y = 1,$$

for time $t \in [0, T]$.

We define the value function U for a given density N as the expected fitness of the representative player starting in $X_t = x$ at time t and who plays optimally:

$$U(x,t) = \sup_V \mathbb{E}^{X_t=x}\left[\int_t^{+\infty} \left(g(X_s,s) - \frac{\nu}{2}V^2(X_s,s)\right) e^{-\int_t^s \mu(X_\xi,\xi)\,\mathrm{d}\xi}\,\mathrm{d}s\right], \quad x \neq \partial \tag{6}$$

conditional on the representative playing the optimal strategy V. The exponent in the expression (6) is the conditional probability of the player being alive. We would like to find the optimal velocity field V which maximizes the expected fitness of the representative player.

The integral in the expression (6) exists by the dominated convergence theorem Rudin et al (1976) because both terms g and V are bounded functions and the integral in the exponent is a nonnegative bounded number. Invoking the Feynman-Kac formula Kac (1949), the fitness U from (6) is the solution to:

$$\frac{\partial U}{\partial t} + \sup_v \left(LU + g - \frac{\nu v^2}{2}\right) = 0, \tag{7}$$

where the generator L is defined as the differential operator:

$$LU = v\frac{\partial U}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 U}{\partial x^2} - \mu U.$$

Similar to Thygesen (2022), we can use the duality argument between the forward and backward Kolmogorov equations to establish that reflection at the boundaries $x \in \{0, H\}$ from (5) corresponds to a homogeneous Neumann boundary condition for the function U:

$$\frac{\partial U}{\partial x}(x,t) = 0 \quad \text{for} \quad x \in \{0, H\}$$

The interval of our interest for the control problem is $[0,T]$ due to the periodicity assumption. The boundary condition for the value function on the interval is $U(x,0) = U(x,T)$, meaning that the expected fitness of the representative player at $t = 0$ is the same as at $t = T$, assuming that the player survives during the one day time interval.

As the function inside the supremum in (7) is a concave quadratic function of the argument v, the global maximum exists and is attained at $V = \frac{1}{\nu}\frac{\partial U}{\partial x}$.

Substituting the form for the optimal velocity V into the Hamilton-Jacobi-Bellman equation we arrive to the following mean field system:

$$\begin{cases} \frac{\partial N}{\partial t} = -\frac{\partial (NV)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2} & (x,t) \in (0,H)\times(0,T) \\ \frac{\partial U}{\partial t} + \frac{1}{2\nu}\left(\frac{\partial U}{\partial x}\right)^2 + \frac{\sigma^2}{2}\frac{\partial^2 U}{\partial x^2} + g - U(\mu_0 + \mu_1 N) = 0 & (x,t) \in (0,H)\times(0,T) \\ \int_0^H N(y,t)\,\mathrm{d}y = 1 & t \in [0,T] \\ U(x,0) = U(x,T) & x \in [0,H] \\ N(x,0) = N(x,T) & x \in [0,H] \\ (NV - \frac{\sigma^2}{2}\frac{\partial N}{\partial x})(x,t) = 0 & x \in \{0,H\} \\ \frac{\partial U}{\partial x}(x,t) = 0 & x \in \{0,H\} \\ V = \frac{1}{\nu}\frac{\partial U}{\partial x} \end{cases} \tag{8}$$

The PDE system (8) is similar to the one from Thygesen and Mazuryn (2022) with a couple of major differences: now there is a diffusion term in the Fokker-Plank equation due to the randomness in the vertical position of the representative player. And, since we don't impose the quasi-static approximation for the value function, the mortality term in the Hamilton-Jacobi-Bellman equation includes U instead of a constant approximation of the expected fitness.

Our modelling set-up is not covered by the contemporary existence and uniqueness theorems in the mean field game theory literature Lasry and Lions (2007); Carmona (2016); Carmona and Delarue (2018a,b), therefore we use the verification theorem approach for the Hamilton-Jacobi-Bellman equation Oksendal (2013): if we can solve the PDE system (8), then we have found a Nash equilibrium of the vertical game and the optimal control exists and indeed is given by $V = \frac{1}{\nu}\frac{\partial U}{\partial x}$. Numerical analysis will reveal if the solution is locally unique, i.e. if the differential equations are locally well-posed.

2.3 PDE-constrained optimization formulation

In this section we aim to show that the Nash equilibrium in the differential mean field game can also be found through a related (but different) optimization over the population. One of the reasons to consider this equivalence is due to flexibility of choice for numerical methods when solving the vertical game. We can use optimization-based methods for solving a PDE-constrained optimization problem rather than equation-solving methods for the system (8).

For simplicity, we consider the mean field limit where the animals are long lived relative to the day, so that fluctuations in the value function U over the one day time can be neglected. Then a system of PDEs similar to (8) appears by replacing U with a constant approximate fitness F. Each individual in the new game optimizes the fitness functional:

$$J(V) = \mathbb{E}^{X_0=x}\left[\int_0^{24} g(X_s,s) - F\mu(X_s,s) - \frac{\nu}{2}V^2(X_s,s)\,\mathrm{d}s\right], \tag{9}$$

with the state subject to (1). The deterministic version of this game has been extensively studied in the paper Thygesen and Mazuryn (2022) and here we will discuss another analytical approach for finding the Nash equilibrium.

To find the pair (N,V) for the quasi-static vertical game (9) we consider the following PDE-constrained optimization problem:

$$\max_{N,V}\int_0^H\int_0^T\left(g - F\left(\mu_0 + \frac{\mu_1 N}{2}\right) - \frac{\nu V^2}{2}\right)N\,\mathrm{d}s\,\mathrm{d}y, \tag{10}$$

subject to the forward Kolmogorov equation:

$$\frac{\partial N}{\partial t} = -\frac{\partial(NV)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}, \tag{11}$$

with the zero-flux, periodic and normalization conditions on the density N and control V from the PDE system (8). The constant F here is an approximate expected fitness of the representative player until death.

It should be noted that the objective functional (10) in the optimization problem is almost identical to the expected fitness (9) from the formulation of the mean field system. The only difference is in the term which describes interaction between an individual player and the aggregate of other agents $\mu_1 N/2$, which is another manifestation of the intrinsic structure of the mean field game. It turns out that all the players as the whole optimize a slightly different quantity than the total fitness of the population.

The equivalence comes from the fact that the differential game with the objective (9) has a potential structure Lasry and Lions (2007), when the running cost is a functional derivative De los Reyes (2015) of some potential. It turns out that solving a game with the potential structure is equivalent to solving the PDE-constrained optimization problem (10). Similar observations on the differential games have been made in the paper Lasry and Lions (2007) and we include the equivalence argument here because our form of the cost functional is slightly different and to keep the presentation self-contained.

One way to establish the correspondence is to consider the functional equivalent of the method of Lagrange multipliers for the PDE-constrained optimization problem by writing the corresponding optimality system De los Reyes (2015) for the PDE-constrained problem. The Lagrange functional associated to the constrained problem (10) has the following form:

$$L(N,V,p) = \left\langle g - F\left(\mu_0 + \frac{\mu_1 N}{2}\right) - \frac{\nu V^2}{2}, N\right\rangle$$

$$-\left\langle \frac{\partial N}{\partial t} + \frac{\partial (NV)}{\partial x} - \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}, p \right\rangle,$$

where p is a Lagrange multiplier corresponding to the constraint (11). The brackets here indicate inner product, i.e. integrals over both space and time.

We calculate functional derivatives of the Lagrange functional L with respect to each of the variables N, V and p along admissible directions by integrating the corresponding integrals by parts and setting them to be equal to zero.

$$\begin{aligned} L_N(N,V,p)\delta N = &\left\langle g - F(\mu_0 + \mu_1 N) - \frac{\nu V^2}{2} \right. \\ &\left. + \frac{\partial p}{\partial t} + \frac{\partial p}{\partial x}V + \frac{\sigma^2}{2}\frac{\partial^2 p}{\partial x^2}, \delta N \right\rangle \\ &- \oint_{\partial\Omega_{t=\{0,T\}}} p\delta N \cdot \boldsymbol{n}\, \mathrm{d}\alpha - \frac{\sigma^2}{2}\oint_{\partial\Omega_{x=\{0,H\}}} \frac{\partial p}{\partial x}\delta N \cdot \boldsymbol{n}\, \mathrm{d}\alpha \\ &= 0. \end{aligned} \tag{12}$$

$$L_V(N,V,p)\delta V = \left\langle N\left(\frac{\partial p}{\partial x} - \nu V\right), \delta V \right\rangle = 0. \tag{13}$$

$$L_p(N,V,p)\delta p = -\left\langle \frac{\partial N}{\partial t} + \frac{\partial (NV)}{\partial x} - \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}, \delta p \right\rangle = 0. \tag{14}$$

These equalities should hold along any admissible direction δN, δV and δp. We are not particularly concerned about which functional spaces these functions belong to, only them being admissible directions.

The expression (14) yields the forward Kolmogorov equation from the mean field system (8). From (13) we arrive to $V = \frac{1}{\nu}\frac{\partial p}{\partial x}$, which establishes the relation between the adjoint state p and the velocity field V, similar to the one we established between the value function U and the optimal control V in (8). The first term in the equation (12) yields the Hamilton-Jacobi-Bellman equation from (8) replacing the co-state p with the value function U and applying the quasi-static approximation of the expected fitness. The contour integrals give the time periodicity condition for the co-state as a function of time and the homogeneous Neumann boundary condition for p along $\partial\Omega_{x=\{0,H\}}$ part of the domain boundary.

One more thing to note is that the constrained optimization problem (10) optimizes over all admissible pairs (N, V). Due to nonzero diffusivity parameter σ we can optimize over the vertical speed V and retrieve the corresponding optimal density N from the forward Kolmogorov equation due to its well-posedness.

3 Numerical study

In this section we take the system of PDEs (8) and solve it numerically for different parameter scenarios. Specific forms of the harvest and mortality rates are taken from our previous paper and here we briefly present essential parts of the model to make the text self-contained. For a more detailed discussion on the model parameters we refer to Thygesen and Mazuryn (2022). The model is inspired by the vertical migration of zooplankton subject to visual predators like planktivorous fish. It will be shown that daily fluctuations in the light levels at depth cause diel vertical migration of the animals.

3.1 Model set-up

We incorporate only visual predation in the model with the mortality rate μ_0 which corresponds to the chance of being detected and eaten by a predator (planktivorous fish). The encounter risk is proportional to the surface area of a detection sphere – a theoretical concept which denotes a ball around a predator of the critical radius r, where enough scattered photons from a prey arrive on the predator's eye and trigger a neural response.

The surface illumination is a periodic function with a period T:

$$I_s(t) = \frac{I_0}{1 + \exp\left(A\cos(2\pi t/T)\right)}$$

At depth in the water column the light intensity decays exponentially with the absorption coefficient k_1:

$$I(x,t) = I_s(t)\exp(-k_1 x)$$

By r we denote radius of the detection sphere with center at depth x at time t. Utilizing the visual range model with saturation from Aksnes and Utne (1997) yields:

$$r^2 \exp(k_1 r) = \gamma^2 \frac{I(x,t)}{K + I(x,t)}$$

The parameter γ here combines the reflection properties of the prey with the visual sensitivity of the predator eye.

Then the risk rate μ_0 is proportional to surface area of the detection sphere with the scaling constant m plus the baseline mortality μ_{base} – a constant mortality rate due to other causes than predation:

$$\mu_0(x,t) = mr^2 + \mu_{\text{base}}$$

The energy harvest rate g is proportional to the food abundance in the environment – phytoplankton concentration for this specific example. For the sake of simplicity, to avoid explicit modelling phytoplankton distribution in the

Symbol	Parameter	Value	Units
H	Depth	500	m
T	Period	24	hour
I_0	Maximum irradiance	1	W m^{-2} nm^{-1}
K	Saturating light level	1	W m^{-2} nm^{-1}
γ	Maximum detection distance	0.02	m
k_1	Absorption coefficient	0.02	m^{-1}
A	Amplitude of light fluctuations	13	-
ν	Drag	10^{-6}	J h m^{-2}
σ^2	Diffusion	20	m^2 hour^{-1}
μ_1	Density-dependent mortality	1	hour^{-1}
m	Mortality scaling	100	m^{-2} hour^{-1}
μ_{base}	Baseline mortality	10^{-5}	hour^{-1}
k_2	Harvest decay rate	0.02	m^{-1}
g_0	Maximum food availability	0.01	J hour^{-1}
x_{clin}	Mixed layer depth	100	m

Table 1 Model parameters mostly from Thygesen and Mazuryn (2022) with added diffusivity and baseline mortality.

sea, we assume that the harvest rate is time invariant and depends logistically on depth:

$$g(x,t) = \frac{g_0}{1 + \exp(k_2(x - x_{\text{clin}}))}$$

3.2 Numerical methods

To calculate numerical solutions we discretize the system (8) with a spectral element scheme using the FEniCS package. The computational domain $[0,H] \times [0,T]$ is triangulated and the analytical solution is approximated by polynomials with pre-defined degrees on each triangle. In calculations we select first and second order polynomials to approximate the unknown function pair (N,V).

The discretized version of the PDE system is solved by a Newton-type method where we can control the step size. This approach is different from the paper Thygesen and Mazuryn (2022), where we developed the homotopy method and solve a sequence of auxiliary problems to find a Nash equilibrium in the vertical game.

The numerical approximation of the equivalent PDE-constrained optimization problem (10) and its comparison with the mean field system (8) is presented in Appendix B.

3.3 Numerical results

We take the parameters from Table 1 and numerically solve the system of partial differential equations (8). Figure 1 displays the optimal distribution N of the population in the water column for the fixed time period with the optimal vertical velocity field V.

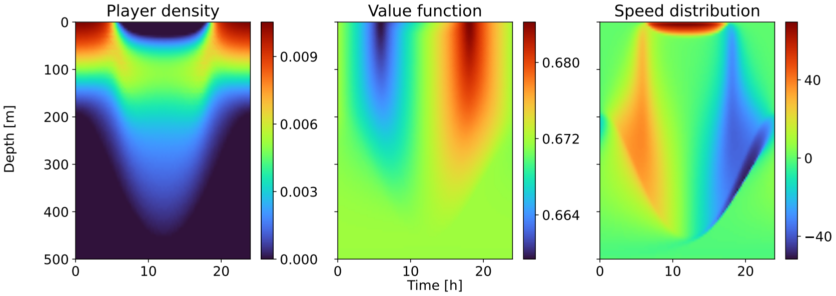

Fig. 1 Nash equilibrium for the model parameters from Table 1. *Left panel*: Optimal density N. *Middle panel*: Value function U. *Right panel*: Vertical velocity field V.

During daytime hours the animals move to deep water layers with low light intensity to reduce the encounter rate with the visual predators as in Figure 1 (left panel). When light intensity decreases at dusk, the players return to upper layers with decreased mortality risk near the surface to benefit from higher nutrient concentration. It should be noted that the optimal density N is symmetric around $t = 12$ hours which, as expected, comes from the symmetry of the model parameters.

Naively, one would anticipate a symmetric velocity profile V by looking at the symmetry of the optimal density in Figure 1 (right panel). In contrast to the density N, the vertical speed field is not an odd function. The model predicts that at around $t = 10$ animals descend faster than they ascend at around $t = 16$ and it is due to high risk of being close to the surface during daytime. The speed distribution shows that if an agent gets in that region by influence of the error $\sigma \, \mathrm{d}B_t$ in the vertical position, then it should leave the region immediately even at a cost of high speed.

The origin of the asymmetry comes from the state dynamics (1) of the representative player. Two processes contribute to the final position of the agent: the player can only control the advection part by choosing appropriate vertical speed, while the diffusion process is left uncontrolled. The agent tries to compensate contribution of the diffusion part to the position in the water column by adjusting its vertical speed. We refer to Appendix A for a more analytical discussion on the observed asymmetry in Figure 1 and numerical study of the analytical model for various noise levels σ.

Figure 2 displays optimal densities N and the corresponding value functions U of simulating several modelling scenarios with modified model parameters. In the top row panels we fix the baseline case from Figure 1 discussed above. We add black lines which correspond to mean trajectories of 3 individual players for a better visualization of impact of the parameters on individual dynamics. In the middle panels, the cost of motion has been increased by multiplying the drag parameter ν with a factor 10. As expected, now the players are less inclined to move and stay in the preferred water level. In the bottom row, the risk rate μ_1 describing density-dependent mortality has been decreased by a factor 10, which can correspond to decreasing predator abundance in the

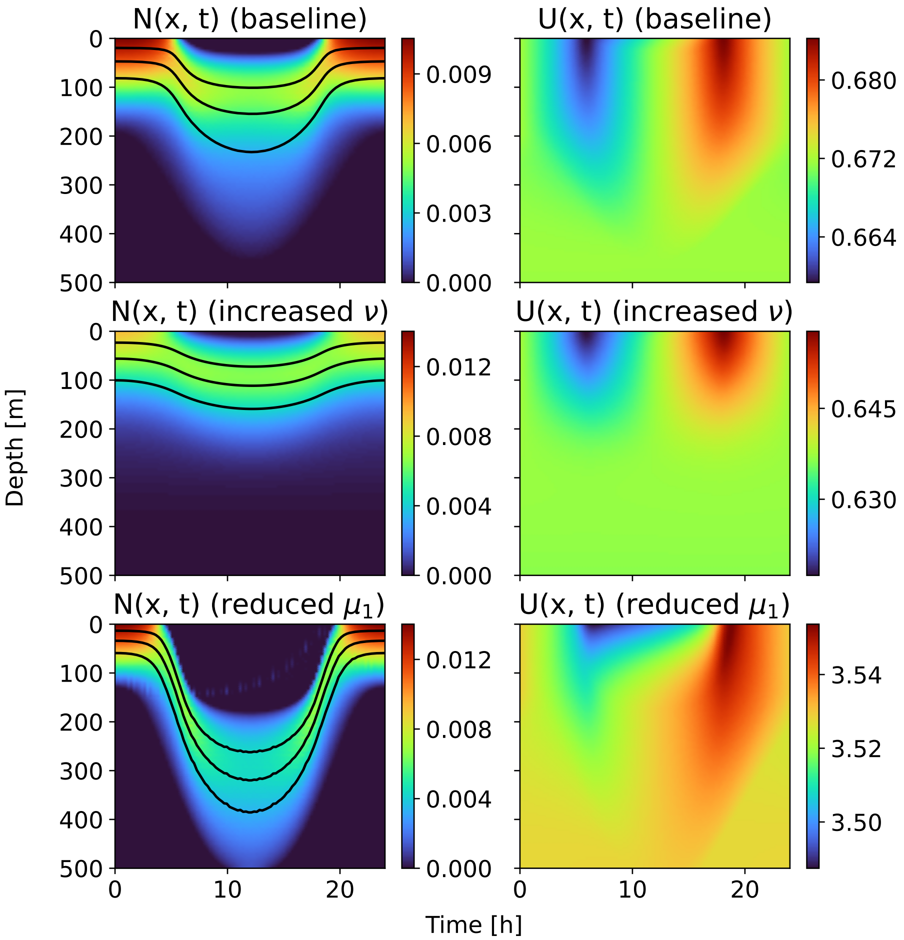

Fig. 2 Sensitivity of the Nash equilibrium for several model set-ups. *Top row*: Baseline case with the parameters from Table 1. *Middle row*: Increased cost of motion ν ($\times 10$). *Bottom row*: Reduced density-dependent mortality μ_1 ($\times 0.1$).

water column. Reduced number of predators makes beneficial high aggregation of the players. Now the fitness is increased (right figure), and, therefore, the animals not only aggregate more but also go deeper during the daytime to avoid the risky region near the surface with high probability of being seen by the predators.

4 Discussion

The starting point of this paper was our model proposed in Thygesen and Mazuryn (2022), and in particular its limitation to the cases where there are no void regions – parts in a water column where the optimal density function has zero values. The issue comes from the fact that it is not clear how to properly define the vertical speed of a player in the void regions without animals. We refer to set-ups with empty regions as the "deep water problem".

In this paper, we have presented a novel model which addresses the issues with the zero concentration regions, covering deep water scenarios by including randomness to the model. Now the players in the vertical game can adjust their vertical position by controlling their vertical speed with random disturbances in the state. The diffusivity ensures that there are, in fact, no strictly void regions. While the model in Thygesen and Mazuryn (2022) used the Euler-Lagrange approach, we have in here employed a Hamilton-Jacobi-Bellman formulation, in which it is well defined what is the optimal vertical speed, even in regions where there are no animals – the speed of a hypothetical agent which happens to find itself there even if it shouldn't be there.

Diffusion terms in PDE models are common in ecology, see for example Okubo and Levin (2001), and randomness can correspond to errors in decision-making of the animals due to incomplete perception of the surrounding environment and emerge from search-type movements. This is reflected in the empirical fact that animals move unpredictably, but it can also result from structure of water flow, i.e. turbulence. In this latter case, though, one would expect correlation between neighboring animals. It is important to emphasize importance of the assumption about independence of white noise processes for each player. Cases with correlated noise, as for the case with turbulence in the water column, lead to systems of stochastic partial differential equations which dramatically increase complexity of analytical and numerical traceability of the resulting models. This type of mean field differential games with common noise is not considered here and serves as a potential extension of the established results in this manuscript.

The model includes the density dependent mortality term, which can be due to higher detection rate of animals in big groups. But this "group" interpretation is only one possible mechanism of the density dependence. As one alternative explanation of the mean field term is density dependent foraging when a higher resource availability typically attracts higher concentration animals which results in a competition for the limited resource.

While deriving the final model we take another approach than in our previous paper Thygesen and Mazuryn (2022). Here we employed the Feymann-Kac formula for establishing the equivalence between optimizing the fitness functional and the Hamilton-Jacobi-Bellman formalism. This allows us to include cases where the fitness fluctuates with time, so that the model framework can also be applied to situations where the environmental variations are not short compared to the life history of the animal. To our knowledge, this is the first explicit application of the Feynman-Kac formula in mathematical analysis within behavioral ecology, even if similar growth/mortality trade-offs are well studied Mangel and Clark (1986).

We disregard the source and mortality terms in the forward Kolmogorov equation due to the short time interval of interest, assuming that the players are long-lived. It is also a technical assumption which allows us to find a time-periodic solution to the Kolmogorov equation. As another potential direction of future research can be relaxing the periodicity assumption in the game and solving the mean field system with all the necessary terms in the Fokker-Plank equation.

We also establish the equivalence between finding a Nash equilibrium for the vertical differential game by solving the mean field system and the PDE-constrained optimization problem. These two approaches allow flexibility in the choice for a more suitable numerical framework for approximating a Nash equilibrium. We test these approaches on two examples and compare the final results. The two constructed examples provide consistent solutions in regions with non-zero concentration of the agents. Numerical issues arise in the optimization approach because the optimization problem is ill-conditioned, in the sense that the criterion is very insensitive to the strategy of animals in regions which are almost-void. One way to address this inconsistency is to use heuristic procedures for estimation of a better guess or use more robust algorithms for numerical optimization. But one should keep in mind that the established equivalence is valid only under the quasi-static approximation, when fluctuations in the value function can be disregarded. Also the equivalence between the two formulations is valid for set-ups with a population of homogeneous players: the agents have symmetric functional and identical set of admissible strategies. This result doesn't directly translate to populations of heterogeneous agents where the symmetry assumption is relaxed.

As a potential perspective for future work can be mentioned expansion of the modelling framework to several interacting populations to cover the multi-player set-up. In the current model we only include implicit presence of the predators through the mortality term, but the model can be expanded to explicitly incorporate several vertical densities of a trophic network in the equations. Similar work with two populations has been done in Thygesen and Patterson (2019) but without taking into account the cost of motion. Another interesting direction to pursue might be, for example, if a population consist of almost-identical animals, which however differ slightly in size, how do they partition the habitat among themselves?

One more possible direction for improvement is to omit the time-scale separation between the vertical game and population dynamics. This will lead to a mean field game formulation with population dynamics where the abundance of predators and preys are time varying quantities. Also, as mentioned earlier, for the sake of simplicity, our final model includes only vertical migration of the agents and disregards horizontal dynamics to avoid this level of generality and keep complexity to a reasonable level. It is also possible to include seasonal migration of animals to the model, when the agents can change their geographic location in the ocean.

To summarize, we have expanded the established PDE framework from Thygesen and Mazuryn (2022) to solve the deep water problem and cover all ranges of depth. Feymann-Kac formalism has been utilized to derive the Hamilton-Jacobi-Bellman equation in the mean field game system. For the derived system of PDEs we formulate the equivalent PDE-constrained problem under the quasi-static approximation and solve both formulations with the numerical scheme based on spectral elements method Kopriva (2009) and validate the model results on several test examples.

Statements and Declarations

Author's contributions

Both authors initiated the study and equally contributed to the conceptualisation of the approach. MM made the analysis of the model, numerical implementation and drafted the initial manuscript. UHT provided supervision. Both authors completed the manuscript.

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Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

Not applicable.

Code availability

The code used to perform the calculations and generate the figures will be placed in a publicly accessible GitHub repository after acceptance of the manuscript.

Appendix A (A)symmetry of the velocity field

In this section we elaborate further on the observed asymmetry in Figure 1 in the optimal velocity field V with the symmetric optimal density N around the midday time. We discuss the observed feature of the velocity field in a more general set up for an arbitrary fixed period $T > 0$.

To start with, we assume that the optimal distribution N is symmetric or an even function as a function of time:

$$N(x, t) = N(x, T - t), \tag{A1}$$

for $x \in [0, H]$ and $t \in [0, T]$.

We aim to show that the symmetry of the density N in the sense (A1) does not imply that the vertical velocity field V is an odd function around on the interval $[0, T]$:

$$V(x, t) = -V(x, T - t). \tag{A2}$$

To show that the equality (A2) does not hold we differentiate the expression (A1) with respect to t and substitute the forward Kolmogorov equation (4) into both sides:

$$\begin{gathered} \frac{\partial N}{\partial x}(x,t) = \frac{\partial N}{\partial x}(x,T-t) \\ -\frac{\partial (NV)}{\partial x}(x,t) + \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}(x,t) = \frac{\partial (NV)}{\partial x}(x,T-t) - \frac{\sigma^2}{2}\frac{\partial^2 N}{\partial x^2}(x,T-t) \end{gathered}$$

Integrating both sides with respect to x from 0 to x and taking into account the zero-flux boundary condition (5) with the periodicity condition (A1) we arrive to:

$$N(x,t)(V(x,t) + V(x,T-t)) - \sigma^2 \frac{\partial N}{\partial x}(x,t) = 0 \tag{A3}$$

If (A2) holds, we reach the conclusion that $\partial N / \partial x = 0$. Thus, the velocity can only be symmetric if the optimal density N is constant in space, which would imply that the velocity profile V is zero everywhere. This argument relies on the assumption that $\sigma > 0$, and that we do in fact get symmetry in absence of diffusion.

For the sake of completeness, to study numerically the behaviour of the vertical speed field, we take the parameters from Table 1 and vary the noise level σ. We also decrease the mortality scaling parameter m by 2 to avoid the low-concentration regions near the surface of the water column to eliminate high speed values there and make the asymmetry more pronounced. Approximate solutions for the corresponding differential mean field game for various values of the diffusivity parameter are shown in Figure A1.

It can be seen that for small values of σ the speed field V approaches an odd function in the sense (A2) (right panel) while the qualitative structure of the surface of the optimal density N doesn't change across the parameter range, with only slight changes in the concentration of players (left panel). Slight differences in the optimal density for small values of σ is due to the fact that the vertical migration is an advection-dominated process and contribution of the diffusion part is negligible. In contrast to small diffusivity values in the upper part of Figure A1, in the lower plots with high noise level σ we observe diffusion-dominated process with higher spread of the agents in the vertical game and more pronounced asymmetry in the optimal speed V as expected.

Appendix B Numerical comparison of the MFG system and the PDE-constrained problem

In this section we examine the equivalence between the mean field system (8) with the quasi-static approximation, when the value function U is replaced by the constant expected fitness F, and the PDE-constrained optimization problem (10) from numerical viewpoint. To compare these methods we construct two test cases to examine corresponding numerical approximations.

For the first example we take the model parameters from Table 1 and find the corresponding numerical solutions for the optimal density N and the optimal velocity V. Numerical approximations of the solution are shown in Figure B2.

One can notice almost identical optimal densities N and optimal controls V of the population in the water column. There are two sources of the observed discrepancy: left column comes from the system (8), where we don't impose the quasi-static approximation of the fitness, and the value function fluctuations can be seen in Figure 1. Right column assumes constant fitness in the formulation of the corresponding PDE-constrained optimization problem. Another possible explanation of the difference in the approximate solutions can be numerical: we compare the numerical results from calculations with reasonable run-time. It turns out that for the chosen set of model parameters the optimization problem requires significant amount of computational time. Also the velocity fields V differ in void regions with low concentration of the players. It can be due to a poor choice of the initial guess for the optimization problem (10) with the initial speed profile being too far from the optimal one. The Newton-type algorithm, which has been utilized in the calculations, doesn't change the values of V due to the zero gradient of the objective function in that region.

For the second test example we select a parameter set without void regions in the optimal density N. We use the constructed example from Appendix A where the mortality scaling m have been reduced to make the region near the surface more attractive to the animals. The numerical solutions are shown in Figure B3.

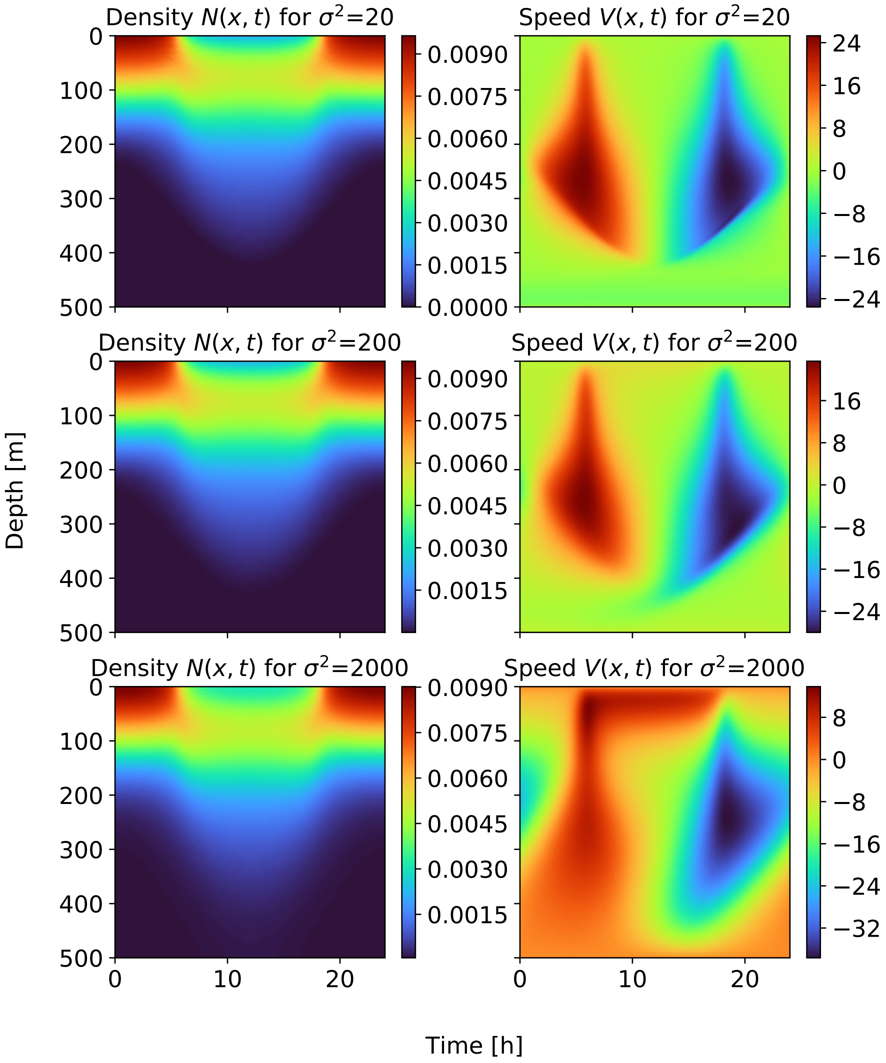

Fig. A1 Asymmetry manifestation in the vertical speed V for varying noise level σ.

With no regions with sharp transition to numerically zero concentration in the optimal density near the surface both methods provide almost identical numerical approximations of the solutions to the problem. Again, as in the previous test example, there are two possible sources of the observed difference in the numerical solution: validity of the quasi-static approximation and the computational aspect of the PDE-constrained optimization formulation.

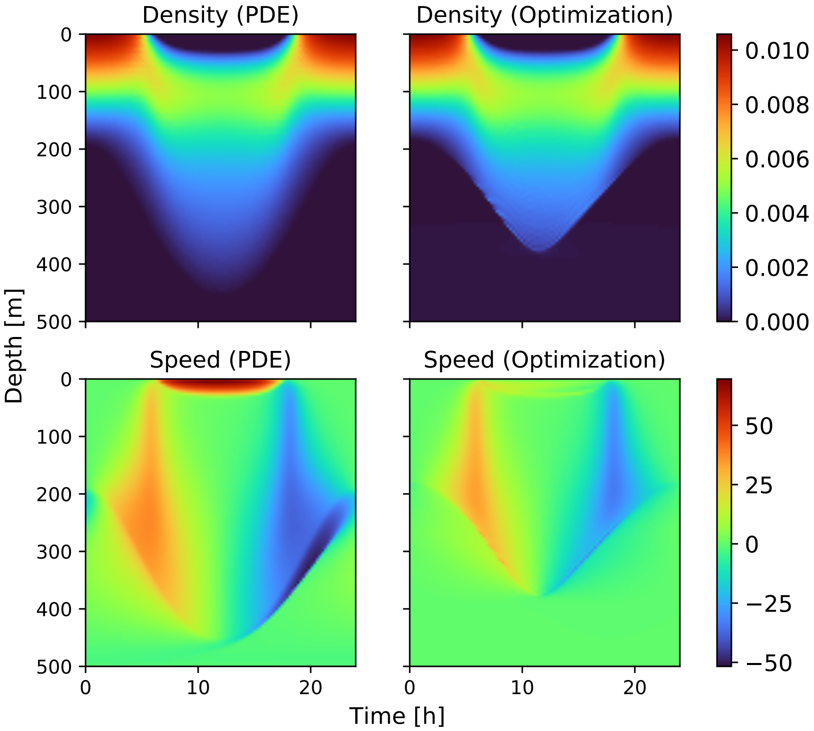

Fig. B2 Nash equilibrium for the parameters from Table 1. *Left column*: Mean field PDE system. *Right column*: PDE-constrained formulation.

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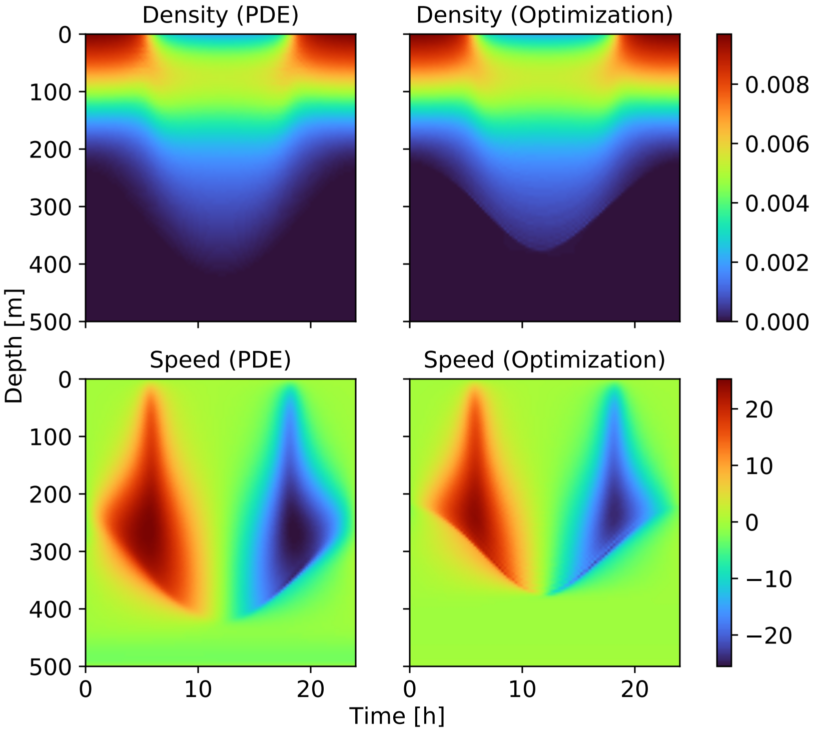

Fig. B3 Nash equilibrium for the second case with no void regions in the optimal density. *Left column*: Mean field PDE system. *Right column*: PDE-constrained formulation.

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PAPER C

Multispecies Mean Field Games for Diel Vertical Migrations

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Multispecies mean field games for diel vertical migrations

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Abstract

We propose and explore a framework for diel vertical migrations in a water column which is based on mean field games. Our model includes two populations of players, that interact as predators and prey. Using mean field game theory, we pose a system of partial differential equations which governs the Nash equilibrium where all players of each species behave optimally. We solve these partial differential equations numerically. Next, we conduct a sensitivity study where we examine the response of population-level quantities to changes in the total abundance of predators and prey. These quantities include the growth and mortality experienced by a single individual. This allows us to identify the emergent form of components in dynamic models of the two populations.

1 Introduction

Predator-prey models form the base of most ecosystem models, and this justifies the continued effort in improving the fidelity of these models. The most fundamental of all predator-prey models, the celebrated Lotka-Volterra equations (Murray, 1989), assume that first order mass action holds: In standard notation, the number of prey consumed by predators is βNP where N is the number of prey, P is the number of predators, and β is a constant. Moreover, the specific growth rate of prey is constant, as is the mortality of the predators. This implicitly assumes that the behavior of the animals in the system is unaffected by the number of animals.

Within theoretical ecology, there is an abundant literature on functional responses, i.e. how the vital rates of an individual vary in response to the abundance of other animals (first and foremost, the abundance of its prey, but also the abundance of its conspecifics and predators). Most basically (Murray, 1989) the type II functional response (also known as Holling's disk equation) states that the growth rate of predators increases but decelerates, when the abundance of their prey is increased. The original explanation for this phenomenon relates to handling time: A predator spends some time searching for prey, and some time processing the individual prey after capture. As the prey abundance is increased, the searching time decreases, and eventually the predator will spend all its time handling prey, at which point a further increase in prey density will not result in increased uptake. It is well known Murray (1989) that these functional responses have profound implications for the dynamics of ecosystems. For example, in the original Lotka-Volterra system, the equilibrium is a center, but when a type II functional response is included, the equilibrium becomes unstable, as an increased prey abundance reduces the mortality of the individual prey. Similarly, when density dependent mortality is included - e.g., the exponential growth of prey is replaced by the logistic growth model - this stabilizes the equilibrium. The combined effect of stabilizing and destabilizing components can yield complex dynamics, for example the bifurcations in the now classic Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971).

While the early studies of functional responses were motivated by empirical observations, and laboratory experiments in simple settings such as doves collecting grain, and synthesized in mechanistic models, more recent studies have focused on the behavorial changes that are induced when individuals adapt to fluctuations in their environment; for example, (Křivan, 1996). To model these behavioral changes, the paradigm assumes that animal behavior has been selected by evolution to be optimal in the given environment, whatever it is. Thus, evolution also favors animals that can identify and adapt to fluctuations in their environment. Here, what is optimized is lifetime reproductive success; essentially, one's number of descendants.

While the study of optimal behaviors initially studied the optimal dynamic response to given environments (Stephens and Krebs, 1987; Mangel and Clark, 1988; Houston and McNamara, 1999), focus has later been on the interaction between the many individuals that constitute an ecosystem. This changes the problem from a single-sided optimization problem to one of a game. In the context of evolutionary ecology, game theory initially studied pairwise interactions (such as the hawk/dove game, (Maynard Smith and Price, 1973)), but it was from the beginning recognized that these animals were "playing the field"; i.e. they have for practical purposes infinitely many possible opponents. When the animals are characterized by an internal state, and aim to maximize their lifetime reproductive success, we are thus lead to dynamic games between individuals which constitute a population.

To approach such problems, the theory of mean field games (Lasry and Lions, 2007) can be applied. Here, the object of study is games with a large number of symmetrically interacting agents. The symmetry assumption on the players makes the limit in traceable and allows to derive equations for describing a Nash equilibrium. In this paper, we consider mean field games with several interacting populations, based on the theoretical framework for mean field games with several types of players (Bensoussan et al., 2018; Fujii, 2019).

The research idea behind the current manuscript is therefore that we can employ the theory of mean field games to derive the optimal behavior of animals in a given ecosystem. This allows us to compute vital rates of individuals - how long do they live, how many offspring do they produce on average - and thereby the net population growth rates. As the population grows, we can assume that animals have been selected by evolution to adapt their behavior, so that they remain optimal. Therefore, we derive emergent population dynamics and ultimately ecosystem dynamics.

To pursue this program, we consider a specific case, aiming to explore the feasibility and technical difficulties. As a case, we chose the coupled diel vertical migrations of two species, a prey species and a predator species. Here, the driving dynamics is day/night cycles in light and the vertical structure of the ocean: The areas near the surface are productive, due to the light which penetrates only the top layer of the ocean, and therefore rich in phytoplankton that can be exploited by a grazer such as a planktonic copepod. At the same time, the light makes the grazer vulnerable to predation by animals that use light to identify their prey, such as a fish larvae. Thus, the grazers are attracted to the surface during the nighttime but repulsed during the daytime, and diel vertical migrations emerge. Diel vertical migrations are observed throughout the aquatic regime, basically for organisms of all sizes and in every aquatic ecosystem, and have been exmined thoroughly, both empirically and theoretically. The present manuscript builds on our earlier contributions (Thygesen et al., 2016; Thygesen and Patterson, 2019; Thygesen and Mazuryn, 2022; Mazuryn and Thygesen, 2022), and we refer to the more detailed review there. Our specific starting point is the mean field game model for diel vertical migration from (Thygesen and Mazuryn, 2022) and its extension to cover the deep water problem in (Mazuryn and Thygesen, 2022). In the present contribution, we extend the previous results to explicitly incorporate two species, one of predators and one of prey.

We assume that the mean field limit holds and describe Nash equilibrium in terms of a system of partial differential equations. We include random disturbances in the vertical position, so that each individual is faced with the problem of optimizing its expected lifetime reward subject to a stochastic differential equation which governs its state dynamics. We assume that different players are affected by independent noise, disregarding the possibility that noise could be correlated or that players are exposed to common noise or shocks (Carmona and Delarue, 2018a,b).

2 Methods

The model for diel vertical migration incorporates two populations, predators and prey, both distributed in a water column $[0, H]$. By X_t is denoted the vertical position of a representative player at time t and by V_t its vertical speed. In control theory terminology, X_t and V_t are state and control, respectively.

To identify the evolutionarily optimal migration strategies, we pose a mean field game between these players. This game is resolved in terms of a system of four partial differential equations, viz. two Fokker-Planck equations governing the spatial distributions of the two species, and two Hamilton-Jacobi-Bellman equation governing the fitness of the animals and the optimal strategies. The derivation of these equations is similar to the single-species case that we considered in (Mazuryn and Thygesen, 2022), but with the added complexity of two interacting populations. The interaction is in that the payoff to an individual of one species depends on the strategies of its conspecifics as well as those of the individuals of the other species.

We first consider a representative prey player. The state of this individual is its vertical position X_t^{prey}, which evolves according to the stochastic differential equation:

$$\mathrm{d}{X_t}^{\mathrm{prey}} = V_t^{\mathrm{prey}}\,\mathrm{d}t + \sigma^{\mathrm{prey}}\,\mathrm{d}B_t^{\mathrm{prey}}, \tag{1}$$

where the prey agent controls its position by adjusting the vertical speed V_t^{prey}, but is subject to random fluctuations in the form of standard Brownian motion B_t^{prey} scaled with constant noise level σ^{prey}. The prey is reflected at the boundaries of the domain, i.e., at the surface $x = 0$ and at the bottom $x = H$. We do not include this reflection term explicitly in the equation governing the animal position, but in the following, we will add it as a boundary condition on the Fokker-Planck equation.

The fitness of this representative prey is defined as its net energy surplus over its lifespan, depending on its strategy V^{prey}:

$$J^{\mathrm{prey}}(V^{\mathrm{prey}}) = \mathbb{E}\left[\int_0^{\tau^{\mathrm{prey}}} g(X_s, s) - \frac{\nu^{\mathrm{prey}}(V_s^{\mathrm{prey}})^2}{2}\,\mathrm{d}s\right]. \tag{2}$$

Here, the expectation is with respect to the stationary distribution of a player following the strategy V^{prey}. The integrand is the instantaneous energy surplus, which is obtained from an energy harvest rate $g(X_s, s)$ and an energetic cost of locomotion, which is quadratic in the velocity V_s^{prey}. This particular choice for the locomotion is justified for small organisms such as copepods, where viscous drag dominates the energy budget; beyond this, we choose this form mainly for mathematical convenience. In this fitness functional, τ^{prey} is the random time of death of the animal. That is, the stochastic process X_t follows (1) for $t < \tau^{\mathrm{prey}}$ and enters the special coffin state $X_t = \partial^{\mathrm{prey}}$ after the death at $t = \tau^{\mathrm{prey}}$ (Øksendal, 2013). The time of death τ^{prey} is constructed as a Markov time, given in terms of the mortailty $\mu^{\mathrm{prey}}(X_t, t)$. This is the killing rate of the process, i.e. the rate with which the process jumps from state X_t to the coffin state ∂^{prey}. This mortality is composed of a predation risk, which is independent of prey density but depends on local predator density, as well as time t and position x, and a density-dependent mortality rate inflicted by conspecifics, yielding a total mortality:

$$\mu^{\mathrm{prey}}(x,t) = \beta(x,t) C^{\mathrm{pred}} N^{\mathrm{pred}}(x,t) + \mu_1 C^{\mathrm{prey}} N^{\mathrm{prey}}(x,t). \tag{3}$$

We refer to the last term also as the intraspecific density dependent mortality. In the total mortality, $\beta(x,t)$ can be seen as the clearance rate of a predator, which depends on light levels, since we assume that predators predominantly use vision to detect prey. $C^{\mathrm{pred}} N^{\mathrm{pred}}(x,t)$ is the local predator density; with C^{pred} giving the total predator abundance and $N^{\mathrm{pred}}(x,t)$ being the probability density of the position of an individual predator. We take C^{pred} to be a dimensionless number, viz. the number of individuals in the system; an alternative would have been to consider C^{pred} a density of animals per surface area. With our choice, the dimension of β is length per time, indicating the vertical range that a predator can scan for prey per time unit. Similarly, $\mu_1 C^{\mathrm{prey}} N^{\mathrm{prey}}$ is a mortality experienced by the individual prey due to interactions with other prey and therefore depending on the local prey density.

To reiterate, the functional (2) is the expected accumulated energy of the representative agent over its lifetime period assuming that it follows the strategy V^{prey} leading to the trajectory X_t. The expression formalizes the trade-off the representative prey agent faces between harvesting energy in regions where g is high and at the same time minimizing risk by avoiding regions with high concentration of predators N^{pred} and/or high light abundance β, all subject to the cost of locomotion. In our case study in the following, the upper levels of the ocean near the surface offers both the potential for fast energy accumulation (i.e., high g) but at the same time high exposure to predation (i.e., high β).

We now shift attention to a representative predator. Its state trajectory is given by the Itô equation

$$\mathrm{d}X_t^{\text{pred}} = V_t^{\text{pred}}\,\mathrm{d}t + \sigma^{\text{pred}}\,\mathrm{d}B_t^{\text{pred}}, \tag{4}$$

so that also the predator controls its position through its velocity V_t^{pred}, but is perturbed with a constant noise level σ^{pred}. The fitness functional of the representative predator has the following form:

$$J^{\text{pred}}(V^{\text{pred}}) = \mathbb{E}\left[\int_0^{\tau^{\text{pred}}} \varepsilon C^{\text{prey}}\beta N^{\text{prey}} - \frac{\nu^{\text{pred}}(V_s^{\text{pred}})^2}{2}\,\mathrm{d}s\right], \tag{5}$$

where we have omitted arguments (X_s^{pred}, s) for brevity. The random time of death τ^{pred} is given in terms of a mortality μ^{pred}, as for the prey. For the sake of simplicity, we take the predator mortality to be constant:

$$\mu^{\text{pred}}(x,t) = \mu_2.$$

The energy budget of the predator involves an energy gain derived from predation as well as a loss term corresponding to the cost of locomotion. The energy gain from predation corresponds to the mortality experienced by the prey, although we include a conversion effiiency ε. That is, the local rate of predation events is $C^{\text{prey}}N^{\text{prey}}\beta C^{\text{pred}}N^{\text{pred}}$, corresponding to first order mass action. Seen from the point of view of the individual prey, this leads to a mortality $\beta C^{\text{pred}}N^{\text{pred}}$, while seen from the point of view of the individual predator, it leads to a predation rate of $\beta C^{\text{prey}}N^{\text{prey}}$. We see that the predator should favor regions with high concentration of prey, but also regions with high clearance rates β; at the same time it should avoid excessive locomotion.

Our interest is in the case where the dynamics are driven by day/night cycles, i.e. a periodic light abundance gives rise to a periodic clearance rate $\beta(x,t)$ with period $T = 24$ hours for each x. That is, we disregard seasonal fluctuations in the surrounding environment, so that we resolve the game at a particular time of the year. For the sake of simplicity, we take the harvest rate g of the prey to be constant. We assume population dynamics are slow enough that we can ignore temporal variation in the population size during the day. Thus, the total biomass in the water column is fixed so that $N^{\text{prey}}(x,t)$ represents a probability distribution of the prey at each point in time, and C^{prey} is considered constant. The analogous statements hold for the predators.

In summary, we search for the vertical distributions for both populations, and the speed profiles as a Markovian closed loop control in the form $V = V(X_t,t)$, for both predators and prey. With the periodicity assumption in hand we are looking for time-periodic solution pairs $(N^{\text{prey}}, V^{\text{prey}})$ and $(N^{\text{pred}}, V^{\text{pred}})$ to the mean field differential game. We derive the governing equations in the next section.

2.1 Mean field system

We now consider the optimal control problem that a representative player faces, given the strategies of all other players in the system. Further, assuming that all players behave optimally, and that all players of the same species are indistinguishable, we pose the system of partial differential equations which governs the mean field limit.

If all prey individuals follow the same strategy V^{prey} and are perturbed by independent noise sources, then the prey density is identical up to scale with the probability density function of the individual prey. In turn, given the stochastic differential equation (1), the probability density $N^{\text{prey}}(x,t)$ of a representative prey is governed by the forward Kolmogorov or Fokker-Planck equation:

$$\frac{\partial N^{\text{prey}}}{\partial t} = -\frac{\partial (N^{\text{prey}} V^{\text{prey}})}{\partial x} + \frac{(\sigma^{\text{prey}})^2}{2} \frac{\partial^2 N^{\text{prey}}}{\partial x^2}. \tag{6}$$

Due to the short time period of the game relative to the lifetime of the agents, we omit mortality and source terms in the forward equation (6); thus, the local population density is only affected by migrations.

We assume that no players enter or exit the domain through the boundary and therefore impose reflective boundary condition for the state equation (1) on the surface and the bottom of the water column $[0, H]$. The no-flux boundary condition has the following form:

$$N^{\text{prey}} V^{\text{prey}} - \frac{(\sigma^{\text{prey}})^2}{2} \frac{\partial N^{\text{prey}}}{\partial x} = 0. \tag{7}$$

Since N^{prey} is a probability density, it normalized:

$$\int_0^H N^{\text{prey}}(y,t)\,\mathrm{d}y = 1. \tag{8}$$

Since probability is conserved under the Fokker-Planck equation with no-flux boundary conditions, this holds for all times t iff it holds for any time t, e.g. $t = 0$.

We now consider the distribution of prey and predators given - i.e., we fix N^{prey} and N^{pred} - and ask how a representative prey should behave in this environment. To this end, we first rewrite the fitness function by taking expectation over the time of death τ^{prey}, and next condition on the initial condition $X_t = x$. We thus obtain the value function:

$$U^{\text{prey}}(x,t) = \sup_V \mathbb{E}^{X_t=x}\left[\int_t^{+\infty}\left(g(X_s,s) - \frac{\nu^{\text{prey}}(V_s^{\text{prey}})^2}{2}\right)e^{-\int_t^s \mu^{\text{prey}}(X_\xi,\xi)\,\mathrm{d}\xi}\,\mathrm{d}s\right]. \tag{9}$$

This is the expected lifetime energy surplus for a prey which is alive at time t and in state $X_t = x \neq \partial$, and which is playing the optimal strategy V^{prey}. The exponential factor in the integral (9) is the conditional probability of the prey surviving the interval $[t,s]$; see Thygesen (2022) for the details of this construction. Thus, the mortality is represented by discounting of future energy harvest.

Combining the Hamilton-Jacobi-Bellman equation and the Feynman-Kac formula (Kac, 1949; Øksendal, 2013), the fitness U^{prey} introduced in (9) is the solution to the following partial differential equation:

$$\frac{\partial U^{\text{prey}}}{\partial t} + \sup_v\left(L^{\text{prey}}U^{\text{prey}} + g - \frac{\nu^{\text{prey}}v^2}{2}\right) = 0, \tag{10}$$

where the differential operator L^{prey} is defined as:

$$L^{\text{prey}}U^{\text{prey}} = v\frac{\partial U^{\text{prey}}}{\partial x} + \frac{(\sigma^{\text{prey}})^2}{2}\frac{\partial^2 U^{\text{prey}}}{\partial x^2} - \mu^{\text{prey}}U^{\text{prey}}.$$

This is the sometimes referred to as the Hamilton-Jacobi-Bellman equation with discounting. Note that the differential operator L^{prey} depends on the densities N^{prey}, N^{pred}, through the mortality, but that we suppress this in the notation, since we consider the environment fixed at this point.

As the expression inside the supremum function in (10) is a concave quadratic function of the argument v, the global maximum exists and is attained at $V^{\text{prey}} = \frac{1}{\nu^{\text{prey}}}\frac{\partial U^{\text{prey}}}{\partial x}$.

Similar to (Thygesen, 2022; Mazuryn and Thygesen, 2022), the duality argument between the forward and backward Kolmogorov equations yields that the reflection at the boundaries $x = 0$ and $x = H$ from (7) corresponds to a homogeneous Neumann boundary condition for the value function U^{prey}:

$$\frac{\partial U^{\text{prey}}}{\partial x}(x,t) = 0. \tag{11}$$

The assumed periodicity reduces the time interval of the differential mean field game to $[0,T]$. The value function on the time interval is periodic, i.e.

$U^{\text{prey}}(x,0) = U^{\text{prey}}(x,T)$, meaning that the expected fitness of the representative player at position $x \neq \partial$ and time $t = 0$ is equal to the expected fitness of the same player at the same position x and $t = T$, conditional on the player surviving the one day time interval.

Gathering all pieces together (6) - (8) and (11) and substituting the form for the optimal velocity V^{prey} into the Hamilton-Jacobi-Bellman equation (10) we arrive to the following prey part of the mean field system:

$$\begin{cases} \frac{\partial N^{\text{prey}}}{\partial t} = -\frac{\partial (N^{\text{prey}} V^{\text{prey}})}{\partial x} + \frac{(\sigma^{\text{prey}})^2}{2} \frac{\partial^2 N^{\text{prey}}}{\partial x^2} \\ \frac{\partial U^{\text{prey}}}{\partial t} + \frac{1}{2\nu^{\text{prey}}} \left(\frac{\partial U^{\text{prey}}}{\partial x}\right)^2 + \frac{(\sigma^{\text{prey}})^2}{2} \frac{\partial^2 U^{\text{prey}}}{\partial x^2} + g - U^{\text{prey}} \mu^{\text{prey}} = 0 \end{cases} \tag{12}$$

which hold for $(x,t) \in (0,H) \times (0,T)$, and the boundary conditions

$$\begin{cases} \int_0^H N^{\text{prey}}(y,t)\,\mathrm{d}y = 1 & t \in [0,T] \\ N^{\text{prey}}(x,0) = N^{\text{prey}}(x,T) & x \in \{0,H\} \\ U^{\text{prey}}(x,0) = U^{\text{prey}}(x,T) & x \in \{0,H\} \\ (N^{\text{prey}} V^{\text{prey}} - \frac{(\sigma^{\text{prey}})^2}{2} \frac{\partial N^{\text{prey}}}{\partial x})(x,t) = 0 & x \in \{0,H\} \\ \frac{\partial U^{\text{prey}}}{\partial x}(x,t) = 0 & x \in \{0,H\} \\ V^{\text{prey}} = \frac{1}{\nu^{\text{prey}}} \frac{\partial U^{\text{prey}}}{\partial x} \end{cases} . \tag{13}$$

With the same reasoning for the predators, using the state equation (4) and the expected fitness functional (5), we arrive at the system of partial differential equations governing the density and fitness of predators:

$$\begin{cases} \frac{\partial N^{\text{pred}}}{\partial t} = -\frac{\partial (N^{\text{pred}} V^{\text{pred}})}{\partial x} + \frac{(\sigma^{\text{pred}})^2}{2} \frac{\partial^2 N^{\text{pred}}}{\partial x^2} \\ \frac{\partial U^{\text{pred}}}{\partial t} + \frac{1}{2\nu^{\text{pred}}} \left(\frac{\partial U^{\text{pred}}}{\partial x}\right)^2 + \frac{(\sigma^{\text{pred}})^2}{2} \frac{\partial^2 U^{\text{pred}}}{\partial x^2} + \varepsilon C^{\text{prey}} \beta N^{\text{prey}} - U^{\text{pred}} \mu^{\text{pred}} = 0 \end{cases} \tag{14}$$

which holds for $(x,t) \in (0,H) \times (0,T)$, and the boundary conditions

$$\begin{cases} \int_0^H N^{\text{pred}}(y,t)\,\mathrm{d}y = 1 & t \in [0,T] \\ N^{\text{pred}}(x,0) = N^{\text{pred}}(x,T) & x \in \{0,H\} \\ U^{\text{pred}}(x,0) = U^{\text{pred}}(x,T) & x \in \{0,H\} \\ (N^{\text{pred}} V^{\text{pred}} - \frac{(\sigma^{\text{pred}})^2}{2} \frac{\partial N^{\text{pred}}}{\partial x})(x,t) = 0 & x \in \{0,H\} \\ \frac{\partial U^{\text{pred}}}{\partial x}(x,t) = 0 & x \in \{0,H\} \\ V^{\text{pred}} = \frac{1}{\nu^{\text{pred}}} \frac{\partial U^{\text{pred}}}{\partial x} \end{cases} . \tag{15}$$

These systems of partial differential equations (12) and (14) with boundary conditions form the final mean field system for solving the vertical differential game. Each PDE system alone is similar to the one derived in

(Mazuryn and Thygesen, 2022), but here, our final system includes two interacting populations in the game and explicitly incorporates the interaction between these two populations in the growth and mortality terms. This allows to resolve the coupled vertical migrations of predators and prey.

3 Model parametrization

Here, we present a numerical study of the mean field model from (12) and (14) with boundary conditions. The functional forms and model parameters build on (Thygesen and Mazuryn, 2022; Mazuryn and Thygesen, 2022) and here we only give a brief overview of the selected parameters to make the manuscript self-contained. See these references for more detailed discussion of the selected functions. The parametrization is inspired by a situation where the prey are copepods (small zooplankton) which are preyed upon by fish larvae. Not all parameters are chosen realistically, so the following study serves mostly as a proof of concept to demonstrate that the framework is operational. We will return to the issue of parametrization in the discussion.

To model the light-dependent clearance rate β which governs the encounters between predators and prey, we start with the illumination at the surface, I_s. This is a T-periodic function of time:

$$I_s(t) = \frac{I_0}{1 + \exp\left(A\cos(2\pi t/T)\right)}.$$

At depth, the light intensity $I(x,t)$ decays exponentially with a constant absorption coefficient k_1:

$$I(x,t) = I_s(t)\exp(-k_1 x).$$

Predators detect prey visually when they enter into a detection sphere centered at the predator. The radius r of this sphere depends on depth x at time t through the light intensity, as developed in the model of visual range with saturation by Aksnes and Utne (1997):

$$r^2 \exp(k_1 r) = \gamma^2 \frac{I(x,t)}{K + I(x,t)}.$$

This relation implicitly defines the distance r of visual detection as a function of depth and time. The detection distance r translates into a clearance rate mr^2, corresponding to predators cruising through the water with constant speed and thus clearing cylindrical volumes. We add a baseline clearance rate β^{base} to ensure that even in dark water, the prey cannot escape predation

Symbol	Parameter	Value	Units
H	Depth	500	m
T	Period	24	hour
I_0	Maximum irradiance	1	W m^{-2} nm^{-1}
K	Saturating light level	1	W m^{-2} nm^{-1}
γ	Maximum detection distance	0.02	m
k_1	Absorption coefficient	0.02	m^{-1}
A	Amplitude of light fluctuations	13	-
ν^{prey}	Drag (Prey)	10^{-6}	J h m^{-2}
ν^{pred}	Drag (Predator)	10^{-9}	J h m^{-2}
$(\sigma^{\text{prey}})^2$	Diffusion (Prey)	20	m^2 h^{-1}
$(\sigma^{\text{pred}})^2$	Diffusion (Predator)	20	m^2 h^{-1}
μ_1	Density-dependent mortality (prey)	1	m h^{-1}
μ_2	Mortality (predator)	10^{-12}	h^{-1}
m	Search rate	25	m^{-1} hour^{-1}
μ_{base}	Baseline mortality	10^{-5}	h^{-1}
k_2	Harvest decay rate	0.02	m^{-1}
g_0	Maximum food availability	0.01	J h^{-1}
x_{clin}	Depth of nutricline	100	m
C^{pred}	Predator abundance	$10 \cdot 10^3$	-
C^{prey}	Prey abundance	10	-

Table 1: Model parameters.

completely; this can be interpreted as prey detection through hydromechanical sensing rather than vision. We therefore obtain a total clearance rate

$$\beta(x,t) = mr^2 + \mu^{\text{base}}.$$

We assume that for the prey, the harvest rate is time invariant and depends logistically on depth:

$$g(x,t) = \frac{g_0}{1+\exp(k_2(x-x_{\text{clin}}))}$$

so that energy harvest is highest at the surface $x = 0$, and transitions at depth x_{clin}.

The specific values for the parameters are given in table 1. These are consistent with the parameters used in (Mazuryn and Thygesen, 2022); in addition, we have added parameters that describe the interaction between predators and prey, but to reiterate, these choices are somewhat arbitrary and serve to verify the model internally rather than validate it against a real-world system.

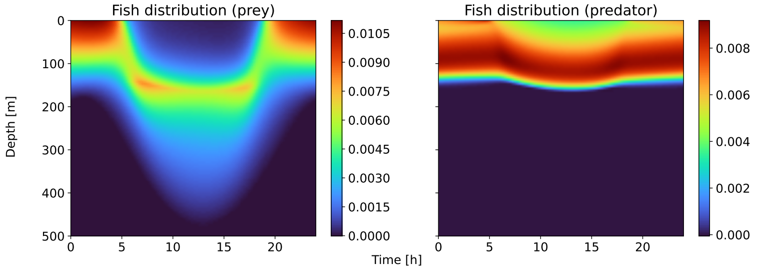

Figure 1: The evolution over a day of the vertical distributions of prey and predators. Parameters from Table 1.

3.1 Numerical methods

The numerical solution to the mean field system has been calculated using the same approach as in Mazuryn and Thygesen (2022), although with the extra complication of two species. Briefly, we employ the spectral element discretization scheme. The computational domain $[0, T] \times [0, H]$ has been triangulated and the unknown solution to the system of partial differential equations (12) - (14) with boundary conditions is approximated by orthogonal polynomials on each element. The final solution to the system is composed of these polynomials on each subdomain.

4 Results

For the base model parameters in Table 1, the numerical solution results in vertical distributions and migrations of the two populations as presented in Figure 1.

We can see that prey players migrate at dawn to deeper levels in the water column to reduce encounter rate with the predators; at dusk, the reverse migration takes place. The predators follow a similar pattern, but with much less movement, presumably because predation rates at depth would be too small to justify the energy spent on the migration.

During the day, the prey agents go deeper than the predators and spread even in the regions with low light intensity and no predators. This is due to the form of the density dependent mortality term in (3), so that these prey are avoiding conspecifics rather than predators. In these regions with absence of predation, the vertical distribution resembles single-species ideal free distribution.

In contrast to the results from (Thygesen and Mazuryn, 2022; Mazuryn and Thygesen, 2022), the vertical distributions of both populations are not symmetrical around $t = 12$: The agents have sharper transition at dawn and slowly return to the surface at dusk. The plausible explanation for this is that the fitness fluctuates significantly over the day.

4.1 Emergent functional responses and population dynamics

In this section we focus on the sensitivity of the model to various parameters, specifically the predator abundance C^{pred} and prey abundance C^{prey}. We then examine how changes in these abundances affect the fitness components and behavior of predators and prey.

With fitness components, we mean summary statistics concerning energy budgets and mortality, since these combine to define the fitness of the animal. For the prey, we compute the total mortality

$$\bar{\mu}^{\mathrm{prey}} = \frac{1}{T}\int_{[0,T]}\int_{[0,H]} (\mu^{\mathrm{prey}} N^{\mathrm{prey}})(x,t)\,\mathrm{d}x\,\mathrm{d}t. \tag{16}$$

This is the mortality averaged both over time and over the population of prey. We also compute the part of this mortality that is due to predation:

$$\mu^{\mathrm{predation}} = \frac{1}{T}\int_{[0,T]}\int_{[0,H]} (\beta C^{\mathrm{pred}} N^{\mathrm{pred}} N^{\mathrm{prey}})(x,t)\,\mathrm{d}x\,\mathrm{d}t. \tag{17}$$

Finally, we compute the average rate of energy surplus experienced by the individual prey:

$$\bar{g}^{\mathrm{prey}} = \frac{1}{T}\int_{[0,T]}\int_{[0,H]} (g N^{\mathrm{prey}})(x,t)\,\mathrm{d}x\,\mathrm{d}t. \tag{18}$$

For the predators, we compute the average harvest rate:

$$\bar{g}^{\mathrm{pred}} = \frac{1}{T}\int_{[0,T]}\int_{[0,H]} \varepsilon C^{\mathrm{prey}} (\beta N^{\mathrm{prey}} N^{\mathrm{pred}})(x,t)\,\mathrm{d}x\,\mathrm{d}t. \tag{19}$$

Figure 2 shows how these population-level rates change as the predator abundance is varied orders of magnitude. The predation mortality (both due to visibility of prey and total risk rate) experienced by the prey in figure 2 (top panel) increases when increasing the predator abundance. Initially, the increase is steep: At this point, mortality is less important than growth, so the prey do not significantly modify their behavior in response to increased predator abundance. As the predator abundance increases further, the prey adapt through predator avoidance, and therefore the mortality curves decelerate. The gap between the two lines is intraspecific density-dependent mortality; this is largely independent of the number of predators, indicating that the prey do not repond by increased aggregation.

The prey growth rate (19) decreases with increasing predator abundance in figure 2 (center panel), since the prey agents adapt to the increasing concentration of predators which makes the prey migrate to deeper layers of the water column where the nutrient concentration is significantly lower.

Finally, in the bottom panel, we see that the predators experience decreased specific growth rates when their abundance increases. This is because increased predator abundance stimulate the prey to increase predator avoidance, so that the individual predator has more difficulties finding prey.

In figure 3, we show the corresponding result when we modify the prey abundance. We see that the individual prey experiences increased mortality (top panel). Most of this is due to increased intraspecific density dependent mortality, i.e., a direct effect. There is also some increased predation mortality, which is an indirect effect.

To examine this indirect effect, we first inspect the prey growth rate (middle panel), which increases with increasing prey abundance. The explanation for this is that as the prey abundance increases, the fitness of the individual prey decreases, due to the intraspecific density dependent mortality. As a result, the individual prey becomes less risk-averse and gives higher priority to growth rather than mortality. Therefore they will spend time closer to the surface to benefit from higher nutrient concentration in these regions, even if this implies more exposure to predators.

This explains why the predation mortality of the individual prey increases when the prey abundance increases. It is also consistent with predator growth rate (lower panel), which increases superlinearly (i.e., accelerating, convexly) with the prey abundance.

5 Discussion

This manuscript contributes to our previous work on diel vertical migration with the mean field game theoretical framework (Thygesen and Mazuryn, 2022; Mazuryn and Thygesen, 2022). Here we develop a game theoretical model to describe the two-species set-up with explicit interactions between the populations. The presented equations in this paper has successfully reproduced the phenomenon of diel vertical migration of marine organisms in the water column. A similar model with two populations in continuous space and time was considered by Thygesen and Patterson (2019) but without tak-

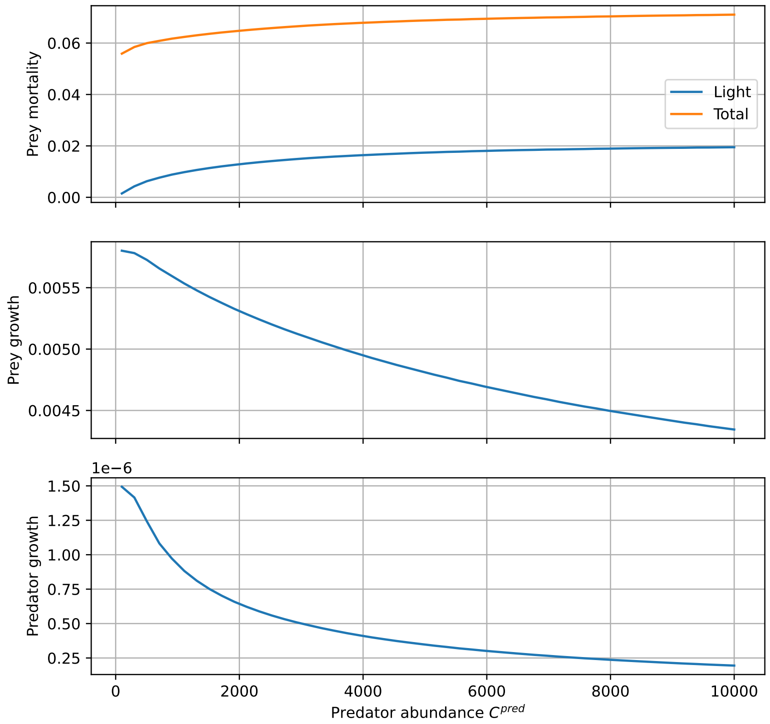

Figure 2: Population-level quantities as function of predator abundance C^{pred}. The blue curve, labelled “light”, indicates predation mortality. Bottom panel: Predator growth rate (19) in the Nash equilibrium.

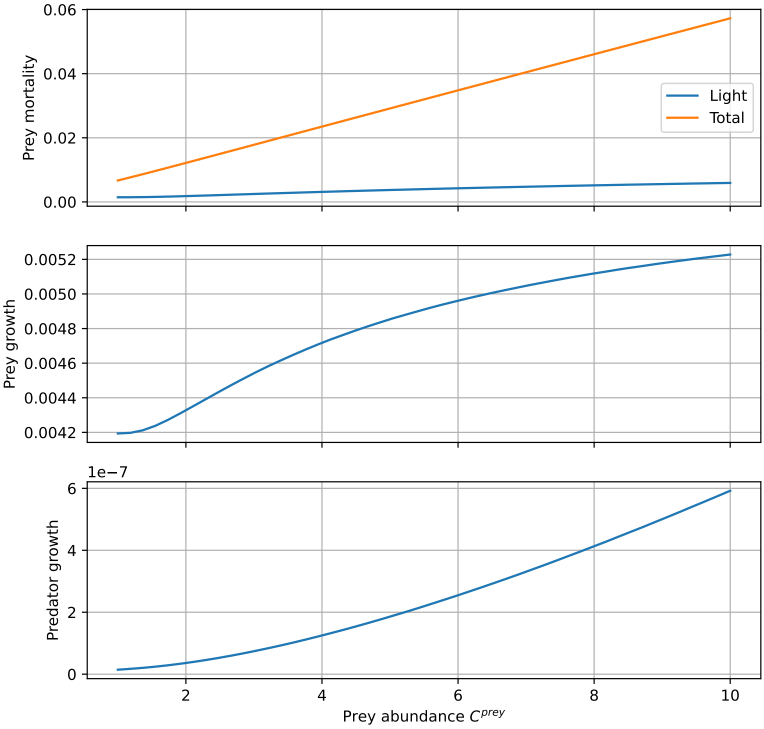

Figure 3: Population-level quantities as function of prey abundance C^{prey}. Panels as in figure 3

ing into account the cost of motion.

We have demonstrated that it is possible to identify the Nash equilibrium and thereby predict the optimal vertical distributions of each species, in the game-theoretic sense. These distributions have, largely, the appearance that one would expect, given the empirical studies in the literature as well as previous theoretical models, both by ourselves and others. Moreover, we have demonstrated that it is possible to predict changes in the behavior, growth, and mortality of organisms as the environment changes; here, exemplified by changes in the abundance of the two species. Ultimately, these emergent functional responses - understood in the broad sense, i.e., how vital rates of organisms depend on their environment - can enter into dynamic models of populations and thereby predict ecosystem dynamics. Extrapolating even further, these models can be used to predict ecosystem services, such as: How many fish will we be able to harvest sustainably from the seas, when we experience global climate change?

Although it is possible to explain qualitatively the resulting functional responses, it is important to realize that they are non-trivial, as direct effects and indirect effects often work in opposite directions, so that detailed studies are needed even to predict the sign of a change. For example, we see that the predator growth rate is an increasing and accelerating (convex) function of the prey density. This phenomenon is known as a Holling type III response within theoretical ecology, and it is often explained with predator behavior: When prey are scarce, it does not pay for the predator to pursue them, and the predator explores other opportunities or wait for better times. Here, the explanation for the phenomenon is different: As prey densities increase, the prey are experience an increased intraspecific density dependent mortality, so their fitness decrease, and they become more willing to expose themselves to predation in order to pursue increased growth.

The specific parameters we have used in our numerical examples were chosen mostly from a mathematical point of view, rather than for ecological realism. That is, we explore the mathematical and numerical properties of the model and the algorithms. Therefore, the contribution in the present state should be seen mostly as a proof of concept which gives results of qualitative nature. In the future, we aim to complete this numerical exploration so that we also bring in higher degree of ecological realism.

It can be argued that our model has an internal inconsistency in that we include the mortality in the Hamilton-Jacobi-Bellman equation, in the form of discounting, but not in the Fokker-Planck equation for the population densities. We argue that this inconsistency is permissible. Consider the analogy of human behavior in traffic: It is fair to say that the risk of death by accident affects human behavior, but also that the mortality is low enough that it can be ignored when describing the flow of traffic and the loads on the road system.

As a potential perspective for future work can be models with explicit population dynamics where the predator and prey abundances are time varying quantities. Here, we do not include mortality terms in the Fokker-Planck equation, due to assumed low mortality rates, but one can expand the model by including these terms explicitly. Then, the periodicity assumption on the solution to the mean field system should be replaced by some other notion of quasi-periodic solutions. This will also include analysis of the slow-fast coupling between behavior (diel vertical migration) and population dynamics. Expanding the time horizon could also involve horizontal movements and seasonal migrations, as well as the growth of individual animals during their lifetimes. This is a formidable research program and our contribution should be seen as a first step in this direction.

More manageable extensions would be to include more sophisticated forms of functional response in the fitness functional. The current model assumes first order mass action at the local level, for given prey density and predator density. It would be possible to include handling times or saturation of the predators, which would give rise to a local type II functional response. One can speculate that this gives the prey an incentive to aggregate, as they can then locally saturate the predators, so that the individual prey experiences decreased predation mortality. Of course, this is countered by the aggregation of predators, as well as the intraspecific density dependent mortality of the prey, but one can anticipate that this in some situations can lead to schooling (or shoaling), which would affect the mean-field limit and could lead to pattern formation.

Another component which could be extended is the nature of the cost of movement. In this manuscript, we have focused on viscous drag, where the power required to move with a given speed is quadratic in the speed. This is applicable for small animals and is even detabable for fish larvae. For larger animals, a cubic cost of motion would be more appropriate, in that it corresponds to the inviscid drag. One can also imagine costs associated with motion that are not related to energy budgets; for example, loss of time spent on foraging, or increased exposure to predators e.g. through larger hydromchanical signatures.

As mentioned earlier, our model builds critically on the assumed independence of white noise processes for each player in the vertical game. But more realistic scenarios are cases with correlated noise, as for the case with turbulence in the water column or some other events experienced by neighbouring agents. Such extensions lead to an analytical machinery with high analytical complexity like systems of stochastic partial differential equations. This type of mean field differential games with common noise is not considered here and serves as a direction for future reseach.

To summarize, we have expanded the established framework from (Thygesen and Mazuryn, 2022; Mazuryn and Thygesen, 2022) to resolve the diel vertical migration with two interacting populations. The model ouput can also be used to calculate and analyse population quantities like experienced growth and mortality rates for individual players, which has been demonstrated on a toy example.

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