



Behavioral games and emergent population dynamics

Frølich, Emil F.

Publication date:
2022

Document Version
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

Citation (APA):
Frølich, E. F. (2022). *Behavioral games and emergent population dynamics*. Technical University of Denmark.

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Behavioral games and emergent population dynamics

Emil F. Frølich

DTU



Kongens Lyngby 2022

Technical University of Denmark
Department of Applied Mathematics and Computer Science
Richard Petersens Plads, building 324,
2800 Kongens Lyngby, Denmark
Phone +45 4525 3031
compute@compute.dtu.dk
www.compute.dtu.dk

Summary (English)

Large-scale models of ecosystems typically do not include explicit habitat choice. This is in spite of adaptive habitat choice being known to have a powerful influence on ecosystems, with indirect effects often being stronger than direct effects. The importance of behavior is particularly pronounced in the aquatic setting, where population dynamics are determined by the diel vertical migration. There is no general toolbox which a working ecologist can apply to add behavior to an ecosystem model. The goal of this thesis is to develop game-theoretic methods to address this shortcoming, and apply the tools to model aquatic ecosystems. This thesis only considers unstructured populations, ignoring the import of ontogeny.

Paper A develops a general method for implementing optimal habitat choice in ecosystems of Lotka-Volterra type, both with continuous and discrete habitats. We apply the method to a predator-prey system, modeling copepods and forage fish in the water column. Paper B focuses on the ecosystem impact of optimal behavior on a tri-trophic ecosystem with a refuge, and how behavior changes the impact of bottom-up and top-down forcing. Finally, the paper investigates the relationship between the Type II and Type III functional responses. Paper C develops a general method to study optimal habitat choice in population games. Paper D couples stochastic mean-field games to predator-prey population dynamics, revealing the emergence of diel migration patterns as a result of ecosystem productivity. Finally paper E is included to show the potential of the methods, but is still a draft. Paper E studies the impact of optimal behavior on a shelf ecosystem, which support the majority of the worlds fisheries.

Summary (Danish)

Modeller af økosystemer inkluderer som oftest ikke habitatvalg. Dette er på trods af at habitatvalg er en af de vigtigste effekter i økosystemer, hvor indirekte effekter af habitatvalg ofte er langt vigtigere end direkte interaktioner. Dette er særligt udtalt i akvatiske økosystemer, hvor populationsdynamikken styres af den daglige vertikale migration. Der findes p.t. ikke en generel værktøjskasse som kan benyttes til at tilføje adfærd til en model af et økosystem. Målet med denne afhandling er at afhjælpe denne mangel gennem udvikling af spilteoretiske værktøjer, samt at benytte disse værktøjer til at undersøge simple økosystemer. Bemærk at alle økosystemer i denne afhandling består af ustrukturerede populationer, d.v.s effekten ontogeni er udeladt.

Artikel A udvikler en generel metode til at implementere habitatvalg i økosystemer med Lotka-Volterra populationsdynamik. Metoden tillader både diskrete og kontinuerte habitater. Artikel B fokuserer på effekten af optimal adfærd i et tre-trofisk økosystem med et refugie. Artiklen fokuserer særligt på effekten af optimal adfærd under henholdsvis øget topprædation og produktivitet. Desuden undersøger artiklen forholdet mellem funktionelle responser af Type II og Type III givet optimal adfærd. Artikel C udvikler en generel metode til at studere optimal adfærd i populations-spil, samt bringer variationelle uligheder ind i teoretisk økologi. Artikel D undersøger et rovdyr-byttedyr spil i en vandsøjle henover et døgn, ved at koble middelfelts spil til populationsdynamik. Dette viser hvorledes den vertikale migration kan forstås som et emergent fænomen fra produktivitet. Endeligt er det blevet valgt at inkludere artikel E, skønt den er en kladde. Dette er for at vise potentialet af metoderne fra artikel D. Artikel E undersøger effekten af optimal adfærd på økosystemer på kontinentalsokler, der understøtter størstedelen af verdens fiskeri.

Preface

This thesis was prepared at DTU Compute in fulfilment of the requirements for acquiring a PhD degree in Applied Mathematics and Computer Science.

Lyngby, 13-October-2022

Two handwritten signatures in blue ink, one on the left and one on the right, positioned below the date.

Emil F. Frølich

Acknowledgements

First and foremost I would like to thank my main supervisor Uffe H. Thygesen, for providing valuable discussions and giving me academic liberty to pursue the projects of my own interest. In addition, I would like to thank my co-supervisor Ken H. Andersen for interesting discussions on the applicability of the work, and an enduring interest in applying the results to real-life settings.

I would like to thank my colleagues, Maksim, Mathias, Niclas, Amos, Christian and Philip for providing an inspiring and informal academic environment. In addition I would like to thank my office mate Mikkel for playing untold hours of foosball. I would also like to thank my colleagues Katrine and Hjørdis for many much-needed coffee-breaks.

The Ph.D. thesis would not have been possible without the support of my girlfriend Lærke Thomsen, who has supported me and helped keep my spirit up the entire way from application to the end. I would also like to thank my parents for supporting me.

Contents

Summary (English)	i
Summary (Danish)	iii
Preface	v
Acknowledgements	vii
I Summary Report	1
1 Introduction	3
1.1 Thesis structure	6
2 Game theory	7
2.1 A brief introduction to game theory	8
2.2 Polymatrix games	11
2.3 Non-linear games	13
2.4 Mean-field games	15
2.5 General ways of finding Nash equilibria	18
2.6 Temporally extended games	19
2.6.1 Lasry-Lions Mean-Field Games	21
3 Behavior and ecosystems	23
3.1 Population games	26
3.2 Mean-field and monomorphic games	27
4 Contributions	33
4.1 Population games in continuous space and time (In print)	34

4.2	Scaling from optimal behavior to population dynamics and ecosystem function	35
4.2.1	Additional results	35
4.3	Population games with instantaneous behavior and the Rosenzweig-MacArthur model	38
4.3.1	Additional results	38
4.4	A predator-prey system with cost of movement	39
4.5	Optimal behavior in a shelf ecosystem	40
4.6	Summary of numerical methods used in the thesis	42
5	Summary and perspectives	47
5.1	Complex ecosystem models with behavior	49
5.2	Better models of individual state	50
5.3	Ontogeny	50
	Bibliography	50
II	Papers	59
A	Solving multispecies population games in continuous space and time	61
B	Scaling from optimal behavior to population dynamics and ecosystem function	73
C	Population games with instantaneous behavior and the Rosenzweig-MacArthur model	107
D	Coupling population dynamics and diel migration patterns	139
E	Optimal behavior in a shelf ecosystem	159

Part I

Summary Report

Introduction

Behavior plays an inescapable role of shaping ecosystems (Stump and Chesson, 2017; Sih et al., 1985), famously illustrated by the return of wolves to Yosemite National Park (Ripple and Beschta, 2004; Laundré et al., 2001). The reintroduction of wolves changed the behavior of elk as they began avoiding open areas, leading to a resurgence of young trees. As such, creating models that incorporate both population changes and behavioral effects while also capturing their interplay is of paramount importance for ecosystem modeling (Schmitz et al., 2004). The goal of this thesis is two-fold in this regard; Firstly, to create general frameworks for modeling population dynamics and behavior, second to study concrete ecosystems using these approaches. In particular, the focus of this thesis is to create models and methods to study aquatic ecosystems.

Though behavior is fundamental in describing ecosystem function, it is still not standard to incorporate it in large-scale ecosystem models. The prime example of a class of models describing large-scale ecosystems are models determining fishing quotas (Kindt-Larsen et al., 2011). Having precise and correct models to determine fishing quotas is of paramount importance as large parts of the worlds populations depend on food-sources from aquatic ecosystems (Tacon and Metian, 2013). When modeling complex aquatic ecosystems behavior is not implemented or implemented indirectly (Ho et al., 2019; van Denderen et al., 2021; Kindt-Larsen et al., 2011). This is despite the fact that fish have rich and varied behavioral patterns over a life-cycle, with their behavior depending on

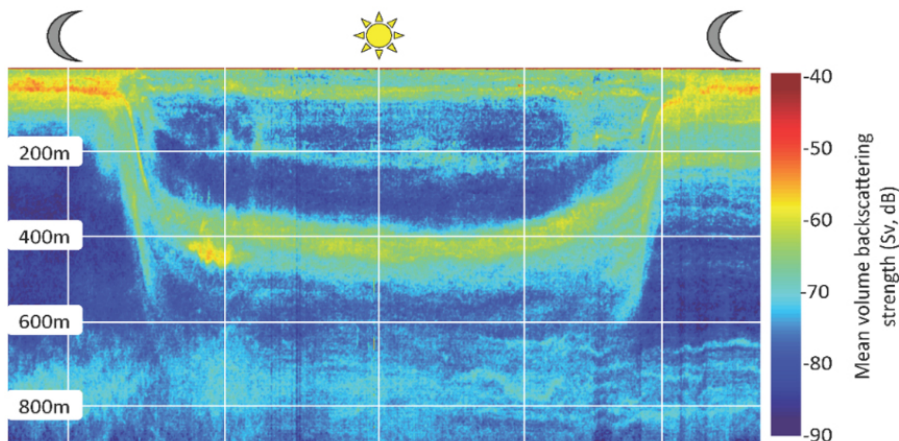


Figure 1.1: An echogram capturing the diel vertical migration, source: <https://oceanexplorer.noaa.gov/explorations/17deepssearch/background/water-column-research/media/fig2-hires.jpg>

both the environment, their age and size (Schadegg and Herberholz, 2017; Biro et al., 2005). A clear example of this is the diel-vertical migration which is the largest animal migration in the world, taking place at sunset and sunrise every day across the world, see Chapter 1. As such, the development of methods to incorporate behavior in ecosystem, particularly aquatic, models is an important problem, which leads to this thesis. The diel vertical migration rules the interaction between fish of differing sizes, with most predator-prey interactions taking place at dawn and dusk (Benoit-Bird and McManus, 2014). The diel vertical migration is a prime example of one of the main behavioral trait in ecological models, namely habitat choice. Understanding how and why animals are distributed as they are, is one of the key challenges in theoretical ecology (Morris, 2003; Fretwell, 1969). This can happen at many different resolutions, both in a fully continuous space and time with explicit movement (Cantrell et al., 2021), and at the level where a habitat is simply divided into two zones, a foraging arena and a safe refuge. A wealth of models have been developed to study the interplay between habitat choice and population dynamics, (Kondoh, 2003; Lima and Dill, 1990; McNamara and Houston, 1992; Abrams, 2010; Werner and Anholt, 1993; Abrams, 1984).

There are many ways to create models incorporating habitat choice based on optimal decision making, one of the primary approaches is to model the interactions as a game and see the emergent effects on the ecosystem, in particular on

the population levels. The basic rationale for modeling interactions as a game is inspired by the idea of Darwinian fitness, where those animals with the highest fitness will outcompete the others (Darwin, 1859). Hence the emergent behavioral strategy of an individual can be expected to lead to fitness maximization. When multiple animals maximize their fitness simultaneously, a game naturally emerges. If we in addition consider a population dynamical equilibrium, then it is reasonable to assume that animals have evolved to follow the strategy that maximizes their fitness. The situation when the system is out of equilibrium is more complicated, but we will come back to this later in the thesis. Modeling behavior by instantaneous optimal habitat choice leads to the emergence of the ideal free distribution, (Fretwell, 1969). The ideal free distribution has had a huge theoretical influence and been validated empirically (Bolker et al., 2003). When movement and population dynamical occur on the same time-scales the situation is more complex, but an analogue of the ideal free distribution can still arise (Cantrell et al., 2021). In this work we develop general tools to study ecosystems with optimal behavior, modeled as optimal habitat choice. Concretely, the contributions consist of the following works:

- In print A general approach for studying Lotka-Volterra habitat selection games, applied to predator-prey system consisting of copopods and forage fish in the north sea. This paper also studies the impact of limited bounded rationality on optimal behavior. The motivation behind this work was expanding the work in (Thygesen and Patterson, 2018) to a multi-species setting, and incorporating population dynamics.
- Resubmitted An idealized predator-prey system of a forage fish and a predator fish, where we study ecosystem impact of optimal behavior through mean-field games. The inspiration for this work was expanding the work in (Kjørboe et al., 2018) to a multi-species setting, and considering the ecosystem impact of optimal foraging.
- Accepted A theoretical development of tools for studying mean-field habitat selection games with instantaneous behavior, applied to an ecosystem modeling the interaction of forage fish and copepods in the arctic summer. The motivation behind this work was to expand the work done in Paper A to the case of non-linear fitness proxies, and to find general criteria for proving uniqueness of Nash equilibria.
- Submitted A predator-prey system with a daily variation in light-levels, modeling copepods and forage fish in the north sea. Using the formalism of temporally extended mean-field games we study the emergent behavior and population levels at the stable point of the populations. The motivation behind this work was to couple the mean-field games of Lasry and Lions (2007) with population dynamics.

Draft A shelf ecosystem with varying benthic and phytoplankton productivity on the diel vertical migration and population levels in a shelf ecosystem. This paper is still in preparation, but we have chosen to include it due to the results it presents and that it shows the feasibility of modeling complex ecosystems. The motivation for this work was to show that the methods developed in the thesis can be applied in real ecosystem models.

1.1 Thesis structure

The dissertation is structured as follows:

- In the first chapter we introduce the motivation and structure of the thesis, and give a brief motivation for each work.
- In the second chapter we introduce the necessary analytical and game-theoretical tools that are used in the papers, highlighting the relationships between the various methods and the problems we face.
- In the third chapter we introduce the problems of modeling interacting populations and their impact on ecosystems. This allows us to introduce population games based on the game-theoretical foundation of the previous chapter. We illustrate the importance of modeling population games as mean-field games.
- In the fourth chapter we briefly summarize the papers that form the basis of the dissertation, presenting the key results and highlighting the connections between the papers.
- In the fifth chapter we conclude on the work that was done in the presented papers, and proposes future work building on the results we have shown.

Note that the bibliography only contains the works referenced in the main body of the thesis. The bibliography of the individual papers can be found in the attached papers.

CHAPTER 2

Game theory

We use game theory to study ecosystems with optimal behavior in this thesis. The roots of game theory are ancient, with the first formal games documented from the dawn of civilization, see Chapter 2. The human interest in games and how to find the best strategies is one of the oldest documented findings (Katz, 2014).

The study of games has been a main driver in the original development of probability theory and statistics (Katz, 2014). The beginnings of informal probability theory was based on studying games of chance (Cardano, 1961). As such, game-theory and probability were originally two sides of the same coin. Further study of expected payoffs in games led to the development of the expectation value (Huygens, 1714), with game-theory and probability theory still intertwined. Finally the correspondence between Pascal and Fermat on games led to the development of discrete probability theory as we know it (Ore, 1960) and the divorce of game theory from probability.

This divorce led to the decline of interest in game theory as a subject in itself, almost disappearing entirely with probability theory taking the center stage. The importance of understanding markets and economic competition increased, and thus game theory as a study in itself reappeared, (Cournot, 1897). This led to the development of game-theory as a general tool for modeling economics, (Von Neumann and Morgenstern, 1947). The paper Von Neumann and Mor-

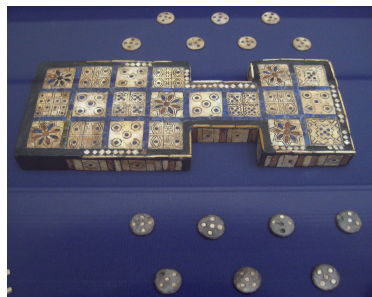


Figure 2.1: The oldest known game, The Royal Game of Ur.
Source:https://upload.wikimedia.org/wikipedia/commons/1/1d/British_Museum_Royal_Game_of_Ur.jpg

genstern (1947) formalized game theory, showing its general applicability in economic modeling and kickstarted the development of abstract game theory. The next step in the development of game theory was to show that every individual can maximize their utility simultaneously in a wide range of games (Nash Jr, 1950). The final step towards game-theory as a tool for studying ecosystem was its application as a tool for explaining animal encounters and strategies (Smith and Price, 1973). Before we can dig into the use of game theory in biology, we review the game theoretic tools and results that we will use.

2.1 A brief introduction to game theory

An N player game consists of a shared strategy space S and the utility functions U_i of the players. Each utility function depend both on the individual choices and the choices of everyone else. Each player i seeks to find the strategy $\sigma_i \in S$ which maximize their utility U_i . A collection of strategies σ_i^{NE} where each player maximizes their individual payoff simultaneously is a Nash equilibrium. At a Nash equilibrium no player gains from deviating from their strategy. Formally, a Nash equilibrium satisfies:

$$\sigma_i^{NE} = \operatorname{argmax}_{\sigma_i \in S} U_i(\sigma_i, (\sigma_j^{NE})_{j=1, j \neq i}^N), \quad \text{for all } i \quad (2.1)$$

If the strategy set S is finite, the Nash equilibrium does not necessarily exist. An example where this occurs is the game rock-paper-scissors. In rock-paper-scissors any strategy can be defeated by the opponent: The key insight in (Nash Jr, 1950) is to consider the expected payoff of a player, under the assumption that a player chooses a strategy randomly based on a probability distribution on the set of possible choices.

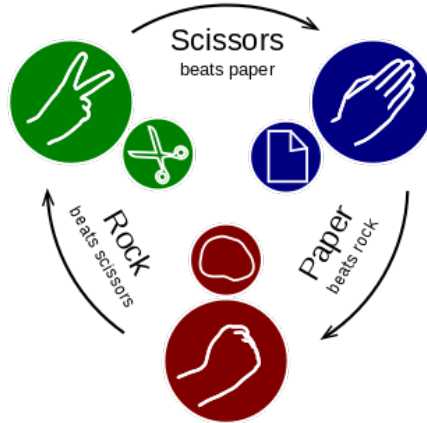


Figure 2.2: Illustration of the game Rock-Paper-Scissors, source: <https://upload.wikimedia.org/wikipedia/commons/6/67/Rock-paper-scissors.svg>

By recasting the possible strategies as finding a probability distribution, we can see that there is a Nash equilibrium in Section 2.1 given by playing each option with probability $1/3$.

This introduction of probability distributions leads to the distinction between mixed and pure strategies. A pure strategy is when the probability distribution is fully concentrated in a single point, whereas a mixed strategy assigns non-zero probabilities to more than one outcome. The distinction can be visualized by thinking in geometric terms. The set of probability measures on a finite set of size n can be modeled as an n -simplex S_n , with point in the simplex representing the support of a probability distribution Section 2.1. Changing to a probabilistic and geometric perspective revealed that Nash equilibria exist in a general class of games (Nash Jr, 1950).

THEOREM 2.1 (EXISTENCE OF NASH EQUILIBRIA) *Consider a game with N players each with utility functions U_i and shared strategy set given by the n -simplex S_n . Then there exists a Nash equilibrium $(\sigma_i^{NE})_{i=1}^N$ satisfying Equation (2.1).*

The theorem was rapidly generalized to the case of compact subsets of metric spaces with continuous utility functions by Glicksberg (1952).

THEOREM 2.2 *Assume K is a compact subset of a metric space, define the*

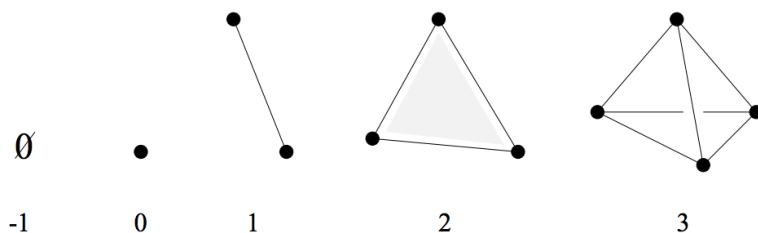


Figure 2.3: Visualization of a simplex, with a zero simplex corresponding to no viable strategies and an n -simplex corresponding to the set of probability distributions over n distinct choices. Source: <https://i.stack.imgur.com/06xtg.png>

strategy space S as the set of probability measures over K , $S = P(K)$. Assume that each player has a continuous utility function U_i . Then there exists a Nash equilibrium $(\sigma_i^{NE})_{i=1}^N$ satisfying Equation (2.1).

These two theorems cover the existence of a Nash equilibrium in the case where the strategy set is finite or compact. The theorems Lemma 2.2 and Lemma 2.1, while forming the foundation of game-theory, are not applicable if the payoff functions are not continuous or the strategy spaces are not compact. Another caveat is that these theorems only guarantee existence of a Nash equilibrium, but provide no clue as how to find it. The problem of finding a Nash equilibrium is highly non-trivial, in particular with a large amount of players (Savani and Von Stengel, 2004). Ecosystems typically involve a large amount of animals interacting, and require a different approach that allow us to handle this. This is where mean-field games, i.e. games where an individual plays the field, come into play. The next subsections focus on introducing specific methods to find Nash equilibria, and determine their existence and uniqueness in a general setting. After this, we introduce mean-field games formally, demonstrating how the methods developed for pairwise games can be used in a mean-field setting.

sults of importance, and state the generalization of the folk-theorem via. variational inequalities as an additional motivation.

2.2 Polymatrix games

Game theory was introduced simultaneously with the advent of linear programming. The development of the two was naturally intertwined for a long while, with a focus on games on simplexes and linear payoff structures. The general structure of the games that were studied alongside the development of linear programming are the polymatrix games:

DEFINITION 2.3 Assume we have N players with strategies σ_i in an m -simplex S_m . Assume all players interact pairwise, where the interaction between players i and j can be described by an interaction matrix A_{ij} . The payoff of player i is:

$$U(\sigma_i, (\sigma_j)_{j=1}^N) = \sum_{j=1, j \neq i}^N \langle \sigma_i, A_{ij} \sigma_j \rangle \quad (2.2)$$

The system $(A_{ij})_{i,j=1}^m$ defines a polymatrix game.

The Nash equilibria of a polymatrix game can be found by interpreting the game as a linear complementarity problem (Lemke, 1970).

DEFINITION 2.4 (LINEAR COMPLEMENTARITY PROBLEM) Given an $m \times m$ matrix M and a vector $q \in \mathbb{R}^m$ the linear complementarity is the problem of finding entry-wise positive vectors w and z such that:

$$\begin{aligned} Mz + q &= w \\ \langle z, w \rangle &\geq 0 \end{aligned} \quad (2.3)$$

The linear complementarity problem originated at the same time as quadratic programming, which is a special case of the linear complementarity problem. The linear complementarity has the benefit that when the real matrix M induces a strictly positive inner product, Lemkes algorithm is guaranteed to terminate and find a solution to the complementarity problem (Lemke, 1970).

The application of linear complementarity problems to polymatrix games was based on iteratively solving a sequence of linear complementarity problems (Eaves, 1973; Rosenmüller, 1971). By shifting all the matrices (A_{ij}) so all payoffs are strictly negative, it is possible to solve a polymatrix game as a single linear complementarity problem (Miller and Zucker, 1991).

THEOREM 2.5 Assume we have a polymatrix game with N players and m strategies and interactions defined by matrices A_{ij} . Define the $1 \times m$ matrix E

consisting of a row of ones. Define the $((N) \cdot m) \times ((N) \cdot m)$ matrix R as

$$R = \begin{bmatrix} 0 & A_{21} & \dots & A_{N1} \\ A_{12} & \dots & A_{N-12} & A_{N2} \\ \vdots & \vdots & \vdots & \vdots \\ A_{1N} & A_{1(N-1)} & \dots & 0 \end{bmatrix} \quad (2.4)$$

Then define $H = R - \max(R) - \varepsilon$. We can then define the final matrix M for the linear complementarity problem:

$$M = \begin{bmatrix} -H & E^T \\ E & 0 \end{bmatrix} \quad (2.5)$$

with the vector $q = (0, \dots, 0, -1, \dots, -1)^T$ where there are N instances of -1 . A Nash equilibrium can now be found by applying Lemkes algorithm to the problem specified by (M, q)

The result of Lemma 2.5 is the principal ingredient in Paper A, but as we consider interacting populations the result has to be modified slightly. Specifically, we had to handle non-zero self-interactions to incorporate density dependence. Exactly how this is done will be covered in the section on mean-field games Section 2.4. Though the Nash equilibrium is guaranteed to exist and can be found through Lemkes algorithm, it does not tell us anything about the number of equilibria. Even a simple game can have multiple Nash equilibria

EXAMPLE 2.1 Consider a two-player matrix game with payoff matrices:

$$\begin{aligned} A_{12} &= \begin{bmatrix} \mathbf{3} & 1 \\ 2 & \mathbf{2} \end{bmatrix} \\ A_{21} &= \begin{bmatrix} \mathbf{3} & 2 \\ 1 & \mathbf{2} \end{bmatrix} \end{aligned} \quad (2.6)$$

This game has two Nash equilibria: $(3,3)$ and $(2,2)$. That these two are Nash equilibria is readily verified, but the question is how do assure ourselves there are no others? If player 1 plays the strategy $(\lambda, 1 - \lambda)$, the payoff of player 2 playing strategy $(1, 0)$ is $3\lambda + (1 - \lambda) = 1 + 2\lambda$. The payoff for playing strategy $(0, 1)$ is $2\lambda + 2(1 - \lambda) = 2$. Hence the best strategy is to play $(1, 0)$ when $\lambda > 1/2$, and $(0, 1)$ otherwise, and a mixed strategy is never a best response. Likewise for player 1.

Example 2.1 illustrates why uniqueness is a desirable trait for a Nash equilibrium. One thing is enumerating Nash equilibria, another is checking whether the enumeration is exhaustive, and comparing the payoffs. Uniqueness of Nash equilibria in polymatrix games can be resolved in part by the theory of P -matrices. A P -matrix is defined as:

DEFINITION 2.6 An $m \times m$ matrix is a P -matrix if every principal minor is positive.

This allows us to state a uniqueness result for Nash equilibria of polymatrix games (Cottle and Stone, 1983):

THEOREM 2.7 *If every principal minor of the matrix R defined by a polymatrix game is a P -matrix, then there is a unique solution to the polymatrix game.*

This is an abstract result, and uniqueness can also be obtained by analyzing a specific game as in (Thygesen and Patterson, 2018).

2.3 Non-linear games

If the payoff functions U_i are non-linear as a function of the player strategies, we need a different methodology than that which we have just presented. Consider a function $f : \mathbb{R}^n \rightarrow \mathbb{R}$ with derivative T . At a minimum x^* the function T satisfies:

$$\langle T(x^*), y - x^* \rangle \geq 0, \quad \text{for all } y \neq x^* \quad (2.7)$$

As an example, we can consider the scalar function

$$U^{mon}(\sigma) = \frac{-10\sigma}{(1+10\sigma)} + \frac{3}{10} \log(1+10\sigma) \quad (2.8)$$

Plotting the function and its derivative $d_\sigma U$ in Section 2.3, it becomes clear that the function is not convex but the minimum is unique. The inequality Equation (2.7) motivates the introduction of variational inequalities, which generalize Equation (2.7).

DEFINITION 2.8 Let K be a convex subset of a real Hilbert space H , and T be a mapping $T : K \rightarrow H$. The variational inequality defined by T over K is denoted $VI(T, K)$ and consists of finding an x such that

$$\langle T(x), y - x \rangle \geq 0, \quad \text{for all } y \in K \quad (2.9)$$

Variational inequalities find broad applications in optimization, and have a rich and developed theory (Hadjisavvas et al., 2006). With Equation (2.7) in mind and using Lemma 2.8 we can recast the problem of finding a Nash equilibrium

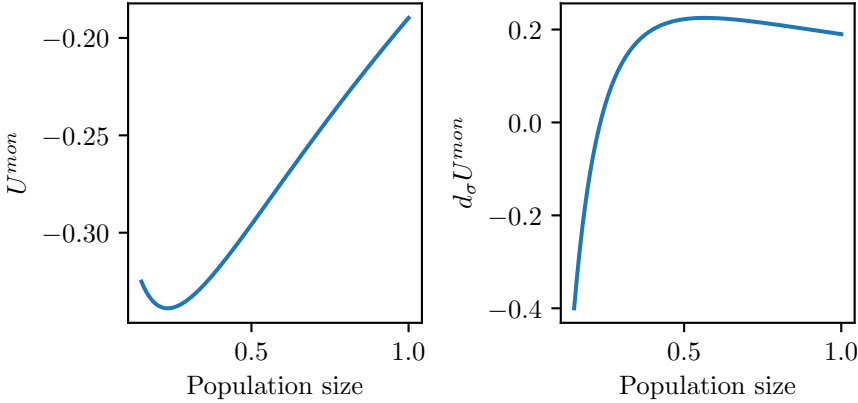


Figure 2.4: A non-convex differentiable function with a unique minimum at the stationary point

as a variational inequality. This allows us to bring the tools of variational inequalities to bear. Consider an N -player game with payoff functions U_i and convex strategy space K . A Nash equilibrium of the game $(\sigma_i^{NE})_{i=1}^N$ solves the system of variational inequalities:

$$\langle -\nabla_{\sigma_i} U_i(\sigma_i^{NE}, (\sigma_j)_{j=1, j \neq i}^N), \sigma'_i - \sigma_i^{NE} \rangle \geq 0 \quad \forall i, \sigma'_i \neq \sigma_i^{NE} \quad (2.10)$$

The advantage of variational inequalities is that the system Equation (2.10) can be recast into a single variational inequality, which we can try to solve. Define the total operator $dU = (\nabla_{\sigma_i} U_i)_{i=1}^N$, a Nash equilibrium can be found by solving the variational inequality over K^N and H^N defined by $-dU$:

$$\langle -dU((\sigma_i^{NE})_{i=1}^N), (\sigma'_i - \sigma_i^{NE})_{i=1}^N \rangle \geq 0, \quad \forall (\sigma'_i)_{i=1}^N \neq (\sigma_i^{NE})_{i=1}^N \quad (2.11)$$

If K is compact, a Nash equilibrium exists by the theorems of Glicksberg and Nash Lemma 2.1, Lemma 2.2. Variational inequalities allow us to answer the question of existence in a more general setting (Maugeri and Raciti, 2009).

THEOREM 2.9 (EXISTENCE OF NASH EQUILIBRIA) *The variational inequality $\langle -dU(\sigma), \sigma' - \sigma \rangle$ has a solution σ^{NE} over K^N if there exists a point $y_0 \in K^N$ such that*

$$\{\sigma' \in K : \langle -dU(\sigma'), \sigma' - y_0 \rangle < 0\} \quad (2.12)$$

is bounded.

When we consider an optimization problem, it is preferable the optimal value is unique so any optimization method will give the same result. Uniqueness is particularly important for Nash equilibria, as the payoffs in one Nash equilibrium can strictly dominate the payoffs at another Nash equilibrium Example 2.1. Typically, we are only interested in the maximal combination of values. Convex functions have unique minima, and are characterized by having monotone derivatives. This can be generalized by variational inequalities.

DEFINITION 2.10 A variational inequality $VI(T, K)$ is strictly pseudomonotone if

$$\langle T(x), y - x \rangle \geq 0 \Rightarrow \langle T(y), y - x \rangle > 0 \quad (2.13)$$

A strictly pseudomonotone variational inequality has at most one solution.

For a proof, see [Hadjisavvas et al. \(2006\)](#).

That strict pseudomonotonicity generalizes monotonicity is illustrated in Section 2.3, as the function U^{mon} has a unique minimum, but its derivative is not strictly increasing.

THEOREM 2.11 (UNIQUENESS OF NASH EQUILIBRIA) *The Nash equilibrium of a game defined with the variational inequality $\langle -dU(x), y - x \rangle \geq 0, \quad \forall y \neq x$ is unique if $-dU$ is strictly pseudomonotone.*

For polymatrix games, we could find the Nash equilibrium by using Lemkes algorithm after rephrasing them as linear complementarity problems. By rephrasing Nash equilibria as variational inequalities, we open up a new set of tools. One of them is to rephrase the variational inequality in terms of a non-linear complementarity problem and solve that. This is the method we used in articles *B* and *C*. Another method is to apply projection-based methods ([Solodov and Svaiter, 1999](#)). We did not explore the potential of this method in our work, as there appears to be a lack of a standard robust implementation.

2.4 Mean-field games

When the number of players in a game grows, the problem of finding Nash equilibria increases exponentially ([Savani and Von Stengel, 2004](#)). The theory of mean-field games was invented to handle this situation. Assuming we have multiple types of players the population of each type is very large and the utility of an individual depends on the average strategy of the other players,



Figure 2.5: A school of fish coordinating their movement by individual actions, a situation which can be modeled by a mean-field game. Source: Christian Holland, <https://www.flickr.com/photos/christianholland/>

then the game can be modeled as a one-shot mean-field game (Aumann, 1964; Carmona, 2004). In the ecological literature, one-shot mean-field games are typically referred to as "playing the field". The prototypical phenomenon to model as a mean-field game is flocking, where large amounts of individuals seem to coordinate their behavior without any central planning as in a school of fish Section 2.4. In a mean-field game the utility functions U_i of an individual are functions of both the strategy of an individual σ_i and the average population strategies $\bar{\sigma}_j$, so $U_i(\sigma_i, (\sigma_j)_{j=1}^N)$. The theory of whether and in what sense a mean-field game represents the limit of an N -player is expansive. We have not gone into details concerning this. An introduction to the theory of which limits tend to mean-field games may be found in Lacker (2020); Lasry and Lions (2007); Carmona and Lacker (2015).

At the Nash equilibrium no individual in a mean-field game gains from diverging

from their strategy. As all players in each group are assumed identical, the payoff of all individuals must be identical. The payoff for an individual is the same as the payoff from following the population mean strategy. For this reason, the Nash equilibrium of a mean-field game must be a solution to the fixed-point problem

$$\bar{\sigma}_i = \operatorname{argmax}_{\sigma_i \in K} U_i(\sigma_i, (\bar{\sigma}_j)_{j=1}^N) \quad (2.14)$$

With Equation (2.14) in hand, we can expand the usefulness of polymatrix games to games with density dependent effects.

THEOREM 2.12 *Assume we have N interacting populations with the interaction of an individual of type i with population j specified by a matrix A_{ij} . Then the Nash equilibrium of the game can be found by solving the linear complementarity problem specified as: Define the $1 \times m$ matrix E consisting of a row of ones. Define the $((N) \cdot m) \times ((N) \cdot m)$ matrix R as*

$$R = \begin{bmatrix} \frac{1}{2}A_{11} & A_{21} & \dots & A_{N1} \\ A_{12} & \dots & A_{N-12} & A_{N2} \\ \vdots & \vdots & \vdots & \vdots \\ A_{1N} & A_{1(N-1)} & \dots & \frac{1}{2}A_{NN} \end{bmatrix} \quad (2.15)$$

Defining $H = R - \max(R) - \varepsilon$ we can define the final matrix M for the linear complementarity problem:

$$M = \begin{bmatrix} -H & E^T \\ E & 0 \end{bmatrix} \quad (2.16)$$

with the vector $q = (0, \dots, 0, -1, \dots, -1)^T$ where there are N instances of -1 . A Nash equilibrium can be found by applying Lemke's algorithm to the problem specified by (M, q)

For a proof of this, see Appendix A in paper A. If we consider the more general case, with N interacting populations and general non-linear utility functions the criterion for a Nash equilibrium in terms of variational inequalities is given by the system of variational inequalities

$$\langle -\nabla_{\sigma_i} U_i |_{\sigma_i = \bar{\sigma}_i} ((\bar{\sigma}_j^{NE})_{j=1}^N), \bar{\sigma}'_i - \bar{\sigma}_i^{NE} \rangle \geq 0 \text{ for all } \sigma'_i \in K \quad (2.17)$$

Using the shorthand dU_i for $\nabla_{\sigma_i} U_i |_{\sigma_i = \bar{\sigma}_i}$, we can define the operator $dU = (dU_1, \dots, dU_N)$. Finding a Nash equilibrium of a mean-field game is equivalent to solving a variational inequality.

THEOREM 2.13 *The Nash equilibrium of the N -player mean-field game with payoff functions $U_i(\sigma_i, (\bar{\sigma}_j)_{j=1}^N)$ and strategy space $K \subset H$ can be found by solving the variational inequality:*

$$\langle -dU((\bar{\sigma}_j^{NE})_{j=1}^N), ((\sigma'_j)_{j=1}^N - ((\bar{\sigma}_j^{NE})_{j=1}^N)) \rangle \geq 0 \text{ for all } (\sigma'_j)_{j=1}^N \neq (\bar{\sigma}_j^{NE})_{j=1}^N \quad (2.18)$$

We apply this result for the first time in Paper B expanding on the result in Paper C.

2.5 General ways of finding Nash equilibria

Though we have theoretical tools establishing the existence of Nash equilibria, actually calculating them can be very hard. There are two general avenues of approach to this problem. The first is direct solution, where a system of equations is posed and then solved. The other is rephrasing the problem as a dynamical system, where the dynamical system is guaranteed to converge to the Nash equilibrium. If we start with the direct methods, we can formulate the Nash equilibrium as a linear or non-linear complementarity problem. This complementarity problem can then be solved, either by dedicated tools such as SICONOS [Acary et al. \(2019\)](#) or by posing it as a feasibility problem for a general purpose optimization algorithm. If we instead consider the variational inequality, the most popular direct approach is using extra-gradient type algorithms. These have not been explored in this work, but would potentially be useful in future work with large-scale systems. We did not explore these algorithms as robust and fast implementations are not readily available, in contrast to the situation for complementarity problems.

The replicator equation is the most well-known approach to finding Nash equilibria in evolutionary games, due to its direct biological interpretation as describing the population dynamics of a collection of phenotypes, e.g. the distribution of populations on a finite set of patches. If we describe the mean fitness by $E(F(x))$ and the fitness at a point i by $F(x_i)$, the equation is:

$$\dot{x}_i = x_i(F(x_i) - E(F(x))) \quad (2.19)$$

The replicator equation essentially assures that the areas with positive fitness increase and the areas with negative fitness decrease in relative population, according to the game dynamics. The Folk Theorem ([Broom and Rychtár, 2013](#)) in evolutionary game-theory describes the strength of this approach, saying that every Nash equilibrium is a stable state of the replicator equation, and that the replicator equation is stable if F is monotone ([Sandholm, 2010](#)). The replicator equation is intrinsically linked to variational inequalities, with regularity of the variational inequality giving stability of the replicator equation ([Migot and Cojocaru, 2021](#), Theorem 6)

THEOREM 2.14 *Assume that F is strictly pseudomonotone, and x^* is a Nash equilibrium. Then x^* is globally asymptotically stable for the replicator equation.*

Hence the Folk Theorem has a much wider validity than is usually assumed, as the stability holds not only for monotone F but pseudomonotone F .

2.6 Temporally extended games

By assuming the payoff functions for the individual players are given by integrals over a time-interval constrained by some differential equation, we enter the realm of differential games. Differential games are riddled with technical assumptions and formal constructions, for this reason we state the theorems in this section in a condensed manner neglecting all considerations of domains of definition, well-posedness and regularity. Stating the theorems in their full generality and with full precision would bring us too far afield. Instead, we refer to where the theorems can be found formulated with full mathematical precision. We start by considering the case of a single player with strategy v in the feasible space K , i.e. the pure optimization problem:

$$\begin{aligned} \max_{v \in K} \int_0^T J(x, v) dt \\ \dot{x} = f(x, t, v) \end{aligned} \quad (2.20)$$

The optimal value V , i.e. the maximal value, and control strategy v for a functional constrained by a dynamical system in Equation (2.20) can be determined by the Hamilton-Jacobi-Bellman (HJB) equation, see Equation (2.21).

$$-\frac{\partial V}{\partial t} = \sup_{v \in K} \left(\frac{\partial V}{\partial x} f(x, v, t) + J(x, v, t) \right) \quad (2.21)$$

THEOREM 2.15 (HAMILTON-JACOBI-BELLMAN) *Given a finite-horizon control problem Equation (2.20) without a terminal reward, the optimal value and strategy can be determined by solving Equation (2.21).*

For a precise version of Lemma 2.15, see (Carmona, 2016). As most motion is not purely deterministic but involves some randomness, it is suitable to instead consider dynamics described by stochastic differential equations. The simplest situation is a deterministic system with a constant noise, leading to the Itô differential equation:

$$dX_t = f(u, X_t, t)dt + \sigma dB_t \quad (2.22)$$

For a discussion of well-posedness and existence of the Itô equation see (Carmona, 2016). The paths of individual fish in the diel vertical migration Chapter 1

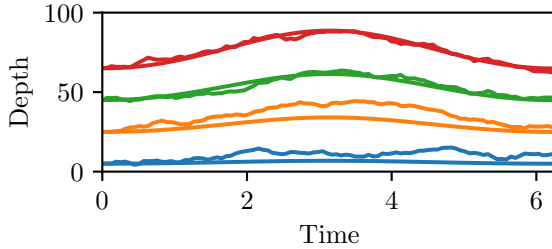


Figure 2.6: Sample paths from an Itô stochastic differential equation with $f(u, x) = ux$, where $u = \sin(t)$ and $\sigma = 1$, plotted along with solutions of the deterministic differential equation.

with the night in the middle of the time interval can be modeled using a stochastic differential equation: The trajectories in Section 2.6 look like plausible paths in a vertical migration, but this mechanistic model has the weakness that it has no dependence on predator numbers. It is well-documented that the diel vertical migration is dependent on the risk of predation and the resource levels (Solberg and Kaartvedt, 2017), so a model of the diel vertical migration should incorporate this. This is where modeling the diel vertical migration as a game comes in, as a game-theoretical model allows for an emergent migration based on the a risk-reward trade-off. Optimizing when the dynamics are given by a stochastic differential instead of a deterministic one forces a change in perspective, namely to optimizing the expected value. The optimal strategy is then the one that maximizes the expected value, this can also be determined by using a version of the HJB equation:

THEOREM 2.16 (VERIFICATION) *Assume the dynamics of a stochastic process can be described by the stochastic differential equation Equation (2.22). A strategy u and value function V with terminal condition $V(x_T)$ which satisfy*

$$-\frac{\partial V}{\partial t} = \sup_{u_i \in K} \left(\frac{\partial V}{\partial x} f(u, x, t) + J(x, u, t) + \frac{1}{2} \sigma \frac{\partial^2 V}{\partial x^2} \right) \quad (2.23)$$

maximize the functional

$$E \left(\int_0^T J(X_t, u, t) dt \right) \quad (2.24)$$

For a precise statement of Lemma 2.16 see (Carmona, 2016) The setup for a differential game can now be defined. We have multiple players, each with

dynamics described either by an SDE or ODE and each player seeks to optimize a functional or the expected value of a functional.

THEOREM 2.17 *Given N players with dynamics given by Equation (2.22) and each with value functions $U_i = E(\int_0^T J_i((X_t^i)_{i=1}^N, (u_i)_{i=1}^N, t) dt)$, a Nash equilibrium is given by a simultaneous solution to the HJB equations for all players. Hence a solution can be found by solving the system:*

$$-\frac{\partial V_i}{\partial t} = \sup_{u_i \in K} \left(\frac{\partial V_i}{\partial x_i} f_i((u_i)_{i=1}^N, (x_i)_{i=1}^N, t) + J_i(x, (u_i)_{i=1}^N, t) + \frac{1}{2} \sigma_i^2 \frac{\partial^2 V_i}{\partial x_i^2} \right) \quad (2.25)$$

with terminal conditions $V_i(T)(x) = D_i(x)$

For a precise statement of Lemma 2.17 see (Carmona, 2016).

As we can see, solving a differential game with N players amounts to solving N coupled HJB equations.

2.6.1 Lasry-Lions Mean-Field Games

If we assume that the populations are very large, then the system in Lemma 2.17 becomes intractable. Instead, we are drawn again to the framework of mean-field games. If we assume that the populations we consider consist of infinitely many individuals, and that the movement of each individual can be described by a stochastic differential equation as in Equation (2.22), we can use the mean-field game framework introduced in Lasry and Lions (2007).

In this framework, each individual uses the optimal strategy as described by the HJB equation, where we optimize at every instant with respect to the population distribution. At the Nash equilibrium, however, no individual gains from diverging from the population mean strategy. Hence the evolution of the population distribution can be described by the Fokker-Planck equation from the SDE's of the individuals. Mean-field games in the sense of Lasry and Lions (2007) result in the distribution of the population being described by a forward-backward pair of partial differential equations. The forward equation captures the dynamics of the distribution, and the backwards equation stems from the individual optimization. Our interest lies in the periodic migration of animals in the water column, hence we are interested in these equations with periodic boundary conditions.

To solve the mean-field game for N populations then entails solving N coupled HJB equations and N Fokker-Planck equations.

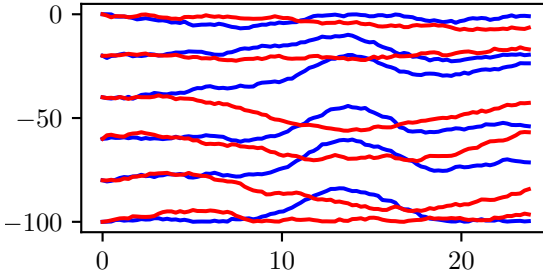


Figure 2.7: Sample paths from the mean-field game solved in paper D, with a consumer and a predator both at population equilibrium.

THEOREM 2.18 *Given N populations each distributed according to φ_i at time t , an individual of population i has dynamics governed by Equation (2.22) and utility function*

$$U_i = E \left(\int_0^T J(X_t, u_i, (\varphi_i)_{i=1}^N, t) dt \right) \quad (2.26)$$

then the Nash equilibrium of the mean-field game is given by the solution to the system of equation pairs:

$$\begin{aligned} -\frac{\partial V_i}{\partial t} &= \sup_{u_i \in K} \left(\frac{\partial V_i}{\partial x_i} f_i(u_i, (\varphi_j)_{j=1}^N, (x_j)_{j=1}^N, t) + J_i(x, (u_i)_{i=1}^N, t) + \frac{1}{2} \sigma_i \frac{\partial^2 V_i}{\partial x_i^2} \right) \\ \frac{\partial \varphi_i}{\partial t} &= -\frac{\partial u_i \varphi_i}{\partial x} + \frac{1}{2} \sigma \frac{\partial^2 \varphi_i}{\partial x_i^2} \end{aligned} \quad (2.27)$$

with terminal conditions $V_i(T)(x) = D_i(x)$.

The important aspect of Lemma 2.18 is that the individuals act given the state of the population, but the state of the population evolves according to the action of all individuals and these two phenomena are in equilibrium. For a precise statement of Lemma 2.18 see (Carmona, 2016).

We develop a method to solve mean-field games in Paper D, applying it to the diel vertical migration. The sample paths based on the work in Paper D can be seen in Section 2.6.1. Remark that these paths are quite similar to those in Section 2.6, but arise organically as a result of a mean-field game. This illustrates that mean-field games can provide emergent behavioral models to replace mechanistic behavioral models of the diel vertical migration.

CHAPTER 3

Behavior and ecosystems

In order to understand ecosystems it is instructive to study their response to forcing of either basal resources or mortality (Hairston et al., 1960). The response of a trophic chain to bottom-up forcing led to the classical ecosystem enrichment hypothesis (Oksanen et al., 1981; Hairston et al., 1960). The ecosystem enrichment hypothesis predicts a population response at every second level in a food chain (Murdoch et al., 2003). The models underlying the ecosystem enrichment hypothesis, however, do not incorporate that animals have dynamic habitat choice. In nature, animals move away from productive zones where the threat of predation is too high instead preferring less productive safe zones Schmitz et al. (2004). Modifying the models of population dynamics to include behavior leads to trophic cascades from indirect effects which dominate the importance of direct effects (Peckarsky et al., 2008; Heath et al., 2014; Wollrab and Diehl, 2015; Abrams and Vos, 2003), and the collapse of the ecosystem enrichment hypothesis (Gonçalves et al., 2014).

Constructing models that can predict where animals forage and population dynamics is a major goal in theoretical biology (Abrams, 2010; Morris, 2003). There are various ways to include habitat-choice dynamics in ecosystem models, Chapter 3. The simplest way to include the importance of behavior in ecosystems is changing the definitions of the functional responses governing the interactions to include density dependence (Arditi and Ginzburg, 1989; Příbylová and Berec, 2015; DeAngelis et al., 1975). Another way is to let each individ-

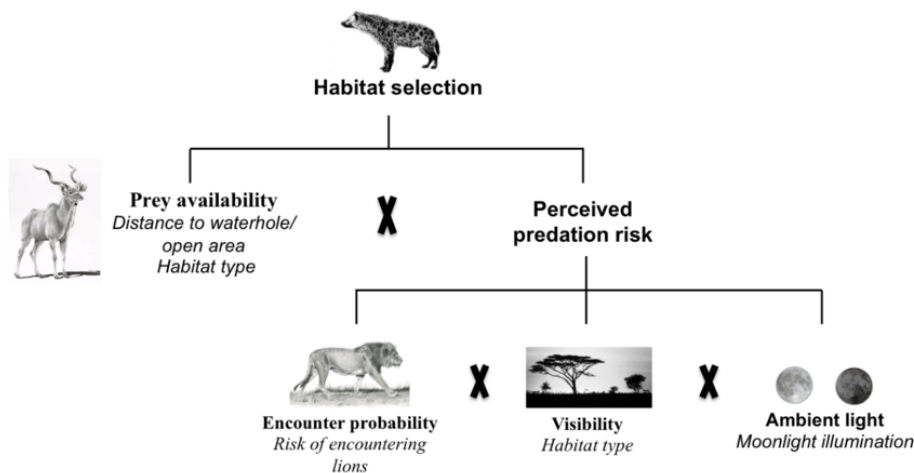


Figure 3.1: Illustration of the choices involved in habitat selection for a hyena on the savanna, source: (Périquet, 2014)

ual move in the direction of higher fitness (Abrams, 2007, 2009; Avgar et al., 2020). Finally, behavior can be modeled by assuming that each animal forages optimally at each instant (Křivan, 2007; Kiørboe et al., 2018; Křivan et al., 2008; Thygesen and Patterson, 2018). As soon as multiple animals are present this approach leads to a game where every animal seeks to optimize its fitness. This is the approach to model ecosystems with optimal habitat choice we have followed in papers A, B and C.

Games have been applied to model behavior almost since the advent of game theory (Smith, 1982), but the general coupling to population dynamics has not followed suit. Game theory quickly found applications in biology. Matrix games are used to model mating and aggressiveness (Smith, 1974; Smith and Price, 1973) and other behavioral patterns with competition (Smith and Price, 1973; Broom and Rychtár, 2013). The next step, which is where the work in this thesis takes off, is games being applied in the context of habitat selection. A theoretical explanation was desired to explain e.g. why all animals do not clump at the most productive spot in a habitat. This led to the development of the ideal free distribution (Fretwell, 1969). The ideal free distribution classically emerged to describe the distribution of a population where all individuals practice instantaneous optimal foraging, where there is no cooperation. It was formulated theoretically, but has been found empirically in a wide range of settings (Williams et al., 2013). The original defining characteristic of the ideal free distribution is that each individual seeks the spot that optimizes their in-

dividual fitness, so the ideal free distribution is naturally coupled to population dynamics.

Though the ideal free distribution assumes instantaneous movement, in reality animals move based on potentially limited information about their environment. The ideal free distribution is, however, still an essential tool as the migration strategies which are stable are generally those which lead to the ideal free distribution at population equilibrium (Cantrell et al., 2010, 2021; Stephen Cantrell et al., 2007; Cressman and Křivan, 2010). Likewise, when the migration dynamics and the population dynamics are on decoupled time-scales the ideal free distribution also emerges as an evolutionarily stable strategy (Cantrell et al., 2020; Cressman and Křivan, 2006), hence following the optimal strategy every instant is a reasonable approximation (Cressman and Křivan, 2006; Křivan, 2007; Ma et al., 2003).

When considering interacting populations, there are basically three time-scales to consider. A slow evolutionary time-scale, in which small changes happen across generations, a medium population-dynamical describing changes in existing populations, and a fast behavioral time-scale where the changes in populations are small. The evolutionary time-scale is clearly separated from the other two, while the population-dynamical and the behavioral time-scale can be intertwined (Abrams, 2007). A full ecosystem model would incorporate all three time-scales explicitly, but constructing such a model is non-trivial due to the curse of dimensionality. As population dynamics and behavior are the two levels which are closest in time-scales and influence each other directly (Abrams, 2010) models with a time-scale of years or months considering this interaction is the norm (Gonçalves et al., 2014; Valdovinos et al., 2010). If there is a full time-scale separation, then behavior, usually movement, can be modeled as instantaneous (Cressman and Křivan, 2006; Křivan, 2013) in a full dynamical model. Instantaneous optimal behavior typically serves to stabilize the population dynamics (Valdovinos et al., 2010).

If we consider the behavior describing habitat choice at a population equilibrium, the situation is more complicated. In this setting, the evolutionary, population-dynamical and behavioral time-scales all interact. If there is no temporal variation in the environment then the evolutionarily stable dispersal strategies are those which lead to a habitat dispersal where each animal has optimal fitness (Cantrell et al., 2010, 2012; Cressman and Křivan, 2010; Křivan et al., 2008). As such, the resultant distribution from distribution and instantaneous optimization are indistinguishable at an evolutionary and population equilibrium. This, however, is predicated on such a stable state existing, which is not always the case under certain behavioral dynamics (Abrams and Roth, 1994b). The case where behavior is either instantaneous or we assume we are at an equilibrium is what we considered in paper A, B, and C. If the environment is temporally

varying, such as is the case for the daily cycle in the ocean, the optimal strategy at equilibrium is no longer the ideal free distribution and movement needs to be incorporated directly (Cantrell et al., 2021). Studying this requires an entirely different toolset, and is the focus of papers D and E.

3.1 Population games

The main topic studied in this thesis is the interaction between different populations, and how their behavior affects population dynamics. The strategies that are safe against invasion are those in which an individual seeks to optimize their fitness, so the definition of a population game should reflect this. This leads back to the definition of a population game where the behavior is that which maximizes the individual per capita growth-rate (Křivan, 2013; Vincent and Brown, 2005; Cressman and Křivan, 2010). An individual in a population game maximizes their own fitness at each instant taking the mean strategy of the population into account, which then modifies the emergent population dynamics (Cressman and Křivan, 2010). A population game can also be defined when movement and migration are not on decoupled time-scales (Cantrell et al., 2021). Our definition of a population game needs to be broad enough to capture population games where each actor has optimal behavior, and the movement can either be instantaneous or explicit. Using the machinery introduced in Chapter 2, we can give a precise definition of a population game, generalizing the definition given in Paper C.

DEFINITION 3.1 Assume there are N interacting populations with average strategies $\bar{\sigma}_i$ and each individual has a strategy s . Each individual has fitness $U_i(s, (\bar{\sigma}_j)_{j=1}^N, (N_j)_{j=1}^M)$, where U_i is a functional. Further assume the population dynamics are of Kolmogorov-type:

$$\dot{N}_i = N_i U_i(\bar{s}_i^{NE}, (\bar{\sigma}_j^{NE})_{j=1}^N, (N_j)_{j=1}^M) \quad (3.1)$$

A population game is when all individuals seek to maximize their fitness U_i with respect to s_i , leading to a mean-field Nash equilibrium $(U_i^{NE})_{i=1}^N$. A population game equilibrium is a simultaneous population and Nash equilibrium.

The study of population games with instantaneous movement is the main focus of the first three papers, with Paper A developing a general method for Lotka-Volterra style games and Paper C generalizing to arbitrary payoff functions. The study in Paper B illustrates the changes in an ecosystem from introducing a population game compared to the case with static behavior. The ideal free

distribution in the single-species case has the attribute that a population following this strategy cannot be invaded, but the situation is more complicated in the multi-species case. The multi-species version of the ideal free distribution should also be invasion proof, and best-response dynamics should converge to the ideal free distribution (Křivan et al., 2008). We were able to define a multi-species version of the ideal free distribution in Section 4.3, based on (Cressman et al., 2001) and the idea of using variational inequalities to formulate evolutionary stability (Migot and Cojocaru, 2021).

DEFINITION 3.2 A Nash equilibrium of a population game with total operator $-dU = (-dU_i)_{i=1}^N$ is an ideal free distribution if at least one component $-dU_i$ is strictly pseudomonotone at the Nash equilibrium.

Apart from population-games with instantaneous behavior, we also studied population games with optimal behavior with explicit movement. In this context, we only studied population game equilibria. As we studied populations where diffusion was part of their movement, they do not exactly follow a simple ideal free distribution at equilibrium. The impact of this on population dynamics was investigated in Section 4.1, where we found that a low level of randomness in the location of an individual did not change the population dynamics to a noticeable degree compared to when they exactly followed an ideal free distribution.

3.2 Mean-field and monomorphic games

The common assumption throughout the mean-field games studied in this thesis is that the key decisions are taken by individuals, acting on the basis of the average behavior of the population. That is, we assume multiple different populations where individuals play the field (Broom and Rychtář, 2014) and have different, i.e. polymorphic, behavior. The underlying assumption here is that individuals of the same type do not cooperate, but rather compete. If instead all individuals have the same behavior and optimize it based on this knowledge, cooperation naturally emerges. This is the situation when the populations are monomorphic.

So far the optimal strategy of an individual is determined from the mean strategy of the population. This is what allows us to study non-linear population games with individual optimization. An alternative is to assume monomorphic populations when studying non-linear population games. In a monomorphic game, all individuals in a population a-priori act as one.

The assumption of monomorphic behavior is usually introduced as a simplifying

assumption in non-linear models (Genkai-Kato, 2007). Incorporating cooperation in models based on fitness optimization increases fitness and causes a divergence from the ideal free distribution (Abrams and Roth, 1994a; Křivan et al., 2008). In both nature and human society, cooperation is commonly observed, and explaining the emergence with a game-theoretical model despite the in-built individual tendencies of Darwinian fitness is non-trivial.

Several key explanatory factors tie directly into the models we consider in this thesis. The first is that anti-social individual choice is no longer beneficial if negative density dependence results over a longer time-horizon (Axelrod and Hamilton, 1981). Another way for cooperation in the sense of monomorphic behavior to emerge is by optimal individual behavior over a life-time taking the structure of populations into account (Akçay and Cleve, 2012). In this thesis, however, we have only considered unstructured populations. Hence the model of assuming polymorphic non-cooperating populations is reasonable.

A final approach to incorporating cooperation, while keeping a polymorphic approach, is to introduce a positive location-specific density dependence. Such effects lead to the evolution of pro-social behavior (Kimmel et al., 2019). As such, a sufficiently concentrated population with sufficiently large positive density effects can be modeled reasonably as monomorphic. This case is not explored in the thesis.

As noted, in the thesis we have studied non-linear population games based on the assumption of polymorphic populations, rather than the monomorphic case. During the research underlying the thesis we invested considerable effort in investigating the difference between population games with monomorphic and polymorphic populations. This allowed us to set up a correspondence between a polymorphic population and a corresponding monomorphic game, which can be used to directly compare a mean-field game and the same game with a monomorphic population. The key is that the Nash equilibria of a mean-field game can often be recovered as the Nash equilibria of a game with monomorphic populations. Comparing the monomorphic game which leads to the mean-field game with the naive monomorphic game can lead to insights as to the impact of assuming a monomorphic population in a given setting is.

DEFINITION 3.3 Consider a mean-field game with populations N_1, \dots, N_M with individual payoffs $U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M)$. Assume $\nabla_{\sigma_i} U_i |_{\sigma_i = \bar{\sigma}_i}$ admits a primitive U_i^{mon} such that $\nabla_{\sigma_i} U_i |_{\sigma_i = \bar{\sigma}_i} = \nabla_{\sigma_i} U_i^{mon}$. We define the monomorphic equivalent game as the game with monomorphic populations specified by the payoff functions U_i^{mon} .

We illustrate the importance of whether a population is assumed to cooperate

or have individual behavior with an example.

The relationship between monomorphic and polymorphic games is clearest in the case of matrix games. Consider a population of size N in a two-patch ecosystem. Assume that the productivity of patch i is $b(i) = 2i$, and that the population has a negative density dependence. This could e.g. reflect competition. The intraspecific competition is described by the matrix

$$A = \begin{bmatrix} -2 & 0 \\ 0 & -4 \end{bmatrix} \quad (3.2)$$

In a mean-field game, the payoff for an individual is $U(\sigma, N\bar{\sigma})$.

$$U(\sigma, N\bar{\sigma}) = N \langle \sigma, A\bar{\sigma} \rangle + \langle \sigma, b \rangle \quad (3.3)$$

This defines a mean-field game, where the Nash equilibrium can be determined by solving a Linear Complementarity Problem by Lemma 2.12. This theorem, however, also has a second interpretation in light of Lemma 3.3. We can see that the game defined by Equation (3.3) is equivalent to the monomorphic game

$$U(\sigma, N\sigma)^{mon} = \frac{N}{2} \langle \sigma, A\sigma \rangle + \langle \sigma, b \rangle \quad (3.4)$$

To find the Nash equilibria of this game we need to solve simple optimization problem, and the Nash equilibrium σ^N is readily found

$$\begin{aligned} \sigma^N &= \begin{pmatrix} \frac{(N-1)}{3N} \\ 1 - \frac{(N-1)}{3N} \end{pmatrix}, & N > 1 \\ \sigma^N &= \begin{pmatrix} 0 \\ 1 \end{pmatrix}, & N \leq 1 \end{aligned} \quad (3.5)$$

If we consider the naive monomorphic game, the optimal strategy is

$$\begin{aligned} \sigma^N &= \begin{pmatrix} \frac{(2N-1)}{6N} \\ 1 - \frac{(2N-1)}{6N} \end{pmatrix}, & N > \frac{1}{2} \\ \sigma^N &= \begin{pmatrix} 0 \\ 1 \end{pmatrix}, & N \leq \frac{1}{2} \end{aligned} \quad (3.6)$$

Comparing Equation (3.5) and Equation (3.6), we see a difference in the Nash equilibria when $N > \frac{1}{2}$. In this case, the population is much more spread out in the monomorphic game, as they coordinate to avoid one another. Meanwhile the population is much more concentrated in the mean-field game as each individual would prefer patch 2. As the populations grow to infinity, the difference between the two equilibria become more and more pronounced.

Consider a habitat-choice game where a consumer in a population of size N with a growth rate given by a Type II functional response. The consumer can either stay in a refuge or go into a foraging arena. In the foraging arena there is a population of predators. The predators also have a Type II functional response. Their satiation level depends on the mean time spent in the arena by the consumers. If we use the instantaneous growth as a fitness proxy and let σ model the time spent in the arena range from $[0, 1]$, this situation is modeled by the payoff function:

$$U(\sigma, \bar{\sigma}) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \frac{\sigma}{1 + c_3 N \bar{\sigma}} \quad (3.7)$$

We seek an equivalent monomorphic payoff function to Equation (3.7). A candidate which fulfills the criteria of Lemma 3.3 is

$$U^{mon}(\sigma, \sigma) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \log(1 + N c_3 \sigma) \quad (3.8)$$

which we recognize as a function with strictly pseudomonotone derivative from Equation (2.20). The utility function in Equation (3.8) can be compared with the naive monomorphic payoff function in Equation (3.9), where we set $\sigma = \bar{\sigma}$ in Equation (3.7).

$$U(\sigma, \sigma) = \frac{\sigma r}{\sigma c_1 + 1} - c_2 \frac{\sigma}{1 + N c_3 \sigma} \quad (3.9)$$

We can now directly see the impact of assuming a polymorphic population and studying a mean-field game. As the growth of $c_2 \frac{\sigma}{1 + c_3 \sigma}$ in Equation (3.9) is smaller than that of $c_2 \log(1 + c_3 \sigma)$ in Equation (3.8), the maximum of $U(\sigma, \sigma)$ will be attained at a larger value of σ . This corresponds to an inherently monomorphic population being more risk-seeking, as individuals will sacrifice themselves for the greater good. Equation (3.7) illustrates that maximizing the individual growth leads to a lower growth rate compared to maximizing the raw pr. capita growth rate as also shown in (Abrams et al., 1993). This is illustrated in the plot below, illustrating density-dependent effects on the population growth rate as a function of the population size N : The pattern emerges that the monomorphic individuals are more willing to take risks and work together to satiate the predator. This stems from the fact that each individual attempts to maximize the per capita growth of the group as a whole, with the knowledge that the entire group will have the same behavior. Mean while the mean-field games induces a risk-averse behavior, as each individual makes a decision based on the behavior of the group, with no assumptions on them acting in the same way. In this way, monomorphic games serve as a model for groups with strong cooperation and coordination and mean-field games are suitable when individuals act independently and selfishly. Which is the more suitable for a given situation depends on the system being modeled, but a reasonable default is going for a mean-field game when considering habitat choice as these are the ones which give rise to ideal-free distributions (Fretwell, 1969; Broom and Rychtář, 2014).

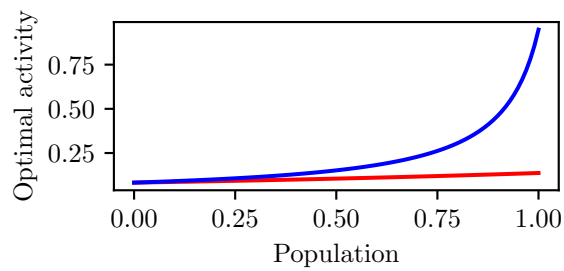


Figure 3.2: The optimal strategy for a monomorphic game Equation (3.9) (blue) and mean-field game Equation (3.7) (red)

CHAPTER 4

Contributions

This thesis presents five papers. Paper A is published, paper C is accepted, paper B is in resubmission after a minor revision, and Paper D is in submission. Paper E is in preparation, and is in a draft state. The first three papers are based on instantaneous optimization, while the fourth and the fifth paper study temporally extended games. There is an overall trend of increasing complexity in the papers, with the first paper being based on linear optimization, the second using variational inequalities to solve mean-field games. The third paper builds the theoretical foundations for using variational inequalities to solve mean-field games coupled with population dynamics, rounding off the study of games with instantaneous optimization. The fourth paper considers a predator-prey system as in the first paper, but now incorporating non-linearities and temporally extended optimization. The fifth paper then applies the approach of the fourth paper to a simple model of a shelf ecosystem, studying emergent population levels and behavioral patterns.

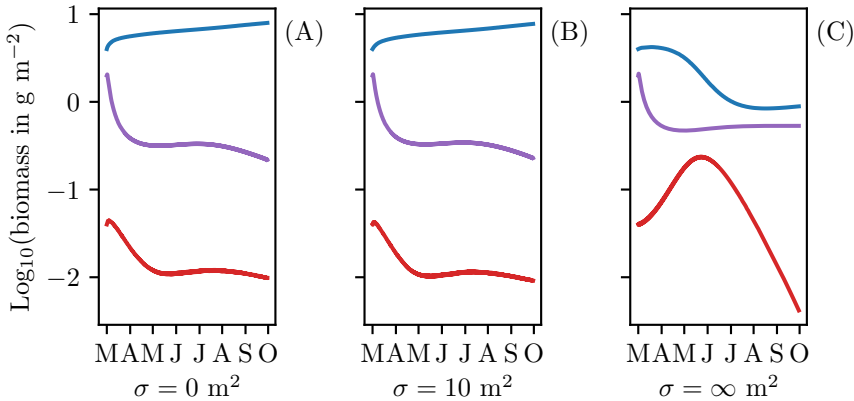


Figure 4.1: Population dynamics with optimal behavior, behavior with bounded rationality and a classic Lotka-Volterra model without behavior. Source: Paper A, figure 1.

4.1 Population games in continuous space and time (In print)

In this paper we introduce a general approach to finding optimal behavior in habitat-choice games in a continuous setting given that the payoffs are non-linear. This is done by introducing a spectral discretization and using the results on solving polymatrix games to solve the resulting linear complementarity in the discretized setting. In addition we introduce a notion of bounded rationality, with a precise description which allows for tuning to real-world data. We illustrate our approach by studying a predator-prey system modeling forage fish and copepods in the north sea, where we can see the delicate interplay between behavior and population dynamics. Our introduction of bounded rationality does not radically change the population dynamics Section 4.1, providing an argument for using unbounded rationality though the reality is more complex. An additional benefit of using bounded rationality is that it produces simulated distributions in the water column that are much more realistic than those without bounded rationality.

4.2 Scaling from optimal behavior to population dynamics and ecosystem function (Minor revision)

In this paper we study a tri-trophic aquatic ecosystem with a resource, a consumer and a predator. The ecosystem is modeled as a mean-field population game with instantaneous behavior, where predators and consumers follow the Nash equilibrium at every instant. Both consumers and predators are modeled as having non-linear functional responses, hence non-linear fitness functions. This increases the sophistication compared to most ecosystem models, as they typically assume at least one of the two groups has a linear functional response. We prove that the Nash equilibrium is unique using the theory of variational inequalities, where we show that the game specified by the payoff functions for the consumer and predator gives rise to a strictly pseudomonotone operator. In the paper we show that optimal behavior essentially buffers away the effect of top-down forcing, and causes bottom-up forcing to result in an increase in all trophic layers Section 4.2. Further, we show that a Type III functional response emerges from a Type II functional response when incorporating instantaneous optimal behavior, both for predators and consumers Section 4.2. The article shows that complex density-dependent effects emerge when incorporating optimal behavior based on non-linear fitness functions.

4.2.1 Additional results

We showed in paper C that the Nash equilibrium was an ideal free distribution, but as the tools from paper C were not available during the preparation of paper B we did not show this in paper B. Exploiting the theoretical tools we developed in paper C, we can now show that the Nash equilibrium is an ideal free distribution in the game we consider in paper B.

PROPOSITION 4.1 (IFD PAPER B) *The Nash equilibrium of a population game with payoffs given by:*

$$\begin{aligned} F_c &= - \left(\varepsilon \frac{\alpha \tau_c R}{(R \tau_c + \alpha/b)} - \frac{\alpha s^{3/4} \tau_c \bar{\tau}_p P}{\bar{\tau}_c \bar{\tau}_p C + \alpha/b} \right) \\ F_p &= - \left(\varepsilon \frac{\alpha s^{3/4} C \bar{\tau}_c \tau_p}{(C \bar{\tau}_c \tau_p + \alpha/b)^2} - \xi \tau_p \bar{\tau}_p \right) \end{aligned} \quad (4.1)$$

is an ideal free distribution if $\varepsilon R \geq s^{3/4} P \tau_p$.

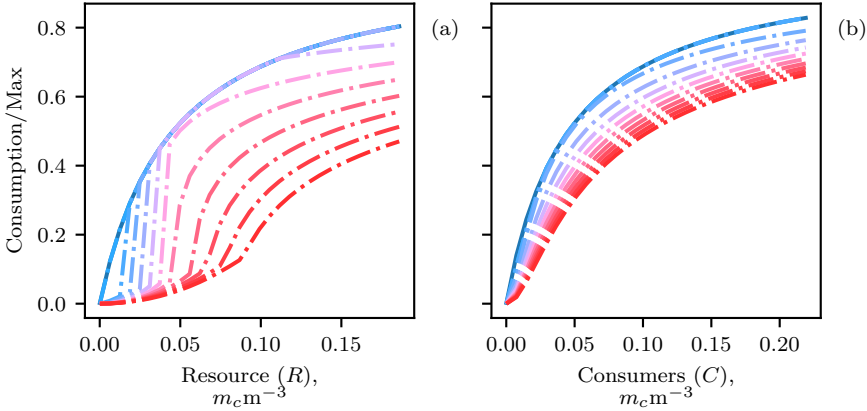


Figure 4.2: The Type III functional response arising from a Type II functional response for consumers (a) and predators (b) when incorporating fast optimal behavior. The gradient from blue to yellow in (a) indicates a change in predator populations, and indicates a change in top-predation in (b). Source: Figure 3, paper B.

PROOF. To show that the Nash equilibrium of the system in Equation (4.1) constitutes an IFD, it suffices to show that the functions $f_1 = -d_{\tau_c} F_c |_{\bar{\tau}_c = \tau_c}$ and $f_2 = -d_{\tau_p} F_p |_{\bar{\tau}_p = \tau_p}$ are strictly pseudomonotone. Consider

$$f_1 = - \left(\varepsilon \frac{\alpha^2 / b \tau_p R}{(R \tau_c + \alpha / b)^2} - \frac{\alpha s^{3/4} \tau_p P}{\tau_c \tau_p C + \alpha / b} \right) \quad (4.2)$$

To simplify the notation, we consider the equivalent formulation

$$f_1(x) = \frac{k_3}{x + k_4} - \frac{k_1}{(x + k_2)^2} \quad (4.3)$$

Both terms in f_1 are positive at 0, have monotone derivatives and the derivative of the first term always dominates the derivative of the second term since $R \geq s^{3/4} P$. Therefore the two functions cross at most once, if:

$$\frac{k_1}{k_2^2} > \frac{k_3}{k_4} \quad (4.4)$$

and f_1 has at most one zero, and is positive afterwards. If f_1 has no zeros, it is either strictly positive or negative, and monotonic. With this consideration out of the way, we can show strict pseudomonotonicity of f_1 . Assume $(y - x)f(y) \geq 0$. If $f(y) = 0$, for $x > y$, then $f(x) > 0$, hence $(x - y)f(x) > 0$. Likewise, if

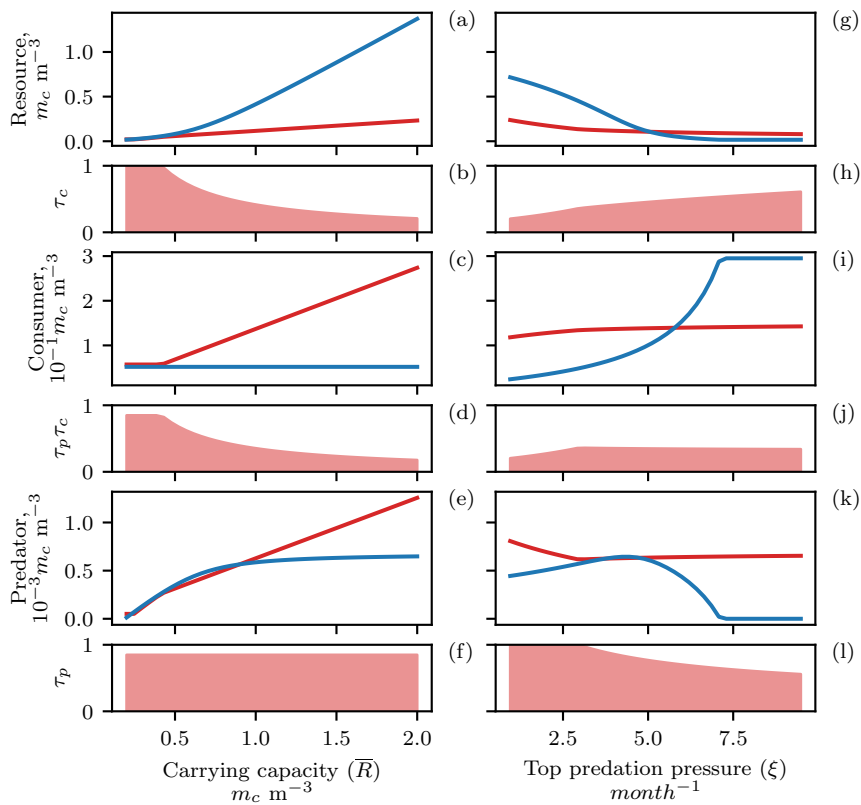


Figure 4.3: Figure from article B showing the impact of optimal behavior on ecosystem examined via. numerical experiments. Source: Figure 4, paper B.

$x < y$, then $f(x) < 0$ and $(x - y)f(y) > 0$. Strict pseudomonotonicity of f_2 is direct, since $f_2'(x)$ is strictly positive. \square

Note the extra necessary condition for the Nash equilibrium in Lemma 4.1 to be an IFD, compared to the case where both species are considered in Paper B. This is due to the fact that an activity level of 0 for the consumer can never constitute a Nash equilibrium in the predator-prey game. This is because the corresponding optimal predator activity of can never have an activity level of 0 as a best response.

4.3 Population games with instantaneous behavior and the Rosenzweig-MacArthur model (Accepted)

We again study a predator-prey system. This time, the focus is on deriving general theory allowing for the systematic study of a large class of population games. This is where we introduce the machinery of variational inequalities to find Nash equilibria of instantaneous mean-field games in a general fashion. We establish criteria for existence and uniqueness for the fixed-points of population games with instantaneous behavior. Having established these, we study a modified Rosenzweig-MacArthur system with varying intraspecific predator competition and fast optimal behavior.

4.3.1 Additional results

In paper (C) we studied the Rosenzweig-MacArthur game with optimal behavior, but we neglected to give a proof of Lipschitz continuity of the solution to the game. The proof follows:

LEMMA 4.2 *The solution to the behaviorally modified Rosenzweig-MacArthur system has Lipschitz continuous solution.*

PROOF. We need to show that f_i are locally Lipschitz and that the solution mappings to the variational inequalities defined by $-dU_c$ and $-dU_p$ are locally Lipschitz. The functions $N_i f_i$ are clearly locally Lipschitz in σ_c, σ_p , respectively and in N_c, N_p .

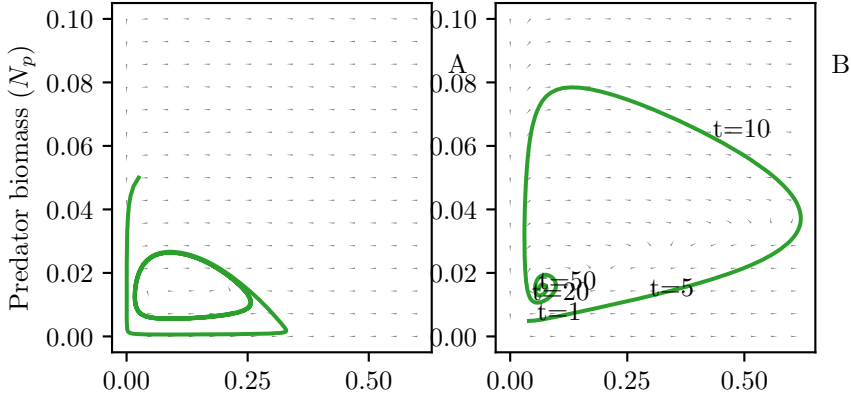


Figure 4.4: Population dynamics of the behaviorally modified Rosenzweig-MacArthur system in paper C, the figure also illustrates that the solution is Lipschitz continuous as shown in Lemma 4.2. Source: Figure 1, paper C.

Denote the solution function as a function of (N_c, N_p) to the variational inequality $VI(-dU_c, P_{2,\mu})$ by S_c . In order to show that S_c is locally Lipschitz, we apply Robinson's implicit function theorem (Robinson, 1991, Theorem 4.2). Two sufficient criteria for this theorem are Fréchet differentiability, and that $-dU_c(\sigma_c, \cdot)$ must be Lipschitz-continuous for every fixed σ_c . As $-dU_c$ has linear growth in N_c , the Lipschitz criterion is satisfied, and the differentiability is clear. Hence S_c is locally Lipschitz continuous. \square

4.4 A predator-prey system with cost of movement (In submission)

In this paper we study the population dynamics and behavioral dynamics of a predator-prey system, where there is day-night cycle.

We impose a cost of motion for both consumers and prey, and model each individual as following an Itô stochastic differential equation. The paper has three main findings: The most important finding at a conceptual level is the emergence of the diel vertical migration in a model coupled to population dy-

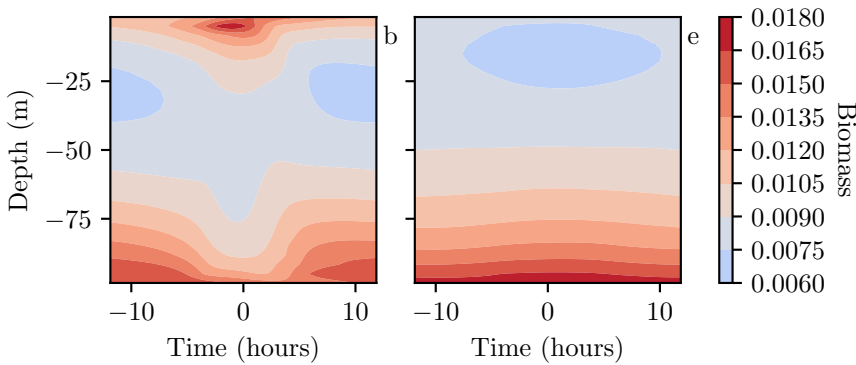


Figure 4.5: Distribution of consumers (A) and predators (B) across the day at the population equilibrium. Source: Figure 5 in paper D.

namics Section 4.4. The second is the rise of different migration patterns as a result of different carrying capacities, where the magnitude and type of migration patterns of zooplankton changes with the carrying capacity Section 4.4(a). Meanwhile forage fish have barely noticeable migrations Section 4.4(b). This again illustrates that behavioral patterns are intimately tied to ecosystem productivity. The third finding is that the energy budget of zooplankton changes radically with increasing carrying capacity, with the relative amount of the total energy going to predation decreasing and the amount going to motion increasing. This results in an increase in both zooplankton and forage fish populations. At the level of model-building, the paper shows that it is possible to couple population dynamics and mean-field games in the sense of Lasry and Lions (2007), as illustrated by the emergent diel vertical migration where we get both the distributions Section 4.4 and population levels Section 4.4.

4.5 Optimal behavior in a shelf ecosystem (In preparation)

In this paper we analyze the impact of benthic and phytoplankton productivity on a shelf ecosystem modeled as a simple food-web, see Section 4.5. We assume each population has optimal behavior, which we model by a mean-field game (Lasry and Lions, 2007). We use the numerical approach as in Paper D. The preliminary results show the powerful effect of behavior, revealing an emergent reverse diel vertical migration of zooplankton accompanied by a normal vertical

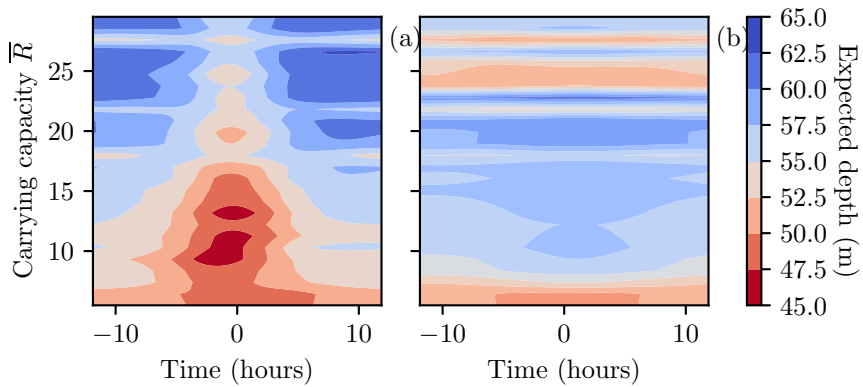


Figure 4.6: The expected diel position of zooplankton (a) and forage fish (b) as a function of carrying capacity. Source: Figure 4 in paper D.

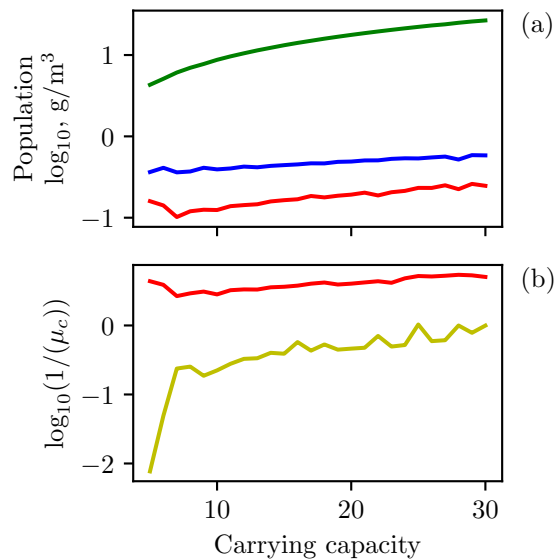


Figure 4.7: Population levels of zooplankton (a,blue) and forage fish (a,red), and energy budget of zooplankton as a ratio to basal metabolism of movement (b,yellow) and predation (b,red).

Model food-web in a shelf ecosystem

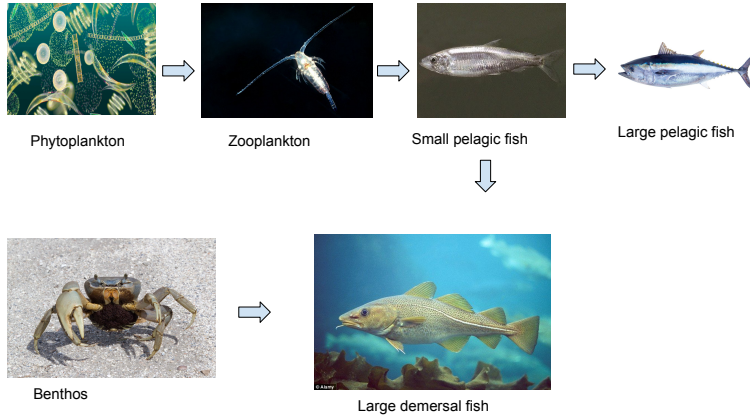


Figure 4.8: A simple food-web describing a shelf eco-system including both benthic and pelagic pathways.

migration of forage fish Section 4.5 The preliminary result also reveal that adaptive behavior has a negative effect on the population levels of the higher levels in the pelagic food-web Benthic productivity, on the other hand, appears to serve as an accelerant of the effect of the phytoplankton productivity Section 4.5.

4.6 Summary of numerical methods used in the thesis

Throughout the writing of this thesis, considerable energy was invested in solving population games, in the sense of resolving a dynamical system and finding Nash equilibria simultaneously. Finding fixed points of a dynamical system along the Nash equilibrium is a non-trivial problem. A first approach which was unsuccessful is modeling the problem as a differential-algebraic equation. This is problematic as the strategy spaces are constrained, so the algebraic equations describing the Nash equilibrium do not lead to a smooth solution curve. Instead, we used three different approaches.

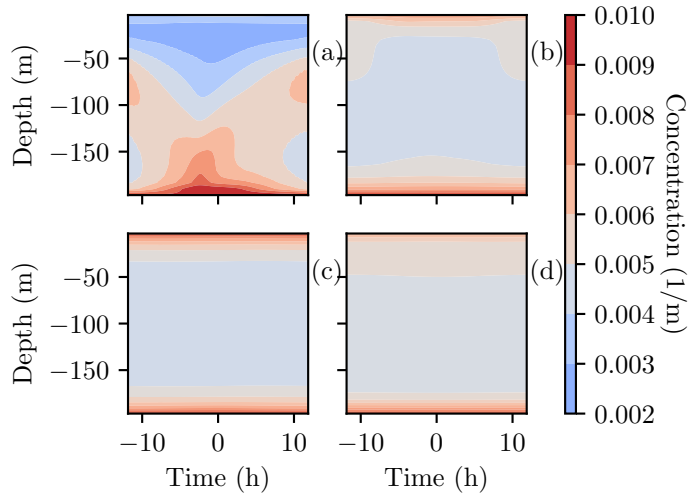


Figure 4.9: Diel vertical migration of zooplankton (a), forage fish (b), large pelagics (c) and large demersals (d) at a carrying capacity of $\bar{R} = 20g$, $\bar{B} = 0.1g$. Source: Paper E, figure 9.

Paper A In the first paper, we simulated the population dynamics using an explicit Newton method, where we solved the inner game at every instant using Lemkes algorithm. In this paper we worked in continuous space, and also studied the impact of bounded rationality. For this reason, we chose to use a spectral discretization (Kopriva, 2009) for the spatial dimension. The typical drawback of a spectral discretization is that mass and discretization matrices become dense, however, this was not a problem as in this specific case as the mass matrices were not directly used by the optimization algorithm. Using a spectral discretization allowed us to solve the equation with an integral kernel by using the method of images, which led to smooth dynamics. Such exponential integrators are viable for a wide variety of otherwise stiff semi-linear systems.

Paper B In the second paper, we used two different approaches to solve the population game. In order to simulate the population dynamics we used an explicit Newton method, finding the Nash equilibrium with the package IPOPT (Wächter and Biegler, 2006) via casadi (Andersson et al., 2019) using the HSL subroutines (HSL, 2007). In order to find the equilibria of the population dynamics, we used a root-finding procedure from SciPy where the inner game was solved as in the simulation.

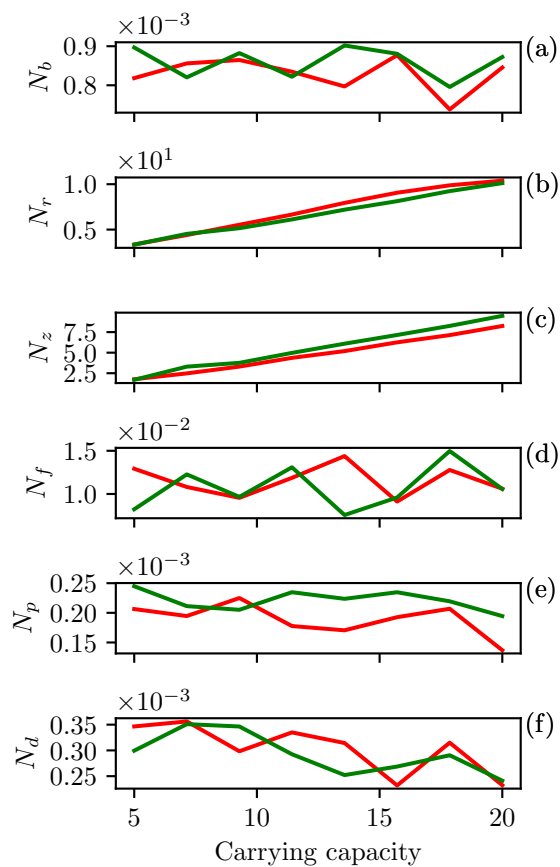


Figure 4.10: Variation in population levels of phytoplankton (a), benthics (b) zooplankton (c), forage fish (d), large pelagics (e) and large demersals (f) as a function of phytoplankton carrying capacity \bar{R} at low (red, 0.01 g) and high (0.1 g) benthic carrying capacities.

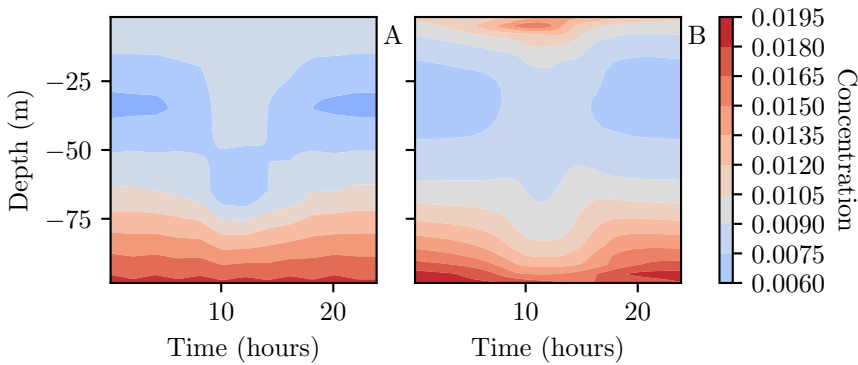


Figure 4.11: Changing strategies with a changing grid. Figure (A) illustrates the optimal strategies with a coarse grid with 12 time-steps and 4 spatial locations. The solution has been linearly interpolated to a 90x30 grid for visual comparison. Figure (B) shows the optimal strategies at population equilibrium with a 90x30 grid.

Paper C In the third paper, we again used an explicit Newton method to simulate the population dynamics coupled with finding the Nash equilibrium as in the previous two papers. In order to find the fix-points of the population dynamics, we posed the joint problem as a complementarity problem. This problem was solved using CasADi ipopt and HSI as in the second paper. This paper again concerned itself with continuous space. To ensure a sparse Hessian matrix for the optimization problem, we used a finite-element discretization.

Paper D In paper D the migrations are modeled explicitly, leading us to require an entirely different approach. Solving the equations in Lemma 2.18 for a mean-field game is notoriously hard. We solve the system by performing an iterative grid-refinement using the software package CasADi, getting a better and better solution of the system. See Section 4.6. For the implementation, see the code on github in the repository https://github.com/jemff/multi_species_water. The difference between figure (A) and (B) in Section 4.6 reveals the benefit of grid refinement for understanding the optimal migration strategies of animals. Meanwhile Section 4.6 indicates that in particular the predator population is indicated by going to a finer grid, with the predator population underestimated on the coarse grid.

In paper (C) we tested the numerical approach of using CasADi and IPOPT

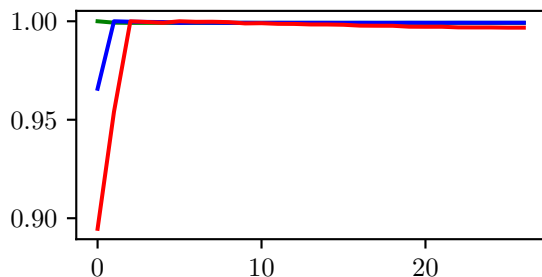


Figure 4.12: Changing populations of resources (green), consumers (blue) and predators (red) with a changing grid. The fineness of the grid varies from 8×4 to 64×32 in 15 steps.

by verifying the results with a dedicated non-linear complementarity solver provided by the package SICONOS (Acary et al., 2019). This produced the same results as using the interior point method with CasADi, so we stuck to using the interior point approach. We also experimented with using a fully implicit Euler method to solve the differential equations with an associated complementarity problem, again using SICONOS. This was more robust than the explicit Euler method, and should be used if the explicit Euler method is unstable.

Summary and perspectives

The main focus of the thesis was studying the impact of behavior, in particular habitat choice, on aquatic ecosystems and population dynamics. In addition, the goal of the thesis was to develop general methods to study ecosystems with optimal behavior. We showed that it is possible to build advanced population-dynamical models with optimal behavior. Our contributions can be divided into two parts, methodological and concrete ecosystem models.

Summarizing the findings from concrete models, in Paper A we illustrate the importance of the interplay of seasonality and population dynamics on behavior in a North Sea ecosystem, while illustrating the population dynamics are relatively unchanged by adding noise to the behavioral decisions. In paper B our modeling results show that behavior has a large effect on ecosystem dynamics, and can fundamentally change the response of an ecosystem to forcing. In addition, optimal behavior leads to complex phenonema, leading to the emergence of Type III functional response. Paper C mainly illustrated the importance of competition in leading to sub-optimal spatial distributions and the impact of carrying capacity on spatial distributions, with the counter-intuitive effect of leading to more spread out populations in less optimal habitats. In paper D we showed that the diel vertical migration can be understood as an emergent behavioral phenonem from forcing, while the zoo of copepod migration patterns observed in nature can be explained in part by resource loads. In addition, we found a breakdown of the ecosystem enrichment hypothesis in papers B, C and

D. Paper E can is a draft, but illustrates how reverse vertical migrations can emerge in complex food-webs and the negative impact of enrichment on higher trophic levels.

To briefly summarize the methodological contributions, we present a unified approach to modeling ecosystems with unstructured populations and optimal behavior, where population interactions can be described by playing the field. Our methods allow for studying the coupling of behavior and populations with both an instantaneous and explicit models of habitat selection and the papers form a toolbox to construct an ecosystem model with optimal behavior.

At a more detailed level, the contributions and foci of each paper are:

1. In the first paper a general model for fast optimal behavior in an ecosystem governed by Lotka-Volterra population dynamics was introduced. We developed the framework in a discrete setting, expanding it to a continuous setting. Expanding to a continuous setting allowed us to explicitly study the impact of bounded rationality on population dynamics. We developed a fast numerical method to resolve the population game, using it on the case of a predator-prey system modeling the North Sea with seasonality. Theoretically, this paper is based on viewing polymatrix games as linear complementarity problems.
2. The second paper focuses on the ecosystem impact of fast optimal behavior in a tri-trophic aquatic ecosystem with fast optimal behavior. The paper is focused on studying the specific ecosystem, and introduces variational inequalities as a tool to show uniqueness of Nash equilibria in population games. In this paper we show that behavior buffers top-down forcing, and that Type III functional responses can emerge from individuals in the setting of a population game.
3. The third paper is theoretical in nature, developing results for existence and uniqueness of both Nash equilibria and population equilibria in population games with instantaneous optimal behavior using variational inequalities. This paper serves to generalize the approach in the first paper, generalizing the approach from Lotka-Volterra models to general Kolmogorov-type models. As such, the paper, provides a theoretical foundation and avenue for further work for the models and methods in papers A and B. We apply the general theoretical results to a behaviorally modified Rosenzweig-MacArthur game which is then analyzed numerically.
4. The fourth paper studies the interplay between the diel vertical migration and population dynamics in a tri-trophic predator-prey system. The fourth paper is also where we begin using coupled Hamilton-Jacobi-Bellman

equations to solve the problem of coupling individual and population-level optimization. Hence we expand the scope of the population games we model to ecosystems with explicit movement, along with fast optimal behavior. This means this means we can study the fixed-points of the ecosystem rather than considering the seasonal changes in population as in paper A. By assuming that movement is modeled as an SDE, we build on the idea of the bounded rationality from paper A. The diel vertical migration of forage fish which arises in this paper is quite different in nature from that observed in Paper A, with essentially no migration. This shows that the diel vertical migration of forage-fish cannot always be explained as a bottom-up phenomenon.

5. The fifth paper studies a shelf ecosystem, focusing on the impact on populations and behavior of benthic and phytoplankton productivity. The fifth paper uses the same methodology as the fourth of temporally extended mean-field games. The paper has three main findings. The first is behavioral in nature, a reverse diel migration for zooplankton naturally emerges at a population fixed-point, while forage fish perform both reverse and normal vertical migrations. These depend on the phytoplankton productivity. The second is that optimal behavior serves to move the effect of enrichment, so only the lower two trophic levels benefit. The third is that increasing the benthic productivity serves to increase the effect of changing phytoplankton productivity. These results on the effect of productivity supplement the findings in paper D, as the rise in forage-fish populations seen there are eliminated by the threat of predation. That forage fish perform diel vertical migrations again as in paper A compared to what we found in paper D shows that both bottom-up and top-down pressures must be incorporated in order to have a workable model of the diel vertical migration.

The work presented in this thesis has focused on general ecosystem models and methods. A next step could be to incorporate the methods presented in this thesis in realistic ecosystem models, incorporating more individual and population-level effects.

5.1 Complex ecosystem models with behavior

The thesis has focused on simple ecosystems, in particular predator-prey systems. These serve as a useful starting point for ecosystem modeling, but real-world ecosystems are complex and consist of a myriad of interacting species in different environments. By using the tools we have developed in the creation of

this thesis, more realistic and complex ecosystems can be modeled. As a starting point, a model of a shelf ecosystem could be expanded to a full ocean model, studying how all the main functional groups interact (van Denderen et al., 2021). Such a model could serve as a stepping-stone to integrate behavior explicitly in complex models of habitat choice, removing the need for heuristics (van Denderen et al., 2021; Ho et al., 2019).

Another avenue of further development could be in models with a mixture of discrete and continuous habitats, as the frameworks we developed in papers A and C readily incorporate such a mixture.

5.2 Better models of individual state

In the models we have considered, the satiation and handling are seen as two sides of the same coin. In reality, satiation happens over a much longer time-scale and affects behavior independently of handling (Fiksen and Jørgensen, 2011). To model an ecosystem where the time-scale is on the order of a day, satiation should be included as a major factor. This would necessitate drawing mechanistic models of satiation into our behavioral models (Andersen, 1999; Fiksen and Jørgensen, 2011). Constructing models incorporating behavior, satiation and population dynamics simultaneously would increase the range of ecosystems across which our methods can be applied, and allow for modeling complex terrestrial ecosystems as well.

5.3 Ontogeny

Here we have only concerned ourselves with unstructured populations, while in reality individual fish start as larvae and go through multiple stages before reaching maturation and being able to reproduce (Andersen, 2019). The fitness that a fish maximizes in reality should be its lifetime fitness, and not the instantaneous growth rate. In certain situations and at equilibrium these two overlap (Sainmont et al., 2015), but generally this cannot be expected to be the case, for example if there are daily variations as is the case in the ocean. Developing models taking the different choices at different life-stages into account could be another way of going forward with the methods and models presented in this thesis. Such models also have the greatest perspectives of being useful for fisheries management, as age-cohorts are a vital to keep track of in this context (Andersen, 2019).

Bibliography

- Abrams, P. A. (1984). Foraging time optimization and interactions in food webs. The American Naturalist, 124(1):80–96.
- Abrams, P. A. (2007). Habitat choice in predator-prey systems: spatial instability due to interacting adaptive movements. The American Naturalist, 169(5):581–594.
- Abrams, P. A. (2009). Adaptive changes in prey vulnerability shape the response of predator populations to mortality. Journal of theoretical biology, 261(2):294–304.
- Abrams, P. A. (2010). Implications of flexible foraging for interspecific interactions: lessons from simple models. Functional Ecology, 24(1):7–17.
- Abrams, P. A., Matsuda, H., and Harada, Y. (1993). Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. Evolutionary Ecology, 7(5):465–487.
- Abrams, P. A. and Roth, J. (1994a). The responses of unstable food chains to enrichment. Evolutionary Ecology, 8(2):150–171.
- Abrams, P. A. and Roth, J. D. (1994b). The effects of enrichment of three-species food chains with nonlinear functional responses. Ecology, 75(4):1118–1130.
- Abrams, P. A. and Vos, M. (2003). Adaptation, density dependence and the responses of trophic level abundances to mortality. Evolutionary Ecology Research, 5(8):1113–1132.
- Acary, V., Bonnefon, O., Brémond, M., Huber, O., Pérignon, F., and Sinclair, S. (2019). An introduction to Siconos. PhD thesis, INRIA.

- Akçay, E. and Cleve, J. V. (2012). Behavioral responses in structured populations pave the way to group optimality. The American Naturalist, 179(2):257–269.
- Andersen, K. H. (2019). Fish ecology, evolution, and exploitation. In Fish Ecology, Evolution, and Exploitation. Princeton University Press.
- Andersen, N. G. (1999). The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting. Journal of Fish Biology, 54(2):287–301.
- Andersson, J. A. E., Gillis, J., Horn, G., Rawlings, J. B., and Diehl, M. (2019). CasADi – A software framework for nonlinear optimization and optimal control. Mathematical Programming Computation, 11(1):1–36.
- Arditi, R. and Ginzburg, L. R. (1989). Coupling in predator-prey dynamics: ratio-dependence. Journal of theoretical biology, 139(3):311–326.
- Aumann, R. J. (1964). Markets with a continuum of traders. Econometrica: Journal of the Econometric Society, pages 39–50.
- Avgar, T., Betini, G. S., and Fryxell, J. M. (2020). Habitat selection patterns are density dependent under the ideal free distribution. Journal of Animal Ecology, 89(12):2777–2787.
- Axelrod, R. and Hamilton, W. D. (1981). The evolution of cooperation. science, 211(4489):1390–1396.
- Benoit-Bird, K. J. and McManus, M. A. (2014). A critical time window for organismal interactions in a pelagic ecosystem. PLoS One, 9(5):e97763.
- Biro, P. A., Post, J. R., and Abrahams, M. V. (2005). Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts. Proceedings of the Royal Society B: Biological Sciences, 272(1571):1443–1448.
- Bolker, B., Holyoak, M., Křivan, V., Rowe, L., and Schmitz, O. (2003). CONNECTING THEORETICAL AND EMPIRICAL STUDIES OF TRAIT-MEDIATED INTERACTIONS. Ecology, 84(5):1101–1114.
- Broom, M. and Rychtář, J. (2013). Game-theoretical models in biology. CRC Press.
- Broom, M. and Rychtář, J. (2014). Asymmetric games in monomorphic and polymorphic populations. Dynamic Games and Applications, 4(4):391–406.
- Cantrell, R. S., Cosner, C., and Lam, K.-Y. (2021). Ideal free dispersal under general spatial heterogeneity and time periodicity. SIAM journal on applied mathematics, 81(3):789–813.

- Cantrell, R. S., Cosner, C., Lewis, M. A., and Lou, Y. (2020). Evolution of dispersal in spatial population models with multiple timescales. Journal of mathematical biology, 80(1):3–37.
- Cantrell, R. S., Cosner, C., and Lou, Y. (2010). Evolution of dispersal and the ideal free distribution. Mathematical Biosciences & Engineering, 7(1):17.
- Cantrell, R. S., Cosner, C., Lou, Y., and Ryan, D. (2012). Evolutionary stability of ideal free dispersal strategies: a nonlocal dispersal model. Can. Appl. Math. Q., 20(1):15–38.
- Cardano, G. (1961). The book on games of chance:(Liber de ludo aleae). Holt, Rinehart and Winston.
- Carmona, G. (2004). Nash equilibria of games with a continuum of players.
- Carmona, R. (2016). Lectures on BSDEs, stochastic control, and stochastic differential games with financial applications. SIAM.
- Carmona, R. and Lacker, D. (2015). A probabilistic weak formulation of mean field games and applications. The Annals of Applied Probability, 25(3):1189–1231.
- Cottle, R. W. and Stone, R. E. (1983). On the uniqueness of solutions to linear complementarity problems. Mathematical programming, 27(2):191–213.
- Cournot, A. A. (1897). Researches into the Mathematical Principles of the Theory of Wealth. New York: Macmillan Company, 1927 [c1897].
- Cressman, R., Garay, J., and Hofbauer, J. (2001). Evolutionary stability concepts for n–species frequency-dependent interactions. Journal of Theoretical Biology, 211(1):1–10.
- Cressman, R. and Křivan, V. (2006). Migration dynamics for the ideal free distribution. The American Naturalist, 168(3):384–397.
- Cressman, R. and Křivan, V. (2010). The ideal free distribution as an evolutionarily stable state in density-dependent population games. Oikos, 119(8):1231–1242.
- Darwin, C. (1859). On the origin of species.
- DeAngelis, D. L., Goldstein, R., and O’Neill, R. V. (1975). A model for tropic interaction. Ecology, 56(4):881–892.
- Eaves, B. C. (1973). Polymatrix games with joint constraints. SIAM Journal on Applied Mathematics, 24(3):418–423.

- Fiksen, Ø. and Jørgensen, C. (2011). Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. Marine Ecology Progress Series, 432:207–219.
- Fretwell, S. D. (1969). On territorial behavior and other factors influencing habitat distribution in birds. Acta biotheoretica, 19(1):45–52.
- Genkai-Kato, M. (2007). Macrophyte refuges, prey behaviour and trophic interactions: consequences for lake water clarity. Ecology Letters, 10(2):105–114.
- Glicksberg, I. L. (1952). A further generalization of the kakutani fixed point theorem, with application to nash equilibrium points. Proceedings of the American Mathematical Society, 3(1):170–174.
- Gonçalves, R. J., van Someren Gréve, H., Couespel, D., and Kiørboe, T. (2014). Mechanisms of prey size selection in a suspension-feeding copepod, *temora longicornis*. Marine Ecology Progress Series, 517:61–74.
- Hadjisavvas, N., Komlósi, S., and Schaible, S. S. (2006). Handbook of generalized convexity and generalized monotonicity, volume 76. Springer Science & Business Media.
- Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control, and competition. The american naturalist, 94(879):421–425.
- Heath, M. R., Speirs, D. C., and Steele, J. H. (2014). Understanding patterns and processes in models of trophic cascades. Ecology letters, 17(1):101–114.
- Ho, H.-C., Tylianakis, J. M., Zheng, J. X., and Pawar, S. (2019). Predation risk influences food-web structure by constraining species diet choice. Ecology letters, 22(11):1734–1745.
- HSL, A. (2007). A collection of fortran codes for large-scale scientific computation. See <http://www.hsl.rl.ac.uk>.
- Huygens, C. (1714). Christiani Hugenii Libellus de Ratiociniis in Ludo Aleae: Or, The Value of All Chances in Games of Fortune; Cards, Dice, Wagers, Lotteries, &c. Mathematically Demonstrated. S. Keimer.
- Katz, V. J. (2014). History of mathematics. Pearson New York.
- Kimmel, G. J., Gerlee, P., Brown, J. S., and Altrock, P. M. (2019). Neighborhood size-effects shape growing population dynamics in evolutionary public goods games. Communications biology, 2(1):1–10.
- Kindt-Larsen, L., Kirkegaard, E., and Dalskov, J. (2011). Fully documented fishery: a tool to support a catch quota management system. ICES Journal of Marine Science, 68(8):1606–1610.

- Kjørboe, T., Saiz, E., Tiselius, P., and Andersen, K. H. (2018). Adaptive feeding behavior and functional responses in zooplankton. Limnology and Oceanography, 63(1):308–321.
- Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. Science, 299(5611):1388–1391.
- Kopriva, D. A. (2009). Implementing spectral methods for partial differential equations: Algorithms for scientists and engineers. Springer Science & Business Media.
- Křivan, V. (2007). The lotka-volterra predator-prey model with foraging–predation risk trade-offs. The American Naturalist, 170(5):771–782.
- Křivan, V. (2013). Behavioral refuges and predator–prey coexistence. Journal of Theoretical Biology, 339:112–121.
- Křivan, V., Cressman, R., and Schneider, C. (2008). The ideal free distribution: a review and synthesis of the game-theoretic perspective. Theoretical population biology, 73(3):403–425.
- Lacker, D. (2020). On the convergence of closed-loop nash equilibria to the mean field game limit. The Annals of Applied Probability, 30(4):1693–1761.
- Lasry, J.-M. and Lions, P.-L. (2007). Mean field games. Japanese journal of mathematics, 2(1):229–260.
- Laundré, J. W., Hernández, L., and Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in yellowstone national park, usa. Canadian Journal of Zoology, 79(8):1401–1409.
- Lemke, C. (1970). Recent results on complementarity problems. In Nonlinear programming, pages 349–384. Elsevier.
- Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian journal of zoology, 68(4):619–640.
- Ma, B. O., Abrams, P. A., and Brassil, C. E. (2003). Dynamic versus instantaneous models of diet choice. The American Naturalist, 162(5):668–684.
- Maugeri, A. and Raciti, F. (2009). On existence theorems for monotone and nonmonotone variational inequalities. J. Convex Anal., 16(3-4):899–911.
- McNamara, J. M. and Houston, A. I. (1992). Risk-sensitive foraging: a review of the theory. Bulletin of mathematical biology, 54(2-3):355–378.

- Migot, T. and Cojocaru, M.-G. (2021). On minty-variational inequalities and evolutionary stable states of generalized monotone games. Operations Research Letters, 49(1):96–100.
- Miller, D. A. and Zucker, S. W. (1991). Copositive-plus lemke algorithm solves polymatrix games. Operations research letters, 10(5):285–290.
- Morris, D. W. (2003). Shadows of predation: habitat-selecting consumers eclipse competition between coexisting prey. Evolutionary Ecology, 17(4):393–422.
- Murdoch, W. W., Briggs, C. J., and Nisbet, R. M. (2003). Consumer-resource dynamics, volume 36. Princeton University Press.
- Nash Jr, J. F. (1950). Equilibrium points in n-person games. Proceedings of the national academy of sciences, 36(1):48–49.
- Oksanen, L., Fretwell, S. D., Arruda, J., and Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. The American Naturalist, 118(2):240–261.
- Ore, O. (1960). Pascal and the invention of probability theory. The American Mathematical Monthly, 67(5):409–419.
- Peckarsky, B. L., Abrams, P. A., Bolnick, D. I., Dill, L. M., Grabowski, J. H., Luttbeg, B., Orrock, J. L., Peacor, S. D., Preisser, E. L., Schmitz, O. J., et al. (2008). Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology, 89(9):2416–2425.
- Périquet, S. (2014). Sharing the top: how do spotted hyaenas cope with lions?: apex predator coexistence in a wooded savana. PhD thesis, Université Claude Bernard-Lyon I.
- Příbylová, L. and Berc, L. (2015). Predator interference and stability of predator–prey dynamics. Journal of mathematical biology, 71(2):301–323.
- Ripple, W. J. and Beschta, R. L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience, 54(8):755–766.
- Robinson, S. M. (1991). An implicit-function theorem for a class of nonsmooth functions. Mathematics of operations research, 16(2):292–309.
- Rosenmüller, J. (1971). On a generalization of the lemke–howson algorithm to noncooperative n-person games. SIAM Journal on Applied Mathematics, 21(1):73–79.
- Sainmont, J., Andersen, K. H., Thygesen, U. H., Fiksen, Ø., and Visser, A. W. (2015). An effective algorithm for approximating adaptive behavior in seasonal environments. Ecological Modelling, 311:20–30.

- Sandholm, W. H. (2010). Population games and evolutionary dynamics. MIT press.
- Savani, R. and Von Stengel, B. (2004). Exponentially many steps for finding a nash equilibrium in a bimatrix game. In 45th Annual IEEE Symposium on Foundations of Computer Science, pages 258–267. IEEE.
- Schadegg, A. C. and Herberholz, J. (2017). Satiation level affects anti-predatory decisions in foraging juvenile crayfish. Journal of Comparative Physiology A, 203(3):223–232.
- Schmitz, O. J., Krivan, V., and Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions.
- Sih, A., Crowley, P., McPeck, M., Petranka, J., and Strohmeier, K. (1985). Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics, 16(1):269–311.
- Smith, J. M. (1974). The theory of games and the evolution of animal conflicts. Journal of theoretical biology, 47(1):209–221.
- Smith, J. M. (1982). Evolution and the Theory of Games. Cambridge university press.
- Smith, J. M. and Price, G. R. (1973). The logic of animal conflict. Nature, 246(5427):15–18.
- Solberg, I. and Kaartvedt, S. (2017). The diel vertical migration patterns and individual swimming behavior of overwintering sprat sprattus sprattus. Progress in Oceanography, 151:49–61.
- Solodov, M. V. and Svaiter, B. F. (1999). A new projection method for variational inequality problems. SIAM Journal on Control and Optimization, 37(3):765–776.
- Stephen Cantrell, R., Cosner, C., Deangelis, D. L., and Padron, V. (2007). The ideal free distribution as an evolutionarily stable strategy. Journal of Biological Dynamics, 1(3):249–271.
- Stump, S. M. and Chesson, P. (2017). How optimally foraging predators promote prey coexistence in a variable environment. Theoretical Population Biology, 114:40–58.
- Tacon, A. G. and Metian, M. (2013). Fish matters: importance of aquatic foods in human nutrition and global food supply. Reviews in Fisheries Science, 21(1):22–38.
- Thygesen, U. and Patterson, T. (2018). Oceanic diel vertical migrations arising from a predator-prey game. Theoretical Ecology, 12(1):17–29.

- Valdovinos, F. S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P., and Dunne, J. A. (2010). Consequences of adaptive behaviour for the structure and dynamics of food webs. Ecology letters, 13(12):1546–1559.
- van Denderen, P. D., Petrik, C. M., Stock, C. A., and Andersen, K. H. (2021). Emergent global biogeography of marine fish food webs. Global Ecology and Biogeography, 30(9):1822–1834.
- Vincent, T. L. and Brown, J. S. (2005). Evolutionary game theory, natural selection, and Darwinian dynamics. Cambridge University Press.
- Von Neumann, J. and Morgenstern, O. (1947). Theory of games and economic behavior, 2nd rev.
- Wächter, A. and Biegler, L. T. (2006). On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. Mathematical programming, 106(1):25–57.
- Werner, E. E. and Anholt, B. R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. The American Naturalist, 142(2):242–272.
- Williams, A. C., Flaherty, S. E., and Flaxman, S. M. (2013). Quantitative tests of multitrophic ideal free distribution theory. Animal Behaviour, 86(3):577–586.
- Wollrab, S. and Diehl, S. (2015). Bottom-up responses of the lower oceanic food web are sensitive to copepod mortality and feeding behavior. Limnology and Oceanography, 60(2):641–656.

Part II

Papers

PAPER A

Solving multispecies population games in continuous space and time



Contents lists available at ScienceDirect

Theoretical Population Biology

journal homepage: www.elsevier.com/locate/tpbSolving multispecies population games in continuous space and time[☆]Emil F. Frølich^{*}, Uffe H. Thygesen

Technical University of Denmark, Department of Applied Mathematics and Computer Science - DTU Compute, Building 303B, Matematiktorvet, 2800, Kgs. Lyngby, Denmark



ARTICLE INFO

Article history:

Received 26 August 2021

Available online 28 June 2022

Dataset link: https://github.com/jemff/food_web

Keywords:

Population dynamics

Habitat choice

Game theory

Vertical migration

Predator–prey

ABSTRACT

Game theory has emerged as an important tool to understand interacting populations in the last 50 years. Game theory has been applied to study population dynamics with optimal behavior in simple ecosystem models, but existing methods are generally not applicable to complex systems. In order to use game-theory for population dynamics in heterogeneous habitats, habitats are usually split into patches and game-theoretic methods are used to find optimal patch distributions at every instant. However, populations in the real world interact in continuous space, and the assumption of decisions based on perfect information is a large simplification. Here, we develop a method to study population dynamics for interacting populations, distributed optimally in continuous space. A continuous setting allows us to model bounded rationality, and its impact on population dynamics. This is made possible by our numerical advances in solving multiplayer games in continuous space. Our approach hinges on reformulating the instantaneous game, applying an advanced discretization method and modern optimization software to solve it. We apply the method to an idealized case involving the population dynamics and vertical distribution of forage fish preying on copepods. Incorporating continuous space and time, we can model the seasonal variation in the migration, separating the effects of light and population numbers. We arrive at qualitative agreement with empirical findings. Including bounded rationality gives rise to spatial distributions corresponding to reality, while the population dynamics for bounded rationality and complete rationality are equivalent. Our approach is general, and can easily be used for complex ecosystems.

© 2022 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Population dynamics emerges from behavior of the animals; yet many models of population dynamics and ecosystems ignore behavior. In the past 50 years, game theory has evolved into an invaluable tool for including animal behavior in ecological models. Game theory gives a theoretical toolkit for understanding observed behavior and making predictions for how behavior will change in response to external changes. Game theory has been used to model a wide variety of situations where an animal needs to make a choice, from habitat choice (Křivan, 1997; Kondoh, 2003; Křivan et al., 2008), mating behavior (Rapoport, 1967), and confrontation strategies (Maynard Smith and Price, 1973). The game theoretical models have proven successful, with empirical evidence backing up their validity as a model of animal behavior (Cooper et al., 1989; Bolker et al., 2003; Schmitz et al., 1997).

[☆] This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence, Denmark supported by the Villum Foundation, Denmark.

^{*} Corresponding author.

E-mail addresses: jaem@dtu.dk (E.F. Frølich), uhth@dtu.dk (U.H. Thygesen).

We focus on one specific instance of behavior and how to incorporate it into population games, namely habitat choice for interacting populations. A reasonable assumption for interacting populations in an inhomogeneous habitat, is that all animals seek to find the best spot simultaneously. For a single population this leads to the ideal free distribution (Fretwell, 1969). The population dynamics of a model where every individual is always at the best location is a population game (Křivan and Cressman, 2009). The instantaneous population growth rates in a population game are determined by the instantaneous Nash equilibria of the individual habitat-choice game. Population games have emerged as a powerful tool to incorporate behavior in simple population models (Křivan, 1998; Genkai-Kato, 2007; Cressman and Křivan, 2010; Pinti et al., 2021; González-Olivares and Ramos-Jiliberto, 2003). However, the approach used in these models is not scalable to larger number of species or continuous habitats.

Population games are often simplified by only considering one or two trophic levels, (Křivan, 2007) and (Sadowski and Grosholz, 2019). This is in spite of e.g. mating behavior being influenced by the risk of predation, (Carranza and Valencia, 1999) and (Lima, 2009), naturally leading to a game with at least three types of players. Going to games with larger number of players can explain complex phenomena, which cannot be modeled with only

two types (Pinti et al., 2019). Another simplification concerns the representation of space in habitat selection games. Natural habitats often have continuous fitness gradients (Kawecki and Ebert, 2004), yet population games typically simplify this complex reality to a small finite number of patches, (Valdovinos et al., 2010).

The reason for these simplifications is that finding Nash equilibria is prohibitively hard (Bolker et al., 2003; Pinti et al., 2019), which is why the main focus has been on simple games that are solvable analytically (Křivan, 2007) or with very nice structures, such as the ideal free distribution (Cressman and Křivan, 2010). Because of the general issues with finding Nash equilibria efficiently in large games, complex ecosystems models in continuous space with multiple trophic levels have been beyond the scope of previous models. Creating numerical and theoretical approaches that can resolve the issues of computing Nash equilibria quickly for large numbers of interacting species in continuous settings is essential for extending the success of population games from toy-examples to real-world models. If the issue of finding Nash equilibria quickly and efficiently can be resolved, the question of whether to include behavior in a model or not becomes a question of relevance to the model rather than feasibility.

A critique of game-theoretical models is the assumption that players have perfect information and act in a perfectly rational manner, (Jones, 1999). Perfect information seems unreasonable, as animals do not have perfect state information (Simon, 1955). In addition the minor gain in fitness from the almost-perfect choice to the perfect choice is often outweighed by the higher cognitive or sensorial cost of finding the perfect strategy (Simon, 1956; Cohen et al., 2019). Though these concerns are well-founded, most models end up incorporating perfect rationality and information anyway. Classical satisficing models of bounded rationality cannot be verified empirically (Nonacs and Dill, 1993), and with other attempts (Sih, 1992; Thuijisman et al., 1995) the complexity has prevented the models from being implemented at the population level.

We introduce a method that allows the incorporation of behavior and imperfect decision making in population games in continuous space and time. The approach we introduce can readily be applied to study multi-species population dynamics emerging from a habitat-choice game in both continuous and discrete habitats. Our basic approach is to rephrase a continuous habitat selection game as a single linear complementarity problem (Miller and Zucker, 1991). We incorporate bounded rationality by requiring the strategies solve a diffusion equation, picking the strategy that maximizes the payoff with a given level of noise.

To illustrate the potential of the framework, we apply the method to diel vertical migration in the ocean. At dawn, billions of small fish and zoo-plankton migrate from the upper layers of the ocean to the deeper, darker layers, which can be directly measured as the deep scattering layer, (Sutton, 2013) and (Wang et al., 2014). At dusk, the small fish and zoo-plankton migrate upwards. Here, we study the seasonal interplay between population dynamics and behavior. The model is an extension of the model studied in Thygesen and Patterson (2018) to a population game. We couple the time scales of population dynamics and behavioral time scales, which allows us to examine how the vertical distribution of predators and prey change throughout the seasons and how this influences the population dynamics. We investigate the length and magnitude of the feeding rates of predators and consumers at throughout the day in spring, summer, and autumn of a single year. We examine how the optimal behavior with noise differs from that without noise, and how noise changes the population dynamics.

2. Method

2.1. General continuous model and the discrete motivation

Our general model is that of a population-game (Křivan and Cressman, 2009) where the populations can migrate in a continuous habitat on a much faster time-scale than population dynamics (Cressman and Křivan, 2006). We build up the general approach in a discrete setting, and then translate the structures we have built up into the continuous setting.

2.1.1. Developing a discrete population game

To understand the intrinsic coupling of patch-choice models with population dynamics, start by considering a Lotka–Volterra model with M patches and T types. Assume the interactions of animals of type i with type j at patches k and l is given by the entry (k, l) in the matrix A_{ij} . This general formulation allows for non-local interactions, allowing e.g. for simultaneous modeling of the patch choice of birds prey and mice, where a hawk can equally well prey on many different patches in a field (Bechard, 1982; Tew et al., 2000). The intrinsic growth of type i at patch k is given by a function $G_i(k)$ on $\{1, \dots, M\}$. Assuming that the populations are distributed according to probability distributions $(p_i)_{i=1}^T$ on the patches $\{1, \dots, M\}$, such that N_{ij} is the number of individuals of type i at patch j . The population dynamics of type i with total abundance N_i and distribution p_i becomes:

$$\dot{N}_i = N_i \left(\sum_{k=1}^M p_i(k) \left(\sum_{j=1}^T N_j(A_{ij}p_j)(k) \right) + G_i(k) \right) \quad (1)$$

We define the fitness proxy for an individual of type i at patch k by $H_i(k)$, as the growth of an individual of type i at patch k given that all types are distributed according to $(p_i)_{i=1}^T$.

$$H_i((N_j p_j)_{j=1}^T)(k) = \left(\sum_{j=1}^T N_j(A_{ij}p_j)(k) \right) + G_i(k) \quad (2)$$

If migrations are very fast and the habitat is highly interconnected (Cressman and Křivan, 2006; Abrams et al., 2007), it is reasonable to assume all animals of any type simultaneously seek to find the optimum patch in the sense of seeking k to maximize Eq. (2). The result of this is a Nash equilibrium, where no animal has an advantage in moving. As a consequence, the specific growth rate $H_i((N_j p_j)_{j=1}^T)(k)$ of each animal type i is constant across all patches k where this type is found, and no greater in any patch l that is void of this type ($p_l(k) = 0$). In the single-species case, the resulting patch distribution $p^{*,NE}$ is the ideal free distribution (Fretwell, 1969). The approach of using population dynamics determined by Eq. (1) with optimal strategies determined by the Nash equilibrium defines a population game on discrete patches, and is a successful approach to coupling optimal behavior with population dynamics (Valdovinos et al., 2010; Mougi, 2019; Pinti et al., 2021).

The game specified by Eq. (2) is affine in p_j , and finding the Nash equilibrium is equivalent to finding the Nash equilibrium in a polymatrix game (Howson, 1972; Eaves, 1973). A polymatrix game has so-called polymorphic–monomorphic equivalence (Broom and Rychtár, 2013; Eaves, 1973), so an individual of type j cannot determine whether it is playing against a polymorphic population i with pure strategies, or a monomorphic population with a mixed strategy. The benefit of studying games with polymorphic–monomorphic equivalence is that it is irrelevant how a distribution arises, whether through a single population having following a strategy or the existence of multiple subpopulations (Pinti and Visser, 2019). The monomorphic interpretation

is that all individuals of type i choose their positions randomly according to the distribution p_i , instead of having players pick fixed position $p_i(k)$. Finding the Nash equilibrium $(p_i)^{*,NE}$ of Eq. (2) becomes equivalent to finding the Nash equilibrium of the game:

$$F_i(p_i, (N_j p_j)_{j=1}^T) = \left\langle p_i, \sum_{j=1}^T E_{ij} p_j \right\rangle \quad (3)$$

For simplicity, we restrict ourselves to the case $A_{ii} = 0$, the case $A_{ii} \neq 0$ is covered in the Appendix, where E_{ij} is constructed. We can construct E_{ij} explicitly if we define Γ_i as a matrix where every column is G_i , so $(\Gamma_i p_j)(k) = G_i(k)$. The total payoff matrices E_{ij} for the interaction between type i and j when in Eq. (3) when $A_{ii} = 0$ then become:

$$E_{ij} = N_j A_{ij} + \frac{1}{T} \Gamma_i \quad (4)$$

We recognize Eq. (3) as the growth rate in Eq. (1). Therefore, optimizing the population growth for each type and at the individual level are the same when there is no density dependence ($A_{ii} = 0$). An advantage of this approach to population dynamics is that following the Nash equilibrium of the game Eq. (3) at every instant is an evolutionary stable strategy, i.e. the populations cannot be invaded by mutants (Křivan and Cressman, 2009). These considerations resolve the discrete case, but in nature many habitats are continuous and cannot be described well by discrete patches. However, having a fully-developed discrete model sets the stage for the continuous generalization, and giving us a toolbox of ideas for constructing a population game in continuous space.

2.1.2. The continuous model

The insight of using the monomorphic-polymorphic equivalence is essential in generalizing to the continuous case, since it highlights that the important factor in the individual patch choice Eq. (2) is the overall distribution on patches p_i . To extend population games to continuous space and facilitate the incorporation of imperfect decision making, we consider a habitat described by an interval $[0, z_0]$. We again assume we have T different types. To avoid pathological population interactions, we need to take more care with the possible population distributions in the continuous case. We define the continuous analogues of population distribution across patches by:

$$K = \{ \varphi \in L^2([0, z_0]) : \varphi \geq 0, \int \varphi dz = 1 \} \quad (5)$$

i.e. K is the set of square-integrable probability distributions on $[0, z_0]$, and $\varphi_i \in K$ corresponds to a patch distribution p_i . The quantity $N_i \varphi_i(z)$ gives the population density of type i at z . Interactions between animals of type i and j are given by bounded linear operators $U_{ij} : L^2([0, z_0]) \rightarrow L^2([0, z_0])$, where we again assume $U_{ii} = 0$. A bounded linear operator on $L^2([0, z_0])$ can be thought of as an infinite-dimensional matrix. In case the interactions are local, the operators U_{ij} reduce to multiplication by bounded functions, corresponding to diagonal matrices. This consideration explains why we require square-integrability, since we want to be able to consider purely local interactions. As in the discrete case, we define the local intrinsic growth by a bounded function B_i . Using B_i , K , and U_{ij} we can define the fitness proxy F_i of an individual of type i playing strategy φ_i in the continuous setting:

$$F_i(\varphi_i, (N_j \varphi_j)_{j=1}^T) = \sum_{j=1}^T \int \varphi_i(z) (N_j U_{ij} \varphi_j)(z) dz + \int \varphi_i(z) G_i(z) dz \quad (6)$$

The game given by maximizing all F_i with respect to φ_i is the continuous analogue of a polymatrix game. Since the game again

has polymorphic-monomorphic equivalence, the Nash equilibrium for the individual habitat selection game is also given by finding the Nash equilibrium of the game specified by Eq. (6).

Modeling the population dynamics, we assume that at every instant the animals are distributed according to the Nash equilibrium of Eq. (6). That is, no animal can increase their fitness by unilaterally deviating from their strategy. Denoting the Nash equilibrium by $(\varphi_i^{*,NE})_{i=1}^T$, the population dynamics in the general continuous model are:

$$\dot{N}_i = N_i F_i((\varphi_j^{*,NE})_{j=1}^N, N_j)_{j=1}^N \quad (7)$$

The model we use can theoretically be used for other situations than habitat-choice and population dynamics. As long as the population dynamics can be formulated in way where they are proportional to sums of bilinear payoffs in the strategies, our approach can be used.

2.1.3. Noisy strategies

Our model incorporates that animals are not necessarily perfectly rational: The animal may not be a perfect decision-maker and may choose a slightly sub-optimal habitat, due to imperfect information or limited capacity of information processing, but it can also model errors in our perception of the animal's objectives, or inability to actuate a decision perfectly, for example due to turbulence in the water column. Our model of imperfect rationality is as follows: Say that an animal of type i aims to play the strategy $f_i(\cdot)$, which is a probability density function on $[0, z_0]$. Then our model posits that the animal actually plays a strategy $\varphi_i(\cdot, \sigma)$, which is a smoothed version of $f_i(\cdot)$ obtained by solving the initial value problem for

$$\begin{aligned} \partial_s \varphi_i &= \frac{1}{2} \partial_z^2 \varphi_i \\ \partial_z \varphi_i |_{z=0} &= 0 \\ \partial_z \varphi_i |_{z=z_0} &= 0 \\ \varphi_i(z, 0) &= f_i(z) \end{aligned} \quad (8)$$

on the interval $s \in [0, \sigma]$. Thus, the parameter σ determines the degree of smoothing: With $\sigma = 0$, the animal is perfectly rational ($\varphi_i(z, 0) = f_i(z)$) while with $\sigma = \infty$, we have a completely random decisions where $\varphi_i(z, \infty)$ is a constant function of z , corresponding to a uniform distribution on $[0, z_0]$. Note that s or σ are not connected to time; this smoothing takes place instantaneously at each point in time.

Numerically, this smoothing is performed by first determining the fundamental solution to this initial value problem, ignoring boundaries, which is a Gaussian kernel. Then the boundary conditions are implemented using the method of images (Stakgold and Holst, 2011), resulting in a kernel $S(x)$. Finally, the initial condition is convolved with the kernel $S(x)$.

2.1.4. Spatial discretization

In order to calculate the Nash Equilibrium efficiently, and perform numerical integration precisely we discretize the interval $[0, z_0]$ with a spectral scheme based on Legendre polynomials, (Kopriva, 2009). This allows precise integration and differentiation of piece-wise smooth functions with only relatively few points. Working on a grid with M points, a strategy is a linear combination of normalized hat-functions, where the hat functions are given by:

$$\begin{aligned} \int_{z_{i-1}}^{z_{i+1}} e_i dz &= 1 \\ e_i(z_{i-1}) &= 0, \quad e_i(z_{i+1}) = 0 \end{aligned}$$

where the overall strategy becomes:

$$\varphi_i = \sum_{j=1}^M a_{j,i} e_j, \quad i \in \{1, \dots, N\}$$

$$\sum_{j=1}^M a_{j,i} = 1 \quad i \in \{1, \dots, N\}$$

The strategy of a player, or type, is fully determined by the a_i 's.

When considering non-optimal actors, we need to implement the convolution with $G(x)$, which also assures that the resulting distribution is smooth. An added benefit of incorporating bounded rationality then becomes that our strategy profiles are guaranteed to be smooth, decreasing the number of points required for numerically exact evaluation of the integrals determining the fitness equation (6).

2.1.5. Finding the Nash equilibrium

Finding the Nash Equilibrium in a game in continuous space is usually a hard task, requiring the development of bespoke methods, (Thygesen and Patterson, 2018; Pinti and Visser, 2019). We develop a general method which does not rely on the specific structure of the interactions or habitat, by combining a result on linear complementarity problems (Miller and Zucker, 1991) with an efficient solver.

By discretizing space, we have reduced an uncountable strategy set to a more manageable finite set, with pure strategies e_k . The gain of type k playing strategy e_k against type j playing strategy e_j can be determined as $U_{ij}(e_k, e_j)$, Eq. (6). Evaluating these integrals reduces the continuous game to a discrete habitat choice game equation (2) with payoff matrices A_{ij} determined through the numerical integration $A_{ij}(k, l) = \langle e_k, U_{ij} e_l \rangle$, $k, l \in \{1, \dots, M\}$. The location-specific growth is discretized by defining $G_i(k) = \int B_i(z) e_k(z) dz$. We construct the total payoff matrices E_{ij} for the game between types i and j as in the discrete case Eq. (4). Our discretization has reduced the problem to a polymatrix game, where finding the Nash equilibrium is tractable.

It does not appear to have diffused through the literature, but a Nash equilibrium of a polymatrix game can be found by solving a single linear complementarity problem (Miller and Zucker, 1991). We give a short proof of this using a modification of the argument from Miller and Zucker (1991), specialized to the case of two-player (bimatrix) games but easily generalizable to the general T -player case. Assume that (s_1^*, s_2^*) constitute a Nash equilibrium in mixed strategies with fitnesses $\gamma_1 = \langle s_1^*, E_1 s_2^* \rangle$ and $\gamma_2 = \langle s_2^*, E_2 s_1^* \rangle$ to the first and second player, respectively. Then

$$\langle s_1, 1_n \rangle = \langle s_2, 1_n \rangle = 1$$

since these mixed strategies are probability distributions on strategy space. Here 1_n is a vector of ones. In addition the Nash equilibrium dictates

$$E_1 s_2 = 1_n \gamma_1 - w_1, \quad E_2 s_1 = 1_n \gamma_2 - w_2$$

w_1 and w_2 are non-negative “slack variables” that state that the payoff for the first player can be no greater than the expected payoff γ_1 , but can be smaller for some fixed strategies. These non-optimal strategies, where the slack w_1 is positive, must then be chosen with probability 0, and as a consequence the complementarity condition

$$\langle s_1^*, w_1 \rangle = \langle s_2^*, w_2 \rangle = 0$$

holds. Assume for convenience that all elements in E_1 and E_2 are negative; this can always be obtained without changing the Nash equilibrium by subtracting a constant from E_1 and E_2 . Consequently, the payoffs γ_1 and γ_2 are also negative and thus the

vector $z = (s_1, s_2, -\gamma_1, -\gamma_2)$ satisfies the Linear Complementarity Problem (LCP)

$$z \geq 0, w \geq 0, Hz + \begin{pmatrix} 0 \\ 0 \\ -1 \\ -1 \end{pmatrix} = w, \quad \langle z, w \rangle = 0. \quad (9)$$

where

$$H = \begin{bmatrix} 0 & -E_1 & -1_n & 0 \\ -E_2 & 0 & 0 & -1_n \\ 1_n & 0 & 0 & 0 \\ 0 & 1_n & 0 & 0 \end{bmatrix}$$

Conversely, assume that $z = (s_1, s_2, \gamma_1, \gamma_2)$ and w solve the LCP, then it is straightforward to see that the mixed strategies (s_1, s_2) form a Nash equilibrium with fitnesses at the Nash equilibrium of (γ_1, γ_2) . The assumption that E_1 and E_2 have negative elements imply that the matrix H is copositive plus (meaning, for all $z \geq 0$ with $z \neq 0$ it holds that $\langle z, Hz \rangle > 0$) which assures that the LCP to has a solution, in particular through Lemke’s algorithm.

Solving Eq. (9) was done through two different methods. The interior-point method as implemented in IPOPT, (Wächter and Biegler, 2006), called via the auto-differentiation software CasADi (Andersson et al., 2019), and Lemkes Algorithm implemented in the Numerics package in Siconos, (Acary et al., 2019). Experience showed that Lemkes algorithm was the fastest.

3. Modeling population dynamics and the diel vertical migration

We apply our method to the diel vertical migration of oceanic animals where the game is well-understood, but the interplay between the daily variations and the population dynamics have not been properly investigated. We consider a food-chain in a water column, consisting of a resource R , a consumer C , and a predator P . The resource is thought of as phytoplankton, the consumer as copepods and the predator as forage fish. The predators and consumers are each distributed in the water column according to probability distributions, $\varphi_c(z, t)$, $\varphi_p(z, t)$, and the resource is distributed according to $r(z, t)$.

Forage fish are visual predators, so their predation success is heavily light dependent. The available light decreases with depth in the water column, and varies with the time of day. The light intensity I at depth z is approximately $I(z) = I_0 \exp(-kz)$, and the light-dependent clearance rate of a predator is $\beta_{p,0}$. However, even when there is no light available there is still a chance of catching a consumer if it is directly encountered, so the clearance rate, $\beta_p(z, t)$, of forage fish never goes to 0 even at the middle of the night or at the deepest depths.

$$\beta_p(z, t) = \beta_{p,0} \frac{I(z, t)}{1 + I(z, t)} + \beta_{p,min}$$

We model the light-levels at the surface via the python package pvlb (Holmgren et al., 2018) in the North Sea. The light levels are given by the direct horizontal light intensity at the sea-surface, neglecting more complicated optic effects. The model takes the precipitable water w_a , and aerosol optical depth, aod . We model light decay throughout the water column as $\exp(-kz)$.

In contrast to forage fish, copepods are olfactory predators, and their clearance rate, β_c , is essentially independent of depth and light levels.

$$\beta_c(z, t) = \beta_{c,0}$$

The interactions between the consumer and resource are local, as are the interactions between a predator and a consumer. The local encounter rate between consumers and resources is given by $C\beta_c(z, t)\varphi_c(z, t)r(z, t)$, and the local encounter rate between predators and consumers is $CP\beta_p(z, t)\varphi_c(z, t)\varphi_p(z, t)$.

3.1. Population dynamics

The resource cannot move actively, so its time dynamics are naturally specified locally. The growth of the resource is modeled with a logistic growth, with a loss from grazing by consumers and diffusion from the natural movement of the water. We assume interactions can be described with a Type I functional response, allowing us to eventually use the method developed in Section 2.1. The resource dynamics become:

$$\partial_t r(z, t) = r(z, t) \left(1 - \frac{r(z, t)}{r_{\max}(z)} \right) - \beta_c(z, t)\varphi_c(z, t)C(t)r(z, t) + k\partial_z^2 r(z, t) \quad (10)$$

The total population growth of the consumer population is found by integrating the local grazing rate over the entire water column multiplied by a conversion efficiency ε , subtracting the loss from predation. The growth of the predators is given by the predation rate integrated over the water column. The instantaneous per capita population growth without metabolic losses, of the consumer F_c and predator F_p become:

$$F_c(\varphi_c, \varphi_p) = \int_0^{z_0} \varepsilon \beta_c(z, t)\varphi_c(z, t)r(z, t)dz - P(t) \int_0^{z_0} \beta_p(z, t)\varphi_c(z, t)\varphi_p(z, t)dz \quad (11)$$

$$F_p(\varphi_c, \varphi_p) = C(t) \int_0^{z_0} \beta_p(z, t)\varphi_c(z, t)\varphi_p(z, t)dz$$

Using Eq. (11) we arrive at equations for the predator–prey population dynamics:

$$\begin{aligned} \dot{C} &= C(t) (F_c - \mu_c) \\ \dot{P} &= P(t) (F_p - \mu_p) \end{aligned} \quad (12)$$

We use F_c , F_p , Eq. (11), as our fitness proxies.

3.2. Simulating the model

As in Section 2.1 at any instant, all consumers and predators simultaneously seek to find the strategy that maximizes their fitness (F_c , F_p) Eq. (6). A strategy in our case is a square-integrable probability distribution in the water column, i.e. an element in K , Eq. (5).

Using the notation of Section 2.1, the Nash equilibrium of the instantaneous game is:

$$\begin{aligned} \varphi_c^{*,NE} &= \operatorname{argmax}_{\varphi_c \in K} F_c(\varphi_c, \varphi_p^{*,NE}) \\ \varphi_p^{*,NE} &= \operatorname{argmax}_{\varphi_p \in K} F_p(\varphi_c^{*,NE}, \varphi_p) \end{aligned} \quad (13)$$

We apply the method of Eq. (9) to find the Nash equilibrium of the discretized system. Using the Nash equilibrium Eq. (13) we are able to solve the time-dynamics for the predator–prey system Eq. (12) by a Euler scheme. The dynamics of the resource are more complicated due to the diffusion term, Eq. (10). We solve the partial differential equation for the resource using the method of exponential time-differencing (Hochbruck and Ostermann, 2010) with a first-order approximation of the integral. Using exponential time-differencing guarantees a stable solution, though the system may be stiff (Hochbruck and Ostermann, 2010).

3.3. Model parameters

Following Yodzis and Innes (1992), we parameterize the clearance and loss rates in a metabolically scaled manner following Kleiber’s law, (Yodzis and Innes, 1992), using scaling constants

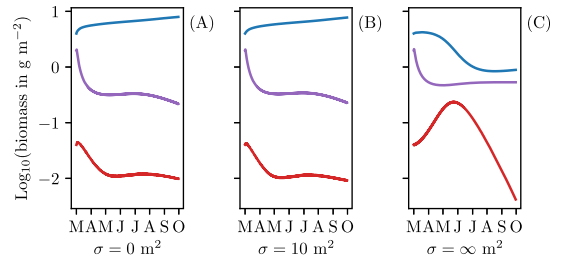


Fig. 1. Total populations of consumers (blue), predators, (red) and resources (purple) from 1st of April to 1st of October. We vary the rationality, from total rationality (A), bounded rationality ($\sigma = 10$), (B) and fully irrational, $\sigma = \infty$, (C), corresponding to a simple Lotka–Volterra model.

from Andersen (2019, Table 3). We use the default parameters in the clear-sky model, modeling a sequence of moonless nights. This is a bit of a simplification, but it should not have a great effect on our results as moonlight at full moon has an intensity 10^{-6} of sunlight at noon (Biberman, 1971). The North Sea is modeled with a rather high attenuation coefficient k , (Table 1). We use the notation $\mathcal{N}(0, \sigma^2)$ for the normal distribution with mean 0 and variance σ^2 (see Table 1).

4. Results

We study a tri-trophic system over a period of time from spring to fall, in order to capture the seasonal variations in population levels and vertical migrations. We restrict ourselves to a single seasonal cycle so we do not have to take the radically changed resource dynamics during winter into account, and can avoid questions of hibernation and other seasonal adaptations for low-resource environments. We compare three different cases of behavioral optimization: perfect rationality, ($\sigma = 0 \text{ m}^2$), bounded rationality ($\sigma = 10 \text{ m}^2$), and a fully irrational system with a uniform distribution throughout the water column ($\sigma = \infty \text{ m}^2$) as a reference. The system with a uniform distribution reduces our dynamic to Lotka–Volterra dynamics and is included as a reference system, to showcase the dynamics without behavior.

4.1. Population dynamics

Fig. 1 shows the seasonal-term population dynamics for the system we consider, comparing the population levels for the models with perfect rationality (Fig. 1(A)), bounded rationality (Fig. 1(B)) and full irrationality (Fig. 1(C)).

In the system with full irrationality Fig. 1(C) we see very unstable population dynamics, with the consumer population having crashed and stabilized again and the predator population rapidly decreasing at the end of the simulation. In contrast, both bounded and perfect rationality result in stable population dynamics (Fig. 1(A,B)). All three models have an initial large population growth, but the behavioral optimization rapidly dampens the population dynamics, as the increase in predator populations leads to a corresponding decrease in the willingness of consumers to take risks (Fig. 1(A,B)). In the summer, the effect of a much shorter night is visible in the resource dynamics on the long term (Fig. 1(A,B, J, J), purple), since the resource population increases, leading to more risk-willing consumers and a higher predator-population (Fig. 1(A,B, J, J), red). Surprisingly this is not enough to counter the rise in consumer numbers (Fig. 1(A,B, J, J), blue)).

The population levels for the model with bounded and perfect rationality are essentially indistinguishable, so the decrease in fitness from the decrease in optimality is not that great. Viewed on a long time-scale the underlying daily variation is practically invisible.

Table 1
Parameter values used in the model of the diel vertical migration.

Name	Abbreviation	Value	Source
Precipitable water	w_a	1 g m ⁻³	Gueymard et al. (1995)
Aerosol optical depth	aod	0.1	Gueymard et al. (1995)
Light decay	k	0.1 m ⁻¹	Gueymard et al. (1995)
Ocean depth	z_0	90 m	McGlade (2002)
Predator mass	m_p	20 g	Appx. Wheeler (1975)
Consumer mass	m_c	0.05 g	$\frac{1}{400}m_p$ (Andersen, 2019, Table 3)
Consumer clearance rate	β_c	32 m ³ yr ⁻¹	Andersen (2019, Table 3)
Predator clearance rate	$\beta_{p,0}$	2800 m ³ yr ⁻¹	Andersen (2019, Table 3)
Consumer metabolic rate	μ_c	0.24 yr ⁻¹	Andersen (2019, Table 3)
Predator metabolic rate	μ_p	21 yr ⁻¹	Andersen (2019, Table 3)
Minimal attack rate	$\beta_{p,min}$	$5 \cdot 10^{-3}\beta_p$	Thygesen and Patterson (2018)
Phytoplankton growth	λ	100 yr ⁻¹	Arin et al. (2002)
Phytoplankton max	r_{max}	10 $\sqrt{(0, 6)}$ g m ⁻³	Assumed
Irrationality	σ	10 m ²	Assumed
Diffusion rate	k	500 m ² yr ⁻¹	Schaechter (2009, Marine Habitats)
Initial consumers	C_0	4 g m ⁻²	Assumed
Initial predators	C_0	0.04 g m ⁻²	Assumed
Initial resources	r_0	4 $\sqrt{(0, 6)}$ g m ⁻³	Assumed

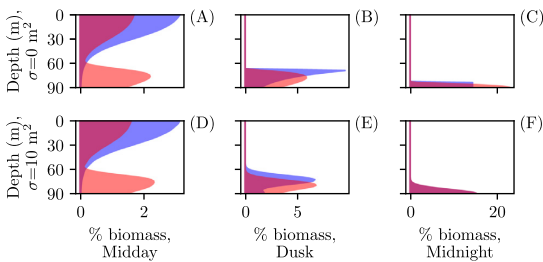


Fig. 2. Daily distribution of consumers *blue* and predators *red* at noon (A,D), dusk (B,E) and at midnight, (C,F) with full (A–C) and bounded rationality (D–F) on the 22nd June (Summer solstice). Remark that the purple color indicates an overlap in ranges.

4.2. Bounded rationality and perfect rationality

The plots in Fig. 2 show snapshots of consumer and predator distributions in the water column at dawn, midday and dusk on summer solstice. Fig. 2(A–C) show the distributions with perfect rationality, and Fig. 2(D–F) show the migration with bounded rationality. Any significant differences in behavioral choices between our model of bounded rationality and perfect rationality become visible when viewing the resulting distributions simultaneously. As expected, a pattern of vertical migration emerges with the emergence of a deep scattering layer of fully rational consumers at noon Fig. 2(A, blue). Most of the predators are also present in this layer Fig. 2(A, red), excepting a few hanging out higher in the water column deterring upward consumer migration, corresponding to the modeling results of Pinti and Visser (2019). At dusk, Fig. 2(B) the predators have a greater concentration near the surface, while the consumer “box” is beginning to form, yet still with a continuous drop-off to the surface due to the risk from the light. At midnight Fig. 2(C) the consumers are concentrated near the surface, with a discontinuous drop to nothing. The predators follow the consumers, albeit with a continuous shape, both distributions being similar to the results of Thygesen and Patterson (2018).

The behavioral choices with bounded and perfect rationality are strikingly similar, especially at noon (Fig. 2(A, D)). At dusk the consumers with perfect rationality have a large discontinuous peak in their distribution, which declines continuously towards the top of the water column due to the risk from light (Fig. 2(B, blue)), while the consumers with bounded rationality follow the

same overall pattern of moving towards the surface, (Fig. 2(E, blue)). The increased concentration of consumers with bounded rationality at the top of the water column (Fig. 2(E, blue)) must be balanced by the wider breadth of the consumer distribution. Due to the slightly higher concentration of bounded rationality consumers at the top, predators with bounded rationality have a peak in their distribution slightly higher in the water column than the fully rational ones (Fig. 2(B, E, red)). Apart from the location, the predator distributions are otherwise quite alike, with the rational predators having an emergent almost-smooth distribution. At midnight the distribution of fully rational consumers has a discontinuous dropoff (Fig. 2(C, blue)). Due to the forced dispersion, the consumers with bounded rationality are more spread out (Fig. 2(F, blue)), but the distribution looks like a smoothed version of the fully rational distribution. In contrast to the consumers, the fully rational predators and the predators with bounded rationality have almost the same distribution, where they spread out at night, with the highest concentration in the top of the water column (Fig. 2(C, red)).

4.3. Seasonal variation

The heatmaps in Fig. 3 illustrate the seasonal variation of the daily migration of consumers (Fig. 3(A–C)) and predators (Fig. 3(D–F)), by focusing on the equinoxes and the summer solstice.

The vertical migration (Fig. 3) is apparent throughout the seasons. Both consumers and predators are highly concentrated at the top of the water column during nighttime, and at day they scatter to the deep, with a transition during dusk as illustrated in Fig. 2(B,D). Looking at the consumers (Fig. 3(A–C)), there is a clear seasonal variation in the speed of the migration and the size of the consumer “box” at nighttime. In the spring, (Fig. 3(A)) the consumer migration is very fast, due to a relatively large predator population from the initial boom, so each individual consumer is at very high risk in the spring. The day-night transition is quite fast during the equinox. Predators follow the consumers (Fig. 3(D)), but with a continuous distribution. At the summer solstice, (Fig. 3(B,D)) the migration has changed character with a more protracted duration, occasioned by a slower change in light levels than in the spring. In addition the predator population has declined a bit from its spring high, and is slowly rising again (Fig. 1), leading to a less risky environment for the consumers. The shape of the distributions of predators and consumers is the same as in the spring, with the only major difference being the shape of the migration.

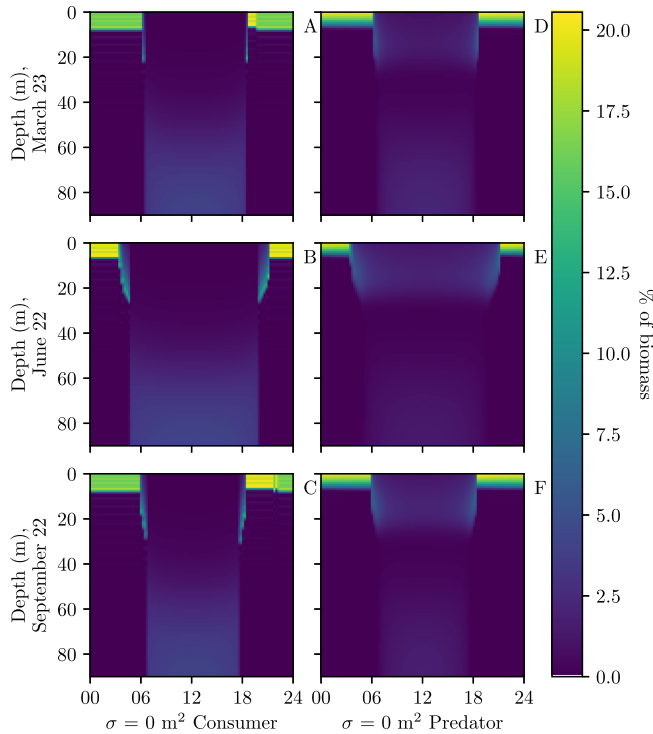


Fig. 3. Vertical distribution of consumers (A–C) and predators (D–F) at spring equinox (March 22), summer solstice (June 22) and fall equinox (September 23).

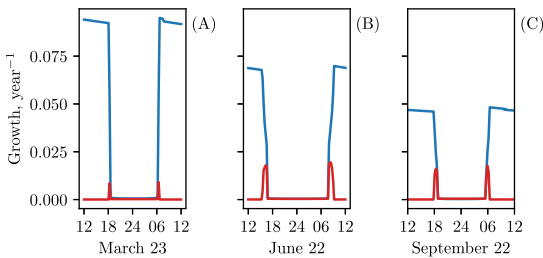


Fig. 4. Seasonal comparison of consumer (blue) and predator, (red) feeding patterns on March 22 (spring equinox) (A), 22 June (summer solstice) (B) and 23 of September (fall equinox) (C).

Moving the hands on the clock forward to the fall equinox, we see a different pattern (Fig. 3(C,F)) compared to the spring equinox. The vertical migration is slower in the fall than the spring, which can be seen by the width of the intermediate states in Fig. 3(C,F). The change in speed comes from an individual consumer being in less danger than in the spring, due to the decline in predator populations and rise in consumer populations (Fig. 1).

4.4. Feeding rates

Fig. 4 shows the seasonal variations in the daily feeding patterns of consumers (blue) and predators (red), by zooming in on the spring equinox, summer solstice and fall equinox.

At all three points in time, consumers have a constant feeding level throughout the night (Fig. 4), due to the vertical migration

(Fig. 3). In spite of the predator and consumer populations being overlaid at night (Fig. 3(A,C)), the predators have practically no feeding activity at night (Fig. 4). This illustrates the advantage of the diel vertical migration for the consumers.

The main feeding time for predators is at dawn and dusk, Fig. 4, again illustrating the efficacy of the diel vertical migration as a predator-avoidance strategy for the consumers. In the spring, there is a large amount of predators and not that many consumers, so the individual consumers get to eat more as evidenced by the high peaks (Fig. 4(A, blue)), while the individual predators go hungry (Fig. 4(A, red)). The duration of predator feeding is largest in the summer (Fig. 4(B, red)), where we also see the slowest migration (Fig. 3(B,D)). That individual predator feeding is slightly larger in the summer than in the fall is surprising, since there are more predators in the summer (Fig. 1(JJ vs. S,O, red)). Consumers' increased risk avoidance must also be occasioned indirectly by the increased consumer population from summer to fall leading to less available food, both pr. capita and in total (Fig. 1(A, purple)), and by the longer day-night transition. As the consumer population increases through the seasons, each consumer gets less food during the night (Fig. 4(A–C, blue)) due to intraspecific competition, while the predator feeding level stabilizes Fig. 4(B, D, blue) after the famine (Fig. 4(A, red)).

5. Discussion

Our study of a Lotka–Volterra system with optimal behavior in the water column focuses on both the emergent behavior and population dynamics. The population dynamics were stabilized dramatically by the introduction of optimal behavior, and a slight seasonal dependence appeared. The short-term dynamics show a clear distinction between predator and consumer feeding modes,

where prey feed during night while predators feed at dusk and dawn. By comparing the results for bounded rationality and unbounded rationality on the long and short time scales, we see two different pictures emerge. The behavior predicted by the two different models is similar, but still visibly different. Though the behavior is different, the difference becomes negligible at long-time scales. Of course, the specific effect is a result of the value of the bounded rationality we use. This value was chosen heuristically to smooth the distributions, but not too much. The results illustrate the strength of our numerical approach to studying population games, and underline the importance of robust algorithms and discretization schemes.

Our results illustrate the interplay between population dynamics, seasons, and behavior. Though light levels may be the same at two different times of the year, the migration patterns can differ radically due to the differences in population abundances. Bounded rationality appears to change the population dynamics imperceptibly compared to the results with perfect rationality. Behavior is probably not completely rational in reality, but the change from complete rationality to slightly bounded rationality does not appear important for population dynamics. Assuming perfect rationality appears much more reasonable than full irrationality. At first sight, the intensity of predator–prey interactions at dawn and dusk seem to indicate that models need to be very fine-grained in time to capture population dynamics accurately. Zooming out to the long-term dynamics lends hope that the same dynamic could be captured with a rougher time-discretization.

In terms of the specific case of diel vertical migrations, large-scale geographical studies of the vertical migration indicate that population levels are a driving factor in the diel vertical migration (Klevjer et al., 2016), not just light. This corresponds to the predictions of our model, and shows the importance of modeling behavior explicitly. Our qualitative results on the seasonal variation of the vertical migration tentatively appear to correspond with empirical findings (Wang et al., 2014; Beaugrand et al., 2001; Colebrook, 1979). This agreement is, it must be emphasized, qualitative in nature. If the model was tuned through empirical data to an ecosystem, perhaps it could be used to forecast seasonal changes in vertical migrations.

At the level of general population games, ocean population dynamics are driven by feeding at dusk and dawn (Benoit-Bird and McManus, 2014), and our model provides a purely behavioral justification for this phenomenon. At the same time, our results show that the discontinuous feeding patterns gives rise to smooth long-term population dynamics. The population-level results support the usual approach of assuming perfect rationality in population games with interacting populations, though the behavior of each individual is most likely slightly sub-optimal (Hurly and Oseen, 1999). Slight sub-optimality in the vertical distribution is not that important for overall population levels, so at the population level complete rationality provides almost no evolutionary benefit.

Bounded rationality as we introduce it is potentially testable, contrasting e.g. satisficing models, (Nonacs and Dill, 1993). Empirical studies of copepod vertical migration patterns indicate that their distribution in the water column can be closely approximated by the smooth distribution we get from the model with bounded rationality (Hay et al., 1991; Visser et al., 2001). Our model of bounded rationality passes the first test, but must be compared with more data.

Our approach for solving games in continuous space represents a significant advance over the current state-of-the art (Mariani et al., 2016; Pinti et al., 2021). Interpreting strategies as distributions in space forms one of the two pillars of our approach. This interpretation is heavily inspired by that of static

mean field games (Lasry and Lions, 2007; Blanchet and Carlier, 2016), rather than classical evolutionary game-theory (Hofbauer et al., 1998). Thinking of the strategy of a population as a distribution for each individual rather than each individual being at specific locations turns out to be a powerful tool. Thinking in terms of distributions is what allows us to reformulate the game between predators and prey into a continuous polymatrix game, where the Nash equilibrium can theoretically be found. A theoretical reformulation of the population game cannot stand alone, leading to the second pillar of our project: The introduction of efficient numerical methods. A necessity for efficient numerical methods is stating the problem in a form that is easily solvable, and an efficient algorithm to solve that form. Using a spectral scheme allows us to only use relatively few points for high precision, (Kopriva, 2009), giving half the problem statement. Together with a tractable method of solving polymatrix games (Miller and Zucker, 1991), we have the full restatement of the problem. We then apply fast algorithms from modern optimization software (Andersson et al., 2019; Acary et al., 2019) to solve the restated problem. This combination is fundamentally what allows us to solve a population game in both continuous time and space. In essence, by using the philosophy of mean-field games applied through modern numerical methods we have constructed a general feasible approach to incorporating behavior in models of interacting populations in continuous habitats.

Our population model with the vertical migration shows that transient phenomena and continuous fitness gradients (Kawecki and Ebert, 2004) are naturally at home in a continuous population game. Incorporating these features allows a more fine-grained biological analysis and greater predictive power in models of real-world systems than typical finite-patch models (Křivan et al., 2008; Sadowski and Grosholz, 2019). Our focus has largely been on the interplay between temporal and spatial transients in the vertical migration. If one of these is averaged out, e.g. the time-varying habitat, the model can be adapted to find the equilibrium populations and distributions in inhomogenous habitats. We have used our approach for a one-dimensional habitat, but it can readily be used to accommodate a two-dimensional habitat. More generally, our approach only depends on the bilinearity of the fitness proxy and the population-game setup.

Though intraspecific competition is often more important in shaping behavior than the risk of predation (Křivan and Sirot, 2002), we did not consider the effect in the case we considered for simplicity and to keep the case aligned with (Thygesen and Patterson, 2018). Including the effect of intraspecific competition on population dynamics and behavior could be a next step for a deeper investigation of the case. Performing a multi-year simulation could also reveal interesting patterns, but doing so would complicate the model since it would need to take low-resource adaptations during winter into account. Since our model is in large part a proof-of-concept, we found it best to neglect such phenomena. We consider the case where the equilibrium is unique, but in general there might be many Nash and population equilibria (Křivan and Sirot, 2002). A specific Nash equilibrium can be tracked across changing population levels, if it is used as starting point for finding the Nash equilibrium with a slightly different population, but we are not aware of any method to guarantee that the correct Nash equilibrium is found apart from enumerating all equilibria (Mangasarian, 1964). Hence there can also be no guarantee which equilibrium our method converges to without this procedure. As such, our method is best suited to models with a unique Nash and population equilibrium.

6. Conclusion

Simulating the population dynamics of a predator–prey system through half a year reveal a complex interplay between seasons, behavior and population dynamics. Though our model is simple in nature, it can catch essential features of the seasonal dependence of the diel vertical migration. Though the primary trophic interactions happen abruptly and in a very short time frame when introducing optimal behavior, optimal behavior still serves to stabilize the system. We show that it is possible to include bounded rationality in a systematic fashion, allowing it as a tuning parameter in future models. The usual assumption of perfect rationality seems to be reasonable for population dynamics, but bounded rationality appears to be better at predicting specific distributions. These results are fundamentally only possible due to one of the major contributions of our approach, namely the introduction of efficient numerical methods for solving continuous population games. Whether to include behavior in a model or not reduces to a question of relevance to the model, not feasibility.

CRedit authorship contribution statement

Emil F. Frølich: Designed the study, Realized the model design, Coded the model, Numerical approaches, Analyzed the results, Writing – original draft. **Uffe H. Thygesen:** Designed the study, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data can be generated using the file `data_lemke_generator.py` from the git repository https://github.com/jemff/food_web.

Acknowledgments

All authors approved the version of the manuscript to be published.

Funding

This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence, Denmark supported by the Villum Foundation, Denmark.

Code availability

All code for reproducing the results of this project is available on github https://github.com/jemff/food_web.

Appendix. The density dependent case

We expand on the game defined by Eq. (3), in the case where $A_{ii} \neq 0$. We remark that strategy of an individual is p_i , but the individual and the population do not follow the same strategy a priori. Instead the individual plays the field (Fretwell, 1969), and we denote the population strategy by \bar{p}_i . Hence the payoff for an individual of type i playing against its conspecifics in the notation of Eq. (3) is given by

$$\langle p_i, N_i A_{ii} \bar{p}_i \rangle \quad (\text{A.1})$$

The optimal strategy for an individual of type i against a population playing \bar{p}_i can therefore be found as a optimization problem, where the Karush–Kuhn–Tucker conditions are:

$$\begin{aligned} N_i A_{ii} \bar{p}_i + \mu_i &= \lambda_i \\ p_i, \mu_i &\geq 0 \\ \sum_{i=1}^T p_i(t) &= 1 \\ \langle p_i, \mu_i \rangle &= 0 \end{aligned} \quad (\text{A.2})$$

At the Nash equilibrium, no individual gains from deviating from the population strategy (Lasry and Lions, 2007). This implies that at the Nash equilibrium $p_i = \bar{p}_i$. Inserting this in Eq. (A.2), we arrive at

$$N_i A_{ii} p_i + \mu_i = \gamma_i \quad (\text{A.3})$$

As such, the Nash equilibrium for the game specified by Eq. (A.1) is the same as the equilibrium for the game specified by:

$$\frac{1}{2} \langle p_i, N_i A_{ii} p_i \rangle$$

In conclusion we arrive at an expression for E_{ii} in the case where $A_{ii} \neq 0$

$$E_{ii} = \frac{1}{2} \langle p_i, N_i A_{ii} p_i \rangle + \frac{1}{T} \Gamma_i \quad (\text{A.4})$$

References

- Abrams, P.A., Cressman, R., Křivan, V., 2007. The role of behavioral dynamics in determining the patch distributions of interacting species. *Amer. Nat.* 169 (4), 505–518.
- Acary, V., Bonnefon, O., Brémont, M., Huber, O., Pérignon, F., Sinclair, S., 2019. An Introduction to Siconos (Ph.D. thesis). INRIA.
- Andersen, K.H., 2019. *Fish Ecology, Evolution, and Exploitation: A New Theoretical Synthesis*. Princeton University Press.
- Andersson, J.A.E., Gillis, J., Horn, G., Rawlings, J.B., Diehl, M., 2019. CasADi – A software framework for nonlinear optimization and optimal control. *Math. Program. Comput.* 11 (1), 1–36.
- Arin, L., Morán, X.A.G., Estrada, M., 2002. Phytoplankton size distribution and growth rates in the Alboran sea (SW Mediterranean): short term variability related to mesoscale hydrodynamics. *J. Plankton Res.* 24 (10), 1019–1033.
- Beaugrand, G., Ibañez, F., Lindley, J.A., 2001. Geographical distribution and seasonal and diel changes in the diversity of calanoid copepods in the north Atlantic and North sea. *Mar. Ecol. Prog. Ser.* 219, 189–203.
- Bechard, M.J., 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor* 84 (2), 153–159.
- Benoit-Bird, K.J., McManus, M.A., 2014. A critical time window for organismal interactions in a pelagic ecosystem. *PLoS One* 9 (5), e97763.
- Biberman, L.M., 1971. Natural levels of illumination and irradiance. In: *Photoelectronic Imaging Devices*. Springer, pp. 39–67.
- Blanchet, A., Carlier, G., 2016. Optimal transport and Cournot–Nash equilibria. *Math. Oper. Res.* 41 (1), 125–145.
- Bolker, B., Holyoak, M., Křivan, V., Rowe, L., Schmitz, O., 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* 84 (5), 1101–1114.
- Broom, M., Rychtář, J., 2013. *Game-Theoretical Models in Biology*. CRC Press.
- Carranza, J., Valencia, J., 1999. Red deer females collect on male clumps at mating areas. *Behav. Ecol.* 10 (5), 525–532.
- Cohen, D., Teichman, G., Volovich, M., Zeevi, Y., Elbaum, L., Madar, A., Louie, K., Levy, D.J., Rechavi, O., 2019. Bounded rationality in *C. Elegans* is explained by circuit-specific normalization in chemosensory pathways. *Nature Commun.* 10 (1), 1–12.
- Colebrook, J., 1979. Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north Atlantic ocean and the North sea. *Mar. Biol.* 51 (1), 23–32.
- Cooper, R., Dejong, D.V., Forsythe, R., Ross, T.W., 1989. Communication in the battle of the sexes game: some experimental results. *Rand J. Econ.* 568–587.
- Cressman, R., Křivan, V., 2006. Migration dynamics for the ideal free distribution. *Amer. Nat.* 168 (3), 384–397.
- Cressman, R., Křivan, V., 2010. The ideal free distribution as an evolutionarily stable state in density-dependent population games. *Oikos* 119 (8), 1231–1242.

- Eaves, B.C., 1973. Polymatrix games with joint constraints. *SIAM J. Appl. Math.* 24 (3), 418–423.
- Fretwell, S.D., 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19 (1), 45–52.
- Genkai-Kato, M., 2007. Macrophyte refuges, prey behaviour and trophic interactions: consequences for lake water clarity. *Ecol. Lett.* 10 (2), 105–114.
- González-Olivares, E., Ramos-Jiliberto, R., 2003. Dynamic consequences of prey refuges in a simple model system: more prey, fewer predators and enhanced stability. *Ecol. Model.* 166 (1–2), 135–146.
- Gueymard, C., et al., 1995. SMARTS2: A Simple Model of the Atmospheric Radiative Transfer of Sunshine: Algorithms and Performance Assessment, Vol. 1. Florida Solar Energy Center Cocoa, FL.
- Hay, S., Kiørboe, T., Matthews, A., 1991. Zooplankton biomass and production in the North sea during the autumn circulation experiment, october 1987–march 1988. *Cont. Shelf Res.* 11 (12), 1453–1476.
- Hochbruck, M., Ostermann, A., 2010. Exponential integrators. *Acta Numer.* 19 (May), 209–286.
- Hofbauer, J., Sigmund, K., et al., 1998. *Evolutionary Games and Population Dynamics*. Cambridge University Press.
- Holmgren, W.F., Hansen, C.W., Mikofski, M.A., 2018. pvlb python: A python package for modeling solar energy systems. *J. Open Source Softw.* 3 (29), 884.
- Howson, Jr., J.T., 1972. Equilibria of polymatrix games. *Manage. Sci.* 18 (5-part-1), 312–318.
- Hurly, T.A., Oseen, M.D., 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Anim. Behav.* 58 (1), 59–66.
- Jones, B.D., 1999. Bounded rationality. *Annu. Rev. Political Sci.* 2 (1), 297–321.
- Kawecki, T.J., Ebert, D., 2004. Conceptual issues in local adaptation. *Ecol. Lett.* 7 (12), 1225–1241.
- Klevjer, T.A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V.M., Kaartvedt, S., 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Sci. Rep.* 6 (1), 19873.
- Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299 (5611), 1388–1391.
- Kopriva, D.A., 2009. *Implementing Spectral Methods for Partial Differential Equations: Algorithms for Scientists and Engineers*. Springer Science & Business Media.
- Křivan, V., 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *Amer. Nat.* 149 (1), 164–178.
- Křivan, V., 2007. The Lotka-Volterra predator-prey model with foraging-predation risk trade-offs. *Amer. Nat.* 170 (5), 771–782.
- Křivan, V., Cressman, R., 2009. On evolutionary stability in predator-prey models with fast behavioural dynamics. *Evol. Ecol. Res.* 11 (2), 227–251.
- Křivan, V., Cressman, R., Schneider, C., 2008. The ideal free distribution: a review and synthesis of the game-theoretic perspective. *Theor. Popul. Biol.* 73 (3), 403–425.
- Křivan, V., Siro, E., 2002. Habitat selection by two competing species in a two-habitat environment. *Amer. Nat.* 160 (2), 214–234.
- Křivan, V., 1998. Effects of optimal antipredator behavior of prey on predator-prey dynamics: The role of refuges. *Theor. Popul. Biol.* 53 (2), 131–142.
- Lasry, J.-M., Lions, P.-L., 2007. Mean field games. *Jpn. J. Math.* 2 (1), 229–260.
- Lima, S.L., 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biol. Rev.* 84 (3), 485–513.
- Mangasarian, O.L., 1964. Equilibrium points of bimatrix games. *J. Soc. Ind. Appl. Math.* 12 (4), 778–780.
- Mariani, P., Křivan, V., MacKenzie, B.R., Mullan, C., 2016. The migration game in habitat network: the case of tuna. *Theor. Ecol.* 9 (2), 219–232.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature* 246 (5427), 15–18.
- McGlade, J.M., 2002. The North sea large marine ecosystem. In: *Large Marine Ecosystems*, Vol. 10. Elsevier, pp. 339–412.
- Miller, D.A., Zucker, S.W., 1991. Coperative-plus Lemke algorithm solves polymatrix games. *Oper. Res. Lett.* 10 (5), 285–290.
- Mougi, A., 2019. Adaptive migration promotes food web persistence. *Sci. Rep.* 9 (1), 1–5.
- Nonacs, P., Dill, L.M., 1993. Is satisficing an alternative to optimal foraging theory? *Oikos* 371–375.
- Pinti, J., Andersen, K.H., Visser, A.W., 2021. Co-adaptive behavior of interacting populations in a habitat selection game significantly impacts ecosystem functions. *J. Theoret. Biol.* 110663.
- Pinti, J., Kiørboe, T., Thygesen, U.H., Visser, A.W., 2019. Trophic interactions drive the emergence of diel vertical migration patterns: a game-theoretic model of copepod communities. *Proc. R. Soc. B* 286 (1911), 20191645.
- Pinti, J., Visser, A.W., 2019. Predator-prey games in multiple habitats reveal mixed strategies in diel vertical migration. *Amer. Nat.* 193 (3), E000.
- Rapoport, A., 1967. Exploiter, Leader, Hero, and Martyr: the four archetypes of the 2×2 game. *Behav. Sci.* 12 (2), 81–84.
- Sadowski, J.S., Grosholz, E.D., 2019. Predator foraging mode controls the effect of antipredator behavior in a tritrophic model. *Theor. Ecol.* 12 (4), 531–544.
- Schaechter, M., 2009. *Encyclopedia of Microbiology*. Academic Press.
- Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78 (5), 1388–1399.
- Sih, A., 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* 139 (5), 1052–1069.
- Simon, H.A., 1955. A behavioral model of rational choice. *Q. J. Econ.* 69 (1), 99–118.
- Simon, H.A., 1956. Rational choice and the structure of the environment. *Psychol. Rev.* 63 (2), 129.
- Stakgold, I., Holst, M.J., 2011. *Green's Functions and Boundary Value Problems*. John Wiley & Sons.
- Sutton, T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *J. Fish Biol.* 83 (6), 1508–1527.
- Tew, T., Todd, I., Macdonald, D., 2000. Arable habitat use by wood mice (*Apodemus sylvaticus*). 2. Microhabitat. *J. Zool.* 250 (3), 305–311.
- Thuijsman, F., Peleg, B., Amitai, M., Shmida, A., 1995. Automata, matching and foraging behavior of bees. *J. Theoret. Biol.* 175 (3), 305–316.
- Thygesen, U., Patterson, T., 2018. Oceanic diel vertical migrations arising from a predator-prey game. *Theor. Ecol.* 12 (1), 17–29.
- Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P., Dunne, J.A., 2010. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol. Lett.* 13 (12), 1546–1559.
- Visser, A., Saito, H., Saiz, E., Kiørboe, T., 2001. Observations of copepod feeding and vertical distribution under natural turbulent conditions in the North sea. *Mar. Biol.* 138 (5), 1011–1019.
- Wächter, A., Biegler, L.T., 2006. On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. *Math. Program.* 106 (1), 25–57.
- Wang, Z., DiMarco, S.F., Ingle, S., Belabbassi, L., Al-Kharusi, L.H., 2014. Seasonal and annual variability of vertically migrating scattering layers in the northern Arabian sea. *Deep Sea Res. I: Oceanogr. Res. Pap.* 90, 152–165.
- Wheeler, A., 1975. *Collins guide to the sea fishes of Britain and north-western Europe*, by B.J. Muus and P. Dahlstrom. Collins. *Oryx* 13 (1), 94.
- Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. *Amer. Nat.* 139 (6), 1151–1175.

PAPER B

Scaling from optimal
behavior to population
dynamics and ecosystem
function

Highlights

Scaling from optimal behavior to population dynamics and ecosystem function *

Emil F. Frølich, Uffe H. Thygesen, Ken H. Andersen

- Fast optimal behavior of consumers and predators causes ecosystem resilience to top-down forcing
- Behavior causes a constant partial satiation for consumers and predators in a changing environment
- The emergence of a Type III functional from behavior is general
- Complex trophic interactions can be captured coupling population dynamics and playing the field

Scaling from optimal behavior to population dynamics and ecosystem function

Emil F. Frølich^{a,*}, Uffe H. Thygesen^a, Ken H. Andersen^b

^a*Technical University of Denmark, Department of Applied Mathematics and Computer Science - DTU Compute, Building 303B, Matematiktorvet, 2800, Kgs. Lyngby, Denmark*

^b*Technical University of Denmark, National Institute of Aquatic Resources - DTU Aqua, Building 201, Anker Engelundsvej, 2800, Kgs. Lyngby, Denmark*

Abstract

While behavioral responses of individual organisms can be predicted with optimal foraging theory, the theory of how individual behavior feeds back to population and ecosystem dynamics has not been fully explored. Ecological models of trophic interactions incorporating behavior of entire populations commonly assume either that populations act as one when making decisions, that behavior is slowly varying or that non-linear effects are negligible in behavioral choices at the population scale. Here, we scale from individual optimal behavior to ecosystem structure in a classic tri-trophic chain where both prey and predators adapt their behavior in response to food availability and predation risk. Behavior is modeled as playing the field, with both consumers and predators behaving optimally at every instant basing their choices on the average population behavior. We establish uniqueness of the Nash equilibrium, and find it numerically. By modeling the interactions as playing the field, we can perform instantaneous optimization at the individual level while taking the entire population into account. We find that optimal behavior essentially removes the effect of top-down forcing at the population level, while drastically changing the behavior. Bottom-up forcing is found to increase populations at all trophic levels. These phenomena both appear to be driven by an emerging constant consumption rate, corresponding to a partial satiation. In addition, we find that a Type III functional response arises from a Type II response for both predators and consumers when their behavior follows the Nash equilibrium, showing that this is a general phenomenon. Our approach is general and computationally efficient and can be used to account for behavior in population dynamics with fast behavioral responses

Keywords: population dynamics, predator-prey, game theory, ecosystem, habitat selection

*This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

*Corresponding author

1. Introduction

Animal behavior plays an essential role in shaping ecosystems (Ripple and Beschta, 2004; Laundré et al., 2001; Stump and Chesson, 2017; Sih et al., 1985). While classic ecosystem models ignore behavior (Hairston et al., 1960; Oksanen et al., 1981), by now a wealth of models have considered the impact of adaptive foraging (Kondoh, 2003; Lima and Dill, 1990; McNamara and Houston, 1992; Abrams, 2010; Werner and Anholt, 1993; Abrams, 1984). One of the central mechanisms is risk-sensitive foraging, e.g. the ability of an animal to retreat to a refuge when under risk of predation. Examples of such behavior are abundant, e.g. juvenile fish prefer the littoral zone over the pelagic despite lower food availability (Biro et al., 2005), and tits prefer the interior of forests (Suhonen, 1993). These behaviors are adaptive and can change rapidly in response to changes in perceived predation risk. In both these cases the behavior of the prey acts to reduce the encounter of prey with predators at the expense of feeding.

There are two common approaches to introducing adaptive behavior reflecting risk-sensitive foraging in ecosystem models. First, through direct modification of encounter terms to reflect predator interference, (Arditi and Ginzburg, 1989; Příbylová and Berec, 2015; DeAngelis et al., 1975). Second, by introducing a fitness proxy which the prey or predator optimize individually. This can happen based on instantaneous optimization based on the current state (Křivan, 2007; Kjørboe et al., 2018), over longer time-intervals through dynamic programming (Houston et al., 1999; Thygesen et al., 2016) or through a gradient-climbing approach (Abrams, 2007, 2009a). The instantaneous optimization is suitable for ecosystems where the behavior is habitat choice with highly-interconnected habitats, where the migrations are much faster than the population dynamics (Cressman et al., 2004; Ma et al., 2003). A canonical example of such a system is the ocean with the diel vertical migration (Iwasa, 1982; Pinti et al., 2019). The model of instantaneous shifts in behavior is also justified when considering activity level as the behavioral variable, e.g. swimming speeds (van Someren Greve et al., 2019; Sutton, 2013). When there are multiple animals or species present, the instantaneous optimization approach leads to a game at every instant.

Models studying the impact of refuge use on ecosystems based on instantaneous choice typically assume that both species have linear fitness proxies (Křivan, 2007; Cressman et al., 2004; Malone et al., 2020), or at least that predators have linear fitness proxies (Genkai-Kato, 2007). In the cases when non-linear fitness proxies are included, the model is often simplified by assuming that populations are monomorphic, that is, the entire population always acts as one, (Genkai-Kato, 2007), i.e. they cooperate. By cooperating individuals in a monomorphic population can obtain a higher population growth rate than if each individual plays the field, i.e., optimizes its individual fitness in competition with conspecifics rather than cooperation (Abrams et al., 1993). If the number of individuals in each population is very large and they do not cooperate, the instantaneous population game is naturally modeled as playing the field (May-

nard Smith, 1982). When playing the field each individual's behavior is based on the average strategy of the populations (Parker, 1978; Maynard Smith, 1982), e.g. their distribution in a spatial habitat (Fretwell, 1969). This leads to a Nash equilibrium where all individuals follow the same behavioral strategy (Křivan et al., 2008) rather than assuming it from the start as in a game with monomorphic populations. Population games modeled as playing the field also allow for non-linear fitness proxies in asymmetric games (Křivan and Eisner, 2006; Vincent and Brown, 2005). The monomorphic structure is, however, often imposed due to a lack of a general method to study population dynamics and behavior simultaneously when playing the field. A modeling approach allowing for easy evaluation of Nash equilibria when individuals play the field games is a stepping stone for an integration of behavior into ecosystem ecology (Schmitz et al., 2008).

An important question in community ecology is to predict the response of the system to (slowly) varying forcing. Here, we distinguish between “bottom-up forcing”, such as varying the basal resources available to the system, and “top-down forcing”, such as varying the mortality of the highest trophic levels e.g. by human harvest. According to the ecosystem enrichment hypothesis (Oksanen et al., 1981; Hairston et al., 1960) consumer abundances at equilibrium respond weakly to bottom-up forcing due to top-down control by predators. Top-down forcing classically results in an increase in consumer populations in response to higher mortalities induced on the predator (Oksanen and Oksanen, 2000). Predators eventually go extinct due to the mortality, potentially after increasing in abundance first (Abrams, 2009b). Behavioral adaptations are known to fundamentally change the responses of ecosystems to forcing. Predators can choose to reduce their foraging activity when they are satiated or subjected to predation or harvesting themselves. These non-consumptive effects lead to trophic cascades (Peckarsky et al., 2008; Heath et al., 2014) which are often stronger than those caused by direct effects (Abrams, 2004, 2010). In addition, non-consumptive effects can fundamentally change the nature of the cascade (Wollrab and Diehl, 2015; Abrams and Vos, 2003). A general trend is that bottom-up forcing causes a change in all in population levels when behavioral adaptation is incorporated (Valdovinos et al., 2010; Abrams, 2010; Schmitz et al., 2004). In contrast, predator adaptation attenuates the effect of top-down forcing (Loeuille and Loreau, 2004) while consumer adaptation can either attenuate or accelerate top-down forcing (Abrams, 2009b; Abrams and Vos, 2003). The results for top-down forcing when both predators and consumers are adaptive are more complex, without an overall trend (Abrams, 1992b; Křivan and Cressman, 2009). Generally, the co-adaptive situation has not been investigated in as much depth, especially not with fast behavior and where the behavioral choices take non-linear effects into account (Barbosa and Castellanos, 2005, Chapter 13, p. 292-294), (Pinti et al., 2021; Abrams, 2010).

An ecosystem modeled as a trophic chain has been examined before with delayed behavior, (Abrams, 1992a; Abrams and Roth, 1994b) or with only linear effects (Abrams, 2010; Pinti et al., 2021). A tri-trophic chain with fast adaptive behavior where both predators and consumers play the field and have

to take non-linear effects such as satiation into account has not been studied before. That is, the impact of fast adaptive behavior has not been studied in entire classes of models. In particular, models of systems where choices are made instantaneously based on both individual satiation, (Křivan and Eisner, 2006), and the satiation of their predator, e.g. models of aquatic ecosystems (Heath et al., 2014; Iwasa, 1982; van Someren Greve et al., 2019) have not been investigated.

Here, we develop a modeling approach which allows us to analyze ecosystems where both predators and consumers have instantaneous behavior, where the choices are made by each individual playing the field with their decisions taking individual satiation into account. Assuming that both consumers and predators play the field, allows us to couple individual choices and the behavior of the overall population. We first present a tri-trophic food-chain consisting of a resource, a consumer, and a predator under risk of top-predation. Consumers and predators both adapt their behavior instantaneously according to a behavioral game. Our work examines the individual, the population, and ecosystem level of this system. We investigate the food chain with optimal behavior at equilibrium as a function of resource carrying capacity and mortality of the predator, i.e., the response to bottom-up and top-down forcing. At the population level we compare the consequences of the top-down and bottom-up forcing to both the classical results and other models with optimal behavior. At the individual level, we examine the consumption rate out of equilibrium, investigating the relationship between Type II and Type III functional responses when both consumers and predators have optimal behavior. In addition, we consider the individual consumption rate at equilibrium as an ecosystem feature when fast optimal behavior is included in the model.

2. Methods

Our model is based on the concept of a “foraging arena” where feeding encounters occur under the risk of predation. Individuals may choose to retreat to a refuge to avoid predation risk at the cost of forgone feeding (Gause et al., 1934). An example of a foraging arena is the upper levels of the ocean during the day where visual predators can detect prey at distance. In this case the anti-predator response is vertical migrations of prey towards a refuge in deeper and darker water (e.g. Iwasa, 1982). Another example of a refuge is the shelter offered small birds by trees and bushes from birds of prey. In the following we implement arena-refuge behavioral dynamics in a tri-trophic consumer-resource-predator system where the predator is further exposed to predation from a top-predator or harvester which does not have population dynamics explicitly included in the model (Figure 1). Instead, this population is represented by a parameter. In this way, we can explicitly study the sensitivity of the system to the top-predator population. This models a migratory population of apex-predators with the predators as preferred food-source (Furey et al., 2018; Block et al., 2011).

The presence of a top-predator creates a tradeoff for the predator, as it is unable to feed in the refuge, but by staying in the refuge it avoids the top-predator. Predators and consumers simultaneously and instantaneously maximize their fitness by choosing behavior to form a Nash equilibrium.

We consider a tri-trophic food chain with biomass densities of a resource (R), a consumer (C), and a predator (P). We have in mind a system where individuals move in and out of the arena independently and instantaneously. The population dynamics are:

$$\begin{aligned}\dot{R} &= \lambda \cdot (\bar{R} - R) - R \cdot M_r(\tau_c, C, R), \\ \dot{C} &= C \cdot (G_c(\tau_c, R) - M_c(\tau_c, \tau_p, P, C) - \mu_c), \\ \dot{P} &= P \cdot (G_p(\tau_c, \tau_p, C) - M_p(\tau_p, \xi) - \mu_p),\end{aligned}\tag{1}$$

where the time derivative of a function f is represented as \dot{f} . We ignore the time argument t in the notation, but R, C, P and τ_c, τ_p are implicitly time-dependent.

The behavioral variables τ_c and τ_p take values between 0 and 1 and describe the fraction of time consumers and predators are present in the arena; the resource is described as a chemostat with carrying capacity \bar{R} and renewal rate λ . M_r is the mortality of the resource due to predation by the consumers. For consumers and predators the specific growth rates are G_c and G_p , their mortalities are M_c and M_p , and metabolic losses are μ_c and μ_p . The growth and mortality rates depend on abundances as well as the instantaneous behaviors τ_p and τ_c .

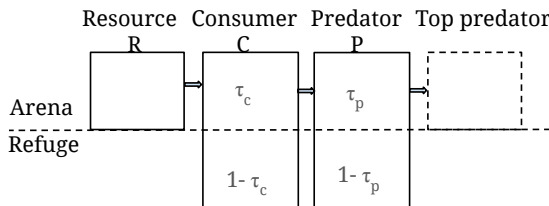


Figure 1: Sketch of the system (Equation (1)) and the arena-refuge concept. Feeding events and predator-prey encounters only occur in the arena. Resources are always in the arena where consumers and predators spend τ_c , respectively τ_p , of their time. This means that e.g. the fraction of the consumer populations which is present in the arena at a given instant is also τ_c . The top-predator tracks the behavior of the predator, and is in the arena τ_p of the time. The population dynamics of the top predator is not represented in the model but acts as an external risk for the predator's foraging.

A type II functional response is our starting point for describing the growth rates of consumers (G_c) and predators (G_p). With conversion efficiency ε and

without behavior this would be:

$$G_c = \varepsilon \frac{a_c \beta_c R}{\beta_c R + a_c}. \quad (2)$$

Here, β_c is the consumer clearance rate and a_c is the maximum consumption rate. For many animals handling time is not the limiting factor for growth but rather prey encounters (Jeschke et al., 2002; Giske and Salvanes, 1995) and to a limited degree processing capacity of the gut. Clearance of resources is only possible in the arena, so the effective consumer clearance becomes $\tau_c \beta_c$. Adjusting for the conversion efficiency the consumer growth rate G_c and resource mortality M_r become (Werner and Anholt, 1993).

$$\begin{aligned} G_c(\tau_c, R) &= \varepsilon \frac{a_c \beta_c \tau_c R}{\beta_c \tau_c R + a_c} \\ M_r(\tau_c, C, R) &= \frac{a_c \beta_c \tau_c}{\beta_c \tau_c R + a_c} C \end{aligned} \quad (3)$$

Note that if the feeding rate is limited by prey-handling as often assumed (Abrams, 1982, 1990; Prowe et al., 2012), with $1/a_c$ being the handling time the correct form of G_c instead becomes

$$\varepsilon \frac{a_c \beta_c \tau_c R}{\beta_c R + a_c}. \quad (4)$$

We only consider a per capita growth rate given by Equation (3).

The consumers suffer a constant metabolic loss, μ_c independent of the time in the arena τ_c . Similarly for the predator, where prey encounters are also limited to the arena:

$$\begin{aligned} M_c(\tau_c, \tau_p, C, P) &= \frac{a_p \beta_p \tau_c \tau_p}{\beta_p \tau_c \tau_p C + a_p} P \\ G_p(\tau_c, \tau_p, C, P) &= \varepsilon \frac{C}{P} M_c(\tau_c, \tau_p, R, C, P) = \frac{a_p \beta_p \tau_c \tau_p C}{\beta_p \tau_c \tau_p C + a_p}, \end{aligned} \quad (5)$$

We now use subscript p on the parameters to indicate the predator. The product $\tau_c \tau_p$ enters in the encounter rate between predators and consumers because we assume that individual consumers and predators move in and out of the arena independently. Movement in and out of the arena is instantaneous, corresponding to a slow-fast system where the population dynamics are much slower than migrations.

The behavior-dependent mortality of the predator emerges from pressure from a top-predator or harvesting. We include the maximal pressure from the top-predator population or maximal harvesting pressure as a parameter ξ . A common feature for apex predators is migrating quickly for food and having diverse food sources (Thygesen et al., 2016; Furey et al., 2018). For these reasons we model that the proportion of apex-predators present in the arena is proportional to the presence of their food, i.e. predators, in the arena. Hence

the top-predator presence can be described by $\xi\tau_p$. The per capita mortality of the predators M_p is then described by their encounters with the proportion of top-predators in the arena, i.e.

$$M_p = \xi\tau_p^2. \quad (6)$$

2.1. Focal individual and playing the field

We consider the specific growth rate F_i for an individual as a fitness proxy. The environment an individual consumer or predator faces is not only shaped by the consumer or predator populations, but also their behavior. Denoting the average of the population behavioral strategies by $\bar{\tau}_i$ where $i \in \{c, p\}$ the average proportion of consumers and predators in the arena are $C\bar{\tau}_c$ and $P\bar{\tau}_p$, respectively. The growth rate for an individual then depends on both $\bar{\tau}_c$ and $\bar{\tau}_p$. Hence each individual plays the field at every instant (Maynard Smith, 1982; Krivan et al., 2008), as they are playing against the habitat choices of the rest of the population.

The growth of a consumer is not impacted by the choices of the rest of the population, but the threat from predation is influenced by the behavior of other consumers and the average predator strategy. The encounter rate of a consumer with an average predator is $a_p\beta_p\tau_c\bar{\tau}_p$, and the satiation of the average predator is

$$\frac{1}{\beta_p\bar{\tau}_c\bar{\tau}_pC + a_p}. \quad (7)$$

With these considerations in mind, the specific growth rate of an individual consumer becomes:

$$F_c(\tau_c, \bar{\tau}_c, \bar{\tau}_p) = G_c(\tau_c, \bar{\tau}_p) - \frac{a_p\beta_p\tau_c\bar{\tau}_pP}{\beta_p\bar{\tau}_c\bar{\tau}_pC + a_p}. \quad (8)$$

As the top-predator or harvester tracks the average predator time in the arena $\bar{\tau}_p$, an individual predator will experience the loss $\xi\tau_p\bar{\tau}_p$. Hence the specific growth of an individual predator becomes:

$$F_p(\tau_p, \bar{\tau}_p, \bar{\tau}_c) = G_p(\tau_p, \bar{\tau}_c) - \xi\tau_p\bar{\tau}_p. \quad (9)$$

For reference we also consider the model where the behaviors τ_c and τ_p are constant in time and equal to 1. This entails that the average behavior is also constantly equal to 1. We refer to this as static behavior, in contrast to the optimal behaviors that continuously maximize the fitness proxy.

2.2. Optimal behaviors, games, and Nash equilibria

We now detail how the individuals at each instant choose their behavior, τ_c and τ_p , to maximize the fitness proxy F_i . Subtleties arise because the fitness depends both on the individual behavioral choice, and average behavior of the population. A key assumption that allows us to resolve this problem is that the populations of both consumers and predators are assumed to be large. If the populations are large, the action of an individual does not change the average

population behavior. With this assumption, the game becomes a game where all individuals play the field. Since no consumer or predator can gain from deviating from the Nash equilibrium, each consumer or predator must follow the average behavior at the Nash equilibrium (Aumann, 1964; Krivan et al., 2008). We refer to this game as the “inner” game, since it is played at every instant and defines the population dynamics.

We consider the Nash equilibrium of the inner game and define the *best responses*:

$$\begin{aligned}\tau_c^*(\tau_p, \bar{\tau}_c) &= \operatorname{argmax}_{\tau_c \in [0,1]} F_c(\tau_c, \bar{\tau}_c, \bar{\tau}_p). \\ \tau_p^*(\tau_c, \bar{\tau}_p) &= \operatorname{argmax}_{\tau_p \in [0,1]} F_p(\tau_p, \bar{\tau}_c, \bar{\tau}_p).\end{aligned}$$

As we assume individuals play the field, we get that $\tau_c^* = \bar{\tau}_c$ at the Nash equilibrium of the game. Hence the Nash equilibria $\bar{\tau}_i^{NE}$ of the respective games where individuals are:

$$\begin{aligned}\tau_c^*(\bar{\tau}_p, \bar{\tau}_c^{NE}) &= \bar{\tau}_c^{NE} \\ \tau_p^*(\bar{\tau}_c, \bar{\tau}_p^{NE}) &= \bar{\tau}_p^{NE}.\end{aligned}\tag{10}$$

Then the the Nash equilibrium of the overall game is defined as the pair of decisions $(\bar{\tau}_c^{NE}, \bar{\tau}_p^{NE})$ such that we are at the Nash equilibrium of both games simultaneously:

$$\begin{aligned}\tau_c^*(\bar{\tau}_p^{NE}, \bar{\tau}_c^{NE}) &= \bar{\tau}_c^{NE}. \\ \tau_p^*(\bar{\tau}_c^{NE}, \bar{\tau}_p^{NE}) &= \bar{\tau}_p^{NE}.\end{aligned}\tag{11}$$

The Nash equilibrium of the inner game depends on the abundances R, C, P , but our notation omits this dependence for compactness. At the Nash equilibrium, no single player has an advantage in changing strategy unilaterally. We show uniqueness of the instantaneous Nash equilibrium in Appendix A. As $\tau_i = \bar{\tau}_i$, $i \in \{c, p\}$ at the Nash equilibrium, we will henceforth just write τ_i^N , $i \in \{c, p\}$ when considering the Nash equilibrium.

2.3. Emergent functional response

The time in the arena of both consumers and predators depend on the Nash equilibrium as defined in Equation (11), found by optimizing the fitness proxies given in Equation (8). The optimal time in the arena depends on both the available food, the concentration of the same type, and the threat from predation. This leads to risk-sensitive foraging behavior, hence risk-sensitive consumption rates.

The consumption rates of a consumer and of a predator as a function of the threat-level and total available resources are of special interest. Given a state (R, C, P) , we can find the corresponding Nash equilibrium $(\tau_c^N(R, C, P), \tau_p^N(R, C, P))$ from Equation (11). Based on the Nash equilibrium and the growth functions (Equation (3) and Equation (5)), we define the dynamical emergent functional

Table 1: Metabolic scaling of parameters with respect to body mass m_i , where $i \in \{c, p\}$. Metabolic costs are a fraction v of maximum growth rate, and the mass of predators is s times larger than the mass of their prey.

Parameter	Symbol	Mass scaling
Max growth	a_i	$\alpha m_i^{3/4}$
Clearance rate	β_i	$b m_i^{3/4}$
Conversion efficiency	ε	-
Metabolic cost	μ_i	$v a_i$
Predator mass	m_p	$s m_c$

response for a consumer with fixed consumer and predator level C_0, P_0 , with a top predation rate ξ_0 :

$$G_{E,c}(R) = G_c(\tau_c^N, \tau_p^N, R, C_0, P_0, \xi_0). \quad (12)$$

and analogously $G_{E,p}(C)$ for the predator. While the functional response in Equation (12) also depends on the abundance of consumers C_0 and of predators P_0 , we are particularly interested in its dependence on the resource level R . This functional response describes how consumption rates respond instantaneously to variations in the resource, i.e. before the dynamic states of the system change.

The consumption rate at equilibrium describes the consumption at the time-scale where the dynamics have stabilized. We refer to this as the *equilibrium* consumption rate. Focusing on the consumer, we vary the basic nutrient loading \bar{R} , and seek the equilibrium in which all abundances are stationary and behaviors are optimal. Denoting the equilibrium point R^*, C^*, P^* as a function of a varying carrying capacity \bar{R} by $(R^*, C^*, P^*)(\bar{R})$, we define:

$$G_{E,c}^*(\bar{R}) = G_c(\tau_c^N(R^*, C^*, P^*), \tau_p^N(R^*, C^*, P^*), R^*(\bar{R}), C^*(\bar{R}), P^*(\bar{R})). \quad (13)$$

The emergent equilibrium consumption rate for a predator is defined in the same terms as a function of the carrying capacity. As the behavior is expected to change due to top-down pressure, we define analogous equilibrium consumption rates for varying top-predation $G_{E,c}^*(\xi)$ and $G_{E,p}^*(\xi)$. The question is how the classical functional responses, given in our notation as $(G_c(1, 1, R), G_p(1, 1, C))$, the equilibrium consumption rate, and the emergent functional responses differ.

2.4. Model parameters and symbols

We parameterize the system by assuming that size-specific constants scale metabolically with mass in accordance with Kleiber's law (Yodzis and Innes, 1992); see table 1.

With the metabolic scaling introduced, the model Equation (1) can be rewritten in terms of half-saturation α/β and consumer-specific mass (See Ap-

Table 2: Numerical value of model parameters used in the sensitivity analysis, simulation and exploration of the relationship between the Type II and Type III functional response.

Symbol	Value	Meaning
α	$1.25 m_c^{1/4}/\text{month}$	Max growth
s	100	Predator:prey mass ratio
b	$27.5 m_c^{1/4} m^3/\text{month}$	Clearance rate coefficient
v	0.07	Ratio between max growth and respiration
\bar{R}	$0.5 m_c \cdot m^{-3}$ (simulation), $1 m_c \cdot m^{-3}$ (sensitivity),	Carrying capacity
λ	0.1/month	Replacement rate
ε	0.3	Efficiency
ξ	1.8 month^{-1} (simulation), 4.8 month^{-1} (sensitivity)	Top-predation rate

pendix B: Metabolic model) as:

$$\dot{R} = \lambda(\bar{R} - R) - \frac{\alpha\tau_c CR}{\tau_c R + \alpha/b} \quad (14)$$

$$\dot{C} = C \left(\varepsilon \frac{\alpha\tau_c R}{\tau_c R + \alpha/b} - \frac{\alpha s^{3/4} \tau_c \tau_p P}{\tau_p \tau_c C + \alpha/b} - v\alpha \right) \quad (15)$$

$$\dot{P} = P \left(\varepsilon \frac{\alpha s^{3/4} \tau_c \tau_p C}{\tau_c \tau_p C + \alpha/b} - v\alpha s^{3/4} - \xi_p \tau_p^2 \right). \quad (16)$$

A predator is usually about 100 times larger than its preferred food-source (Trebilco et al., 2013) giving a predator:prey mass ratio of $s = 100$. We model an aquatic ecosystem, with the values in Table 2, taken from [Table 2.2](Andersen, 2019) with the consumer fish modeled as an anchovy with a mean wet mass of 10 g (Roe Hunter and Leon, 1981). The main impact of this choice is choosing the time-scale.

We summarize the symbols referring to states and specific functions used throughout the paper in Table 3.

2.5. Numerical methods

The Nash equilibrium of the inner game is found with a complementarity-based approach for finding the Nash equilibrium, (Friesz, 2010, Chapter 5). This is implemented as a feasibility problem using IPOPT (Wächter and Biegler, 2006) with the HSL libraries (HSL, 2007) through the framework CasADi (Andersson et al., 2019). In order to perform sensitivity analysis we use a gradient-based continuation method in the state variables, with a fallback to a first-order approximation of the state variable if the continuation fails. This approach is robust, as long as the step size is kept small enough.

3. Results

We analyze the system on three levels: the individual level functional response, the population/ecosystem dynamics, and the ecosystem functions.

Table 3: Summary of notational convention, state variables, symbols and functions used throughout the paper.

Symbol	Meaning
R	Resource concentration
C	Consumer concentration
P	Predator concentration
R^*	Resource concentration at equilibrium
C^*	Consumer concentration at equilibrium
P^*	Predator concentration at equilibrium
G_i	$i \in \{c, p\}$ consumer or predator per capita growth rate.
M_i	$i \in \{c, p\}$ resource, consumer or predator per capita mortality.
$G_{E,i}$	Emergent per capita consumption rate.
$G_{E,i}^*$	Emergent equilibrium per capita consumption rate.
τ_i	$i \in \{c, p\}$ consumer or predator individual strategy.
$\bar{\tau}_i$	$i \in \{c, p\}$ consumer or predator average strategy.
NE	Denotes the Nash equilibrium.
*	Denotes the optimum.

The dynamics of the tri-trophic chain differ markedly between the fixed and optimal behavior (Figure 2). Most striking is how the adaptive behavior stabilizes the system. Early in the simulation, where the population sizes vary the most, the behavior is constantly being adjusted. The system was found to be stable in the range of parameters explored in this study, but no Lyapunov function could be found to show this analytically as in the Lotka-Volterra case (Křivan, 2007).

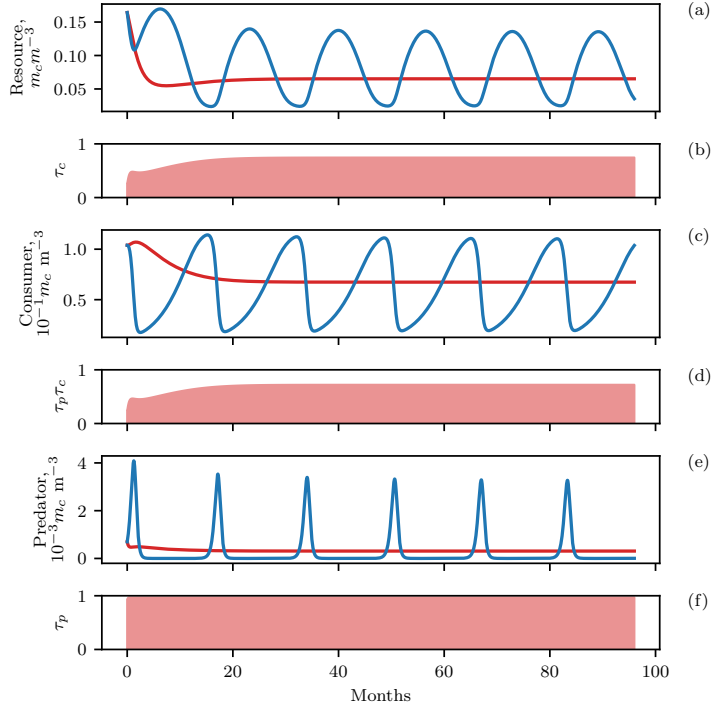


Figure 2: Population dynamics (a, c, e) and behavior (b, d, f) in the system with optimal behavior (red) compared to the system with static (no) behavior (blue). The carrying capacity \bar{R} is $0.5 m_c \cdot m^{-3}$ and the maximal predation pressure ξ is 1.8 month^{-1} .

3.1. Emergent functional responses

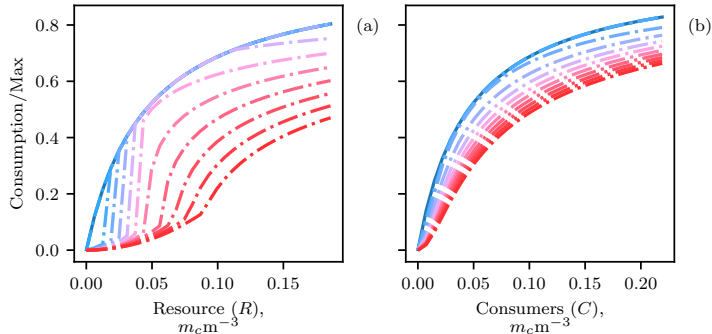


Figure 3: Emergent functional responses, Equation (12), (dash-dotted lines) compared with static functional responses (full blue) for the consumer, $G_{E,c}(C)/a_c$ and $G_c(1,1,C)/a_c$ (a); and the predator $G_{E,p}(R)/a_p$ and $G_p(1,1,R)/a_p$ (b). In (a) we vary the predator population level, from 0 (blue) to $0.16 m_c m^{-3}$ (red) with a fixed top-predation pressure ξ of 1.6 month^{-1} . In (b) we vary the top predation ξ from 0 (dotted blue line) to $15 m_c \text{ month}^{-1}$ (dotted red) with a fixed resource population of $0.1 m_c m^{-3}$. The transition between no threat and the maximal threat level is indicated by a transition from blue via purple to red in both (a) and (b).

The emergent functional responses differ from classical functional responses (Figure 3). We see a continuous transition between prototypical Type III and Type II functional responses for the consumer (Figure 3(a)), emerging from the instantaneous game between predator and consumer. We use the term “fear-based” for this emergence of a type III response, because the consumers respond to increased predator concentration by using the refuge and thereby reducing their intake. Without any predators, we recreate the expected Type II functional response. Notice that some of the curves follow the Type II curve for intermediate resource levels. In this region, the consumer strategy at the Nash equilibrium is at the boundary ($\tau_c = 1$) where consumers are fully active. In contrast, at low resource levels consumers reduce time in the arena as the reward does not justify the risk, while at high resource levels they reduce time in the arena since they can do so without reducing uptake much due to satiation.

The predators also have an emergent Type III functional response (Figure 3(b)), where the slope varies continuously with the maximum predation pressure. Since the Type III-type functional response appears even with no top-predation (Figure 3(b, dotted blue line)) where $\tau_p = 1$, it is also driven by the behavior of the consumers, and does not emerge solely from the predators ‘fear-response’. Instead, the curve reflects that the consumers also increase their time in the arena as their population increases, when the risk to the individual consumer decreases. The phenomenon is clearest at low consumer numbers

where the predator consumption rate does not vary with top-predation pressures (Figure 3(b, full red line, (0-0.05)). In this interval, low consumer numbers driving low a time in the arena for the consumers is the main determining factor.

3.2. Behavior and population levels under top-down and bottom-up forcing

We explore the system response to bottom-up and top-down forcing by varying the carrying capacity of the resource and the maximal risk of predation from top predators (Figure 4) by determining the equilibrium for each parameter value.

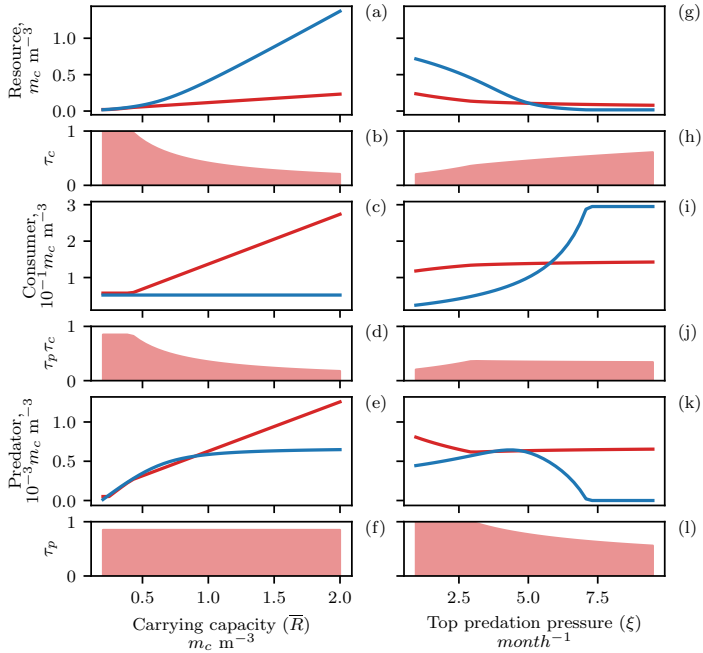


Figure 4: (a-f) Response of the system to bottom-up forcing at the fixed-point under optimal behavior (red lines) and static behavior (blue lines), changing the carrying capacity of the resource while fixing the top predation pressure ξ at 4.8 month^{-1} . (g-l) Response to top-down forcing with color code as before, changing the predation pressure on the predator while fixing the carrying capacity of the resource at $R = 1 m_c m^{-3}$.

Under varying bottom-up forcing the population levels are similar in the static and optimal models until the resources' carrying capacity is above $0.4 m_c m^{-3}$ (Figure 4(a)). Up to this point the predator exerts top-down control on the consumer and keeps its population constant, independent of resource carrying capacity.

Increasing the carrying capacity beyond $0.4 m_c m^{-3}$ changes the trade-off between risk and reward for the consumer towards favoring staying in the refuge. This means that the consumer's consumption stops increasing with the resource productivity (Figure 4(a)). The reduction in time in the arena – and the accompanying reduced predation – makes it possible for the consumer to increase its population in concert with the increase in resource productivity. The predators face a consumer who is less active in the arena (Figure 4(b)). However, the lower availability is more than compensated by the increased consumer population, leading to a constant predator time in the arena (Figure 4(f)). The predator is therefore also able to increase its population. Beyond a carrying capacity of $0.4 m_c m^{-3}$ we therefore have bottom-up control of all populations in the ecosystem. In contrast, in the static case, the top-predator effectively controls the populations of both consumer and predator, and only the resource responds to the bottom-up forcing.

Increasing predation pressure on the predator decreases the time in the arena of the predator (Figure 4(l)), and the resulting decreased predator population causes an increase in consumer time in the arena, (Figure 4(h)). In (Figure 4(l,h)) the time in the arena move in counterpoint. Comparing the trophic-effects of this movement to the model with static behavior, Figure 4(g, i, k), this behavioral dynamic serves to lessen the strength of the trophic cascade from top-down control. Summing up, optimal behavior lets the predators behave more cautiously and the consumers to act more adventurously resulting in resilience from top-down pressure.

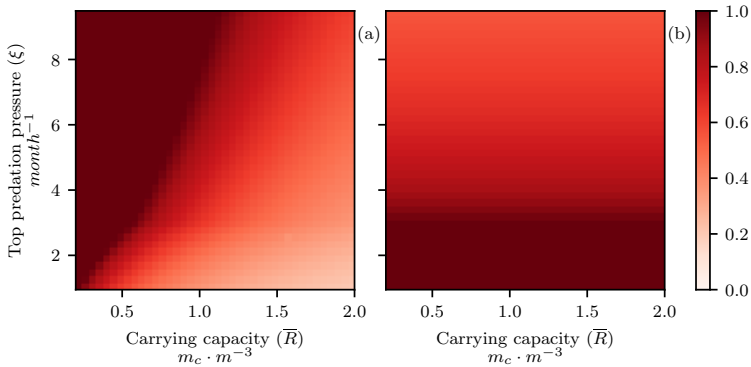


Figure 5: Time in the arena of consumers (τ_c) (a) and predators (τ_p)(b) with varying carrying capacity and top-predation rate and all other parameters kept constant.

Figure 5 shows the time in the arena of consumers and predators at equilibrium for different combinations of carrying capacity \bar{R} and top predation pressure ξ . (For comparison, Figure 4 only varied one parameter at a time). Figure 5 confirms that it is a general pattern that predator time in the arena only decreases due to top-down forcing (Figure 5(b)), while consumer time in the arena (Figure 5(a)) increases from top-down forcing and decreases from bottom-up forcing. This pattern, which was also suggested by Figure 4, appears to be general across parameter space.

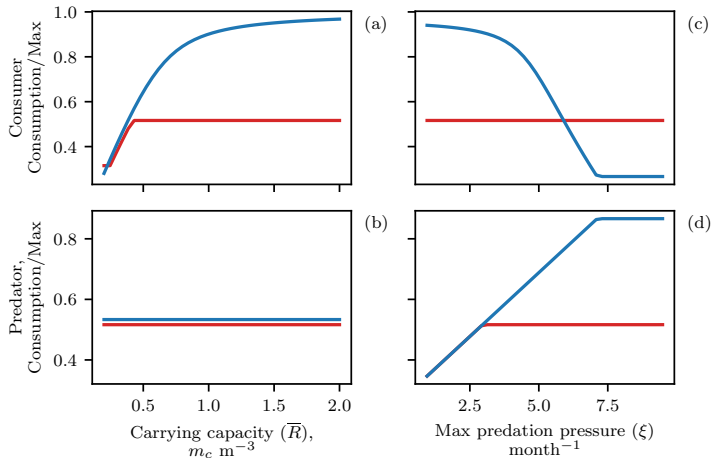


Figure 6: Consumption rates at equilibrium (R^*, C^*, P^*), for predators and consumers with optimal behavior or static behavior with the equilibrium functional responses (Equation (13)) for consumers (a,c) and predators (b,d) as a function of bottom-up (a,b). and top-down forcing (c,d). We use the color code of Figure 4.

Since the fundamental change in the model is the trade-off between risk and satiation that has been introduced from modifying the Type II functional responses, the behavioral phenomena at equilibrium in (Figure 4) may be interpreted as arising from the equilibrium consumption rate levels (Equation (13)) in the model.

Under an increasing carrying capacity with optimal behavior, the consumption rate of the consumers corresponds to a Type II functional response with a lower individual satiation point (Figure 6(a)). The predators again follow the static model, but also have a consumption rate corresponding to a lower satiation (Figure 6(b)). This is quite surprising in light of the change in consumer time in the arena, (Figure 4(b)), and shows that the change is exactly balanced with the increase in consumer population (Figure 4(c)).

When the top-predation pressure is increased, the per capita consumption rate of the predators with and without optimal behavior initially follow the same curve (Figure 6(d)), but the decrease in predator time in the arena (Figure 4(l)) causes a lower maximum. It is a departure from models with only an adaptive consumer (Abrams and Vos, 2003), and indistinguishable from the static paradigm (Oksanen et al., 1981). Without optimal behavior, an increasing consumer population (Figure 4(i),blue) causes the per capita consumption to decrease. Though the consumer time in the arena increases (Figure 4(h)), this causes constant satiation (Figure 6(c,red)). The model appears to have

constant satiation as the underlying property. When the predator time in the arena decreases, the consumer time in the arena increases just enough to keep the predator and consumer satiation constant.

4. Discussion

We have explored the effects of resolving dynamic optimal behavior on population dynamics and behavior in a tri-trophic chain model. The model reveals important differences in population structure and ecosystem function compared to classic models, without fast co-adaptive behavioral responses. The model we consider is one where both consumers and predators optimize, rather than only allowing one trophic level to optimize (Abrams, 1984; Krivan, 2013; Abrams, 2010). This simultaneous time-optimization is implemented by letting both consumers and predators play the field, in the framework of (Vincent and Brown, 2005). The behavioral adaptation makes the system more resilient towards top-down forcing. An increase in populations across all trophic levels was seen under bottom-up pressure. We found that a constant equilibrium consumption rate appears to be the underlying driver of the ecosystem changes. Finally, we have shown that type III functional responses appear as an emergent phenomena for consumers and predators when playing an instantaneous behavioral game.

4.1. Ecosystem response to forcing

Behavior almost entirely absorbs the top-down trophic forcing at each trophic level. In effect, the populations in the system with optimal behavior are almost unaffected by top-down forcing. With static behavior when the top predation pressure is increased, the consumer population grows and the resource population declines (Abrams and Roth, 1994b) while the predator population initially increases before declining to extinction, a so-called hydra effect (Abrams, 2009b). When only the consumers are adaptive the effect of predator mortality is controlled by the response of the consumer (Abrams and Vos, 2003; Abrams, 2009a), and also eventually leads to extinction. In contrast, we see a resilience of the abundances to top-down forcing, and the removal of the hydra-effect. The resilience at all levels is unexpected, as an increase in consumer populations and a distinct change in predator populations was expected (Abrams, 1992b). The non-linear community effects from each individual playing the field are the probable cause of this change, as decreasing the time in the arena for an individual predator does not change its fitness much due to the Type II response while it drastically reduces the loss from top-predation.

It is commonly observed in nature that top-down forcing changes the behavior of the middle species in tri-trophic chains (Heath et al., 2014; Pace et al., 1999; Schmitz et al., 2008). We elaborate on this phenomenon (Abrams and Vos, 2003), as the emergent behavior of the adaptive predator foraging varies counter to the consumer. Density dependence of predator foraging is known to buffer the effect of top-down forcing, (Heath et al., 2014; Schmitz et al., 2004; Abrams, 1992b) e.g. through evolution (Loeuille and Loreau, 2004). Our

model provides a direct behavioral explanation for this damping, instead of a directly introduced density dependence (Heath et al., 2014). Rather than simply damping the population effect of top-down forcing, including optimal behavior through assuming that both consumers and predators play the field seems to eliminate the population effect of top-down forcing entirely, an indirect density-dependence which is hard to model explicitly (Heath et al., 2014). Thus flexible behavior allows greater resilience than evolutionary changes (Loeuille and Loreau, 2004).

When considering bottom-up forcing, all three trophic levels increase their population sizes. The behavior of the predators is constant, while the consumers reduce their time in the arena from the increased availability of resources. These results correspond to the four-trophic model in Abrams (1992b) and the tri-trophic model in Abrams and Roth (1994a).

4.2. Consumption rates

Varying the threat level and keeping all other variables constant reveals a clear risk-sensitivity in the emergent functional response for the consumers, following a classical Type II curve when there is no threat, transitioning to a Type III curve when the threat is high. Previously, a Type III response has been shown to emerge from optimal consumer behavior when predators have static behavior (Abrams, 1982, 1990; Beckerman, 2005; Krivan, 2013; Geritz and Gyllenberg, 2014; Kiørboe et al., 2018), but the addition of risk-averse predators could have attenuated this emergence. Instead, we see that the risk-avoidance of the consumers still drives a Type III response. The situation for the predators is more interesting, as the functional response of adaptive predators preying on adaptive consumers has not been investigated in an as in-depth way. Here, the consumers decrease their time in the arena when the predators increased theirs at low population levels in accordance with predictions (Abrams, 1984) leading to a Type III curve. At higher consumer population levels density-dependent effects, essentially safety in numbers, outweigh the consumer caution, so the continuous transition between the Type II and Type III curves appears as for the consumers. These results reveal that a Type III response of a predator can appear from the predator avoidance of the prey in a behavioral game, rather than being due to an avoidance strategy of the predator itself. The emergence of the Type III curve from a Type II curve is thus a general phenomenon, which also appears when the predators are dynamic. The underlying mechanism for the emergent Type III curve in our model is the trade-off between risk-willingness and foraging, where the gain in foraging becomes less and less due to the satiation inherent in the modified Type II functional response. Satiation versus risk then provides a mechanism which can be tested empirically to assess our model (Gliwicz and Maszczyk, 2007; van Someren Greve et al., 2019).

The fear of predation causes a new equilibrium where the consumption rate is constant across changing environmental conditions, and much lower than expected purely from digestion. Instead of striving for full satiation, there appears to be a constant level of good-enough partial satiation for both consumers and predators. This result is in accordance with results for bottom-up pressure

in single-actor models (Kjørboe et al., 2018). Though the foraging intensity for a consumer increases with top-down pressure and decreases with top-down pressure, the consumption rate stays the same, hence our model illuminates the complicated relationships that can arise when multiple species optimize simultaneously, beyond those considered in Abrams (1992b). The emergence of a constant partial satiation for both predators and consumers with increasing top-predation is surprising, but this maintenance of a constant partial satiation appears to explain the changes in both populations and behavior at the equilibrium. Such partial satiation levels are observed empirically in zooplankton, van Someren Greve et al. (2019), and in fish where stomach content analysis have shown that fish rarely have full stomachs (Armstrong and Schindler, 2011). These observations could be a sign of behavioral adaptation of lower feeding to avoid predation and are in accordance with the good-enough partial satiation emerging from our model.

4.3. Model choices

The parameterization of our model represents a generic aquatic ecosystem with scaling described by metabolic scaling (Yodzis and Innes, 1992). The value for the top-predation and the carrying capacity represent the only free parameters in the model. A tri-trophic food chain with a chemostat can exhibit chaotic behavior (Hastings and Powell, 1991). Chaos is impossible in our model, as it would appear for large values of ε_b^a (Hastings and Powell, 1991), which is constant for our model scaled through Kleibers' law (Yodzis and Innes, 1992). We do not consider imperfect refuges, implemented e.g. through vigilance Malone et al. (2020). An imperfect refuge corresponds to fixing a minimal constant value of τ in our model, and would lead to a greater time spent in the refuge compared to what we find. Including imperfect refuges would therefore only serve to restrict the possibilities that can be explored with the model. We do not consider the evolutionary time-scale, where other traits than refuge use can be modified. Our model could be incorporated in such a model, having a fast time-scale with instantaneous optimization, a medium time-scale of population dynamics, and a slow time-scale of evolution. It is hard to predict what would happen in such a model Abrams and Roth (1994b). Implementing our approach in a more complicated food-web with multiple predators or prey types as e.g. Abrams (1992b); Stump and Chesson (2017) would be interesting, as the numerical approach appears scalable to realistic models rather than only concerning itself with toy models.

4.4. Behavior and games

We model behavior by an instantaneous individual optimization, where the objective is given by the growth of an individual with a modified Type II functional response. This reflects an underlying reality of a migration or activity switch that is much faster than the population dynamics. If not for this fast-slow dynamic, we would need to incorporate explicit migration mechanisms in

our model (Abrams et al., 2007; Ma et al., 2003; Abrams, 2007). Our game-theoretic approach is to treat a population game as playing the field (Broom and Rychtár, 2013; Parker, 1978).

The approach of playing the field has a number of advantages compared to assuming a monomorphic population. Assuming that each individual optimizes their per capita growth in a monomorphic population is fundamentally problematic, as the optimization ceases to be at an individual level since an individual can take the behavior of the rest of the population into account (Abrams et al., 1993). Hence modeling monomorphic populations causes them to take much better decisions at the population level than they would otherwise (Křivan et al., 2008; Abrams et al., 1993). As such in many situations models of population dynamics with individual behavior should be based on playing the field, rather than assuming monomorphic decision makers.

Modeling our game as individuals playing the field keeps the optimization problem at an individual level while possibly allowing for non-linear and density-dependent effects (Vincent and Brown, 2005), such as satiation (Křivan and Eisner, 2006). Incorporating satiation in the fitness proxy causes a non-linearity in the inner game of the model, and is well supported empirically as a factor in behavioral choice (Schadegg and Herberholz, 2017). By assuming that individuals play the field we can model behavior taking satiation of both consumers and predators into account simultaneously without assuming populations of monomorphic individuals. By taking satiation into account, the transition between full presence in the refuge and arena becomes continuous in the state of the system. Using or linear functional responses lead to instantaneous switching in animal preferences, and to discontinuities in population dynamics (Křivan and Schmitz, 2003; Křivan, 2007). The existence of this discontinuity has caused debate about ecosystem models with instantaneous behavior (Abrams, 2010). Attempts at removing this discontinuity have involved attempts at smoothing the transition post-hoc (Fryxell and Lundberg, 1994; Van Baalen et al., 2001). By modeling the system as a game with individuals playing the field with non-linearities in their fitness proxies the continuous habitat transition arises naturally.

The choice of modeling the game as an instantaneous non-linear game where each individual plays the field comes at a cost: We do not have an analytical expression for the Nash equilibrium, as can be found when the fitness proxy is linear (Křivan and Cressman, 2009). In a similar vein, it is infeasible to find an analytical expression for the current state in population games with migrations (Abrams, 2007). An advantage of our approach is that it allows us to handle individual behavior conditioned on non-linear choices, and it fulfills this niche perfectly. There are, however, situations where the game-theoretic approach we advocate is not suitable. We have already mentioned migration games where the migrations and population dynamics happen on the same time-scale as unsuitable for our approach. Another setting where instantaneous optimality is unsuitable is modeling evolution. For instance, slowly changing traits on the evolutionary time-scale can lead to counter-intuitive results such as vigilance evolving into extinction (Matsuda and Abrams, 1994) which is the opposite of

our result. This highlights that the relative time-scales need to be considered before choosing a model with instantaneous optimization. Generally, however, behavior and population dynamics are often on decoupled time-scales (Krivan, 2013). When this decoupling occurs, incorporating behavior as an instantaneous game is a valuable tool and our approach can be used to find complex emergent phenomena.

5. Conclusion

Ecosystem models that include fast behavioral adaptations often neglect non-linear effects on behavior, or only consider a single type of animal. By incorporating the behavior of both predators and consumers, we arrive at a unified model which has explanatory power both at the ecosystem and the individual level. Adding individual behavior taking non-linear tradeoffs into account for both consumers and predators gives rise to complex emergent phenomena. The emergent phenomena expand on results from ecosystems with single-actor optimization, showing the importance of considering the behavior of more than one trophic level.

Declarations

Funding

This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

Code availability

All code for reproducing the results of this project is available on github https://github.com/jemff/predator_preymodel.

Conflict of interest

The authors declare that they have no conflict of interest.

Authors' contributions

E.F.F., U.H.T. and K.H.A. designed the study. E.F.F. realized the model design with help from U.H.T. and K.H.A. E.F.F. coded the model and chose the numerical approaches. E.F.F. analyzed the results with the assistance of U.H.T and K.H.A. E.F.F. wrote the paper with contributions from all authors. All authors read and approved the final version.

Data availability

All data can be generated using the file plots.py from the git repository https://github.com/jemff/predator_preymodel.

References

- Abrams, P.A., 1982. Functional responses of optimal foragers. *The American Naturalist* 120, 382–390.
- Abrams, P.A., 1984. Foraging time optimization and interactions in food webs. *The American Naturalist* 124, 80–96.
- Abrams, P.A., 1990. The effects of adaptive behavior on the type-2 functional response. *Ecology* 71, 877–885.
- Abrams, P.A., 1992a. Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology* 6, 56–72.
- Abrams, P.A., 1992b. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *The American Naturalist* 140, 573–600.
- Abrams, P.A., 2004. Trait-initiated indirect effects due to changes in consumption rates in simple food webs. *Ecology* 85, 1029–1038.
- Abrams, P.A., 2007. Habitat choice in predator-prey systems: spatial instability due to interacting adaptive movements. *The American Naturalist* 169, 581–594.
- Abrams, P.A., 2009a. Adaptive changes in prey vulnerability shape the response of predator populations to mortality. *Journal of theoretical biology* 261, 294–304.
- Abrams, P.A., 2009b. When does greater mortality increase population size? the long history and diverse mechanisms underlying the hydra effect. *Ecology letters* 12, 462–474.
- Abrams, P.A., 2010. Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology* 24, 7–17.
- Abrams, P.A., Cressman, R., Krivan, V., 2007. The role of behavioral dynamics in determining the patch distributions of interacting species. *The American Naturalist* 169, 505–518.
- Abrams, P.A., Matsuda, H., Harada, Y., 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evolutionary Ecology* 7, 465–487.
- Abrams, P.A., Roth, J., 1994a. The responses of unstable food chains to enrichment. *Evolutionary Ecology* 8, 150–171.
- Abrams, P.A., Roth, J.D., 1994b. The effects of enrichment of three-species food chains with nonlinear functional responses. *Ecology* 75, 1118–1130.

- Abrams, P.A., Vos, M., 2003. Adaptation, density dependence and the responses of trophic level abundances to mortality. *Evolutionary Ecology Research* 5, 1113–1132.
- Andersen, K.H., 2019. *Fish Ecology, Evolution, and Exploitation: A New Theoretical Synthesis*. Princeton University Press.
- Andersson, J.A.E., Gillis, J., Horn, G., Rawlings, J.B., Diehl, M., 2019. CasADi – A software framework for nonlinear optimization and optimal control. *Mathematical Programming Computation* 11, 1–36. doi:10.1007/s12532-018-0139-4.
- Arditi, R., Ginzburg, L.R., 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of theoretical biology* 139, 311–326.
- Armstrong, J.B., Schindler, D.E., 2011. Excess digestive capacity in predators reflects a life of feast and famine. *Nature* 476, 84–87.
- Aumann, R.J., 1964. Markets with a continuum of traders. *Econometrica: Journal of the Econometric Society* , 39–50.
- Barbosa, P., Castellanos, I., 2005. *Ecology of predator-prey interactions*. Oxford University Press.
- Beckerman, A.P., 2005. The shape of things eaten: the functional response of herbivores foraging adaptively. *Oikos* 110, 591–601.
- Biro, P.A., Post, J.R., Abrahams, M.V., 2005. Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts. *Proceedings of the Royal Society B: Biological Sciences* 272, 1443–1448.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G., Harrison, A.L., et al., 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–90.
- Broom, M., Rychtár, J., 2013. *Game-theoretical models in biology*. CRC Press.
- Cressman, R., Krivan, V., Garay, J., 2004. Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *The American Naturalist* 164, 473–489.
- DeAngelis, D.L., Goldstein, R., O'Neill, R.V., 1975. A model for trophic interaction. *Ecology* 56, 881–892.
- Fretwell, S.D., 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica* 19, 45–52.
- Friesz, T.L., 2010. *Dynamic optimization and differential games*. volume 135. Springer Science & Business Media.

- Fryxell, J.M., Lundberg, P., 1994. Diet choice and predator-prey dynamics. *Evolutionary Ecology* 8, 407–421.
- Furey, N.B., Armstrong, J.B., Beauchamp, D.A., Hinch, S.G., 2018. Migratory coupling between predators and prey. *Nature ecology & evolution* 2, 1846–1853.
- Gause, G.F., et al., 1934. Experimental analysis of vito volterras mathematical theory of the struggle for existence. *Science* 79, 16–17.
- Genkai-Kato, M., 2007. Macrophyte refuges, prey behaviour and trophic interactions: consequences for lake water clarity. *Ecology Letters* 10, 105–114.
- Geritz, S.A., Gyllenberg, M., 2014. The deangelis–beddington functional response and the evolution of timidity of the prey. *Journal of theoretical biology* 359, 37–44.
- Giske, J., Salvanes, A.G.V., 1995. Why pelagic planktivores should be unselective feeders. *Journal of theoretical Biology* 173, 41–50.
- Gliwicz, Z., Maszczyk, P., 2007. Daphnia growth is hindered by chemical information on predation risk at high but not at low food levels. *Oecologia* 150, 706–715.
- Hadjisavvas, N., Komlósi, S., Schaible, S.S., 2006. Handbook of generalized convexity and generalized monotonicity. volume 76. Springer Science & Business Media.
- Hairton, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *The american naturalist* 94, 421–425.
- Hastings, A., Powell, T., 1991. Chaos in a three-species food chain. *Ecology* 72, 896–903.
- Heath, M.R., Speirs, D.C., Steele, J.H., 2014. Understanding patterns and processes in models of trophic cascades. *Ecology letters* 17, 101–114.
- Houston, A.I., McNamara, J.M., et al., 1999. Models of adaptive behaviour: an approach based on state. Cambridge University Press.
- HSL, A., 2007. A collection of fortran codes for large-scale scientific computation. See <http://www.hsl.rl.ac.uk>.
- Iwasa, Y., 1982. Vertical migration of zooplankton: a game between predator and prey. *The American Naturalist* 120, 171–180.
- Jeschke, J.M., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological monographs* 72, 95–112.

- Karamardian, S., Schaible, S., Crouzeix, J., 1993. Characterizations of generalized monotone maps. *Journal of Optimization Theory and Applications* 76, 399–413.
- Kjørboe, T., Saiz, E., Tiselius, P., Andersen, K.H., 2018. Adaptive feeding behavior and functional responses in zooplankton. *Limnology and Oceanography* 63, 308–321.
- Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299, 1388–1391.
- Křivan, V., 2007. The lotka-volterra predator-prey model with foraging–predation risk trade-offs. *The American Naturalist* 170, 771–782.
- Křivan, V., 2013. Behavioral refuges and predator–prey coexistence. *Journal of Theoretical Biology* 339, 112–121.
- Křivan, V., Cressman, R., 2009. On evolutionary stability in predator–prey models with fast behavioural dynamics. *Evolutionary Ecology Research* 11, 227–251.
- Křivan, V., Cressman, R., Schneider, C., 2008. The ideal free distribution: a review and synthesis of the game-theoretic perspective. *Theoretical population biology* 73, 403–425.
- Křivan, V., Eisner, J., 2006. The effect of the holling type ii functional response on apparent competition. *Theoretical Population Biology* 70, 421–430.
- Křivan, V., Schmitz, O.J., 2003. Adaptive foraging and flexible food web topology. *Evolutionary Ecology Research* 5, 623–652.
- Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the” landscape of fear” in yellowstone national park, usa. *Canadian Journal of Zoology* 79, 1401–1409.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian journal of zoology* 68, 619–640.
- Loeuille, N., Loreau, M., 2004. Nutrient enrichment and food chains: can evolution buffer top-down control? *Theoretical population biology* 65, 285–298.
- Ma, B.O., Abrams, P.A., Brassil, C.E., 2003. Dynamic versus instantaneous models of diet choice. *The American Naturalist* 162, 668–684.
- Malone, M.A., Halloway, A.H., Brown, J.S., 2020. The ecology of fear and inverted biomass pyramids. *Oikos* 129, 787–798.
- Matsuda, H., Abrams, P.A., 1994. Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theoretical Population Biology* 45, 76–91.

- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge university press.
- McNamara, J.M., Houston, A.I., 1992. Risk-sensitive foraging: a review of the theory. *Bulletin of mathematical biology* 54, 355–378.
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* 118, 240–261.
- Oksanen, L., Oksanen, T., 2000. The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist* 155, 703–723.
- Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution* 14, 483–488.
- Parker, G.A., 1978. Searching for mates. *Behavioural ecology: an evolutionary approach* 1, 214–244.
- Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., Orrock, J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J., et al., 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* 89, 2416–2425.
- Pinti, J., Andersen, K.H., Visser, A.W., 2021. Co-adaptive behavior of interacting populations in a habitat selection game significantly impacts ecosystem functions. *Journal of Theoretical Biology* 523, 110663.
- Pinti, J., Kjørboe, T., Thygesen, U.H., Visser, A.W., 2019. Trophic interactions drive the emergence of diel vertical migration patterns: a game-theoretic model of copepod communities. *Proceedings of the Royal Society B* 286, 20191645.
- Přibyllová, L., Berc, L., 2015. Predator interference and stability of predator–prey dynamics. *Journal of mathematical biology* 71, 301–323.
- Prowe, A.F., Pahlow, M., Dutkiewicz, S., Follows, M., Oschlies, A., 2012. Top-down control of marine phytoplankton diversity in a global ecosystem model. *Progress in Oceanography* 101, 1–13.
- Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54, 755–766.
- Roe Hunter, J., Leon, R., 1981. The spawning energetics of female northern anchovy, *engraulis mordax*. *fishery bulletin* 9.
- Schadegg, A.C., Herberholz, J., 2017. Satiation level affects anti-predatory decisions in foraging juvenile crayfish. *Journal of Comparative Physiology A* 203, 223–232.

- Schmitz, O.J., Grabowski, J.H., Peckarsky, B.L., Preisser, E.L., Trussell, G.C., Vonesh, J.R., 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology* 89, 2436–2445.
- Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: The primacy of trait-mediated indirect interactions.
- Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16, 269–311.
- van Someren Greve, H., Kiørboe, T., Almeda, R., 2019. Bottom-up behaviourally mediated trophic cascades in plankton food webs. *Proceedings of the Royal Society B* 286, 20181664.
- Stump, S.M., Chesson, P., 2017. How optimally foraging predators promote prey coexistence in a variable environment. *Theoretical Population Biology* 114, 40–58.
- Suhonen, J., 1993. Predation risk influences the use of foraging sites by tits. *Ecology* 74, 1197–1203.
- Sutton, T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *Journal of fish biology* 83, 1508–1527.
- Thygesen, U.H., Sommer, L., Evans, K., Patterson, T.A., 2016. Dynamic optimal foraging theory explains vertical migrations of bigeye tuna. *Ecology* 97, 1852–1861.
- Trebilco, R., Baum, J.K., Salomon, A.K., Dulvy, N.K., 2013. Ecosystem ecology: size-based constraints on the pyramids of life. *Trends in ecology & evolution* 28, 423–431.
- Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P., Dunne, J.A., 2010. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology letters* 13, 1546–1559.
- Van Baalen, M., Krivan, V., van Rijn, P.C., Sabelis, M.W., 2001. Alternative food, switching predators, and the persistence of predator-prey systems. *The American Naturalist* 157, 512–524.
- Vincent, T.L., Brown, J.S., 2005. *Evolutionary game theory, natural selection, and Darwinian dynamics*. Cambridge University Press.
- Wächter, A., Biegler, L.T., 2006. On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. *Mathematical programming* 106, 25–57.
- Werner, E.E., Anholt, B.R., 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist* 142, 242–272.

Wollrab, S., Diehl, S., 2015. Bottom-up responses of the lower oceanic food web are sensitive to copepod mortality and feeding behavior. *Limnology and Oceanography* 60, 641–656.

Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. *The American Naturalist* 139, 1151–1175.

Appendix A: Uniqueness of the Nash equilibrium

We start by defining the notion of strict pseudomonotonicity:

Definition 1. A function $f : K \rightarrow \mathbb{R}^n$ from a convex set $K \subset \mathbb{R}^n$ is strictly pseudomonotone if for every pair $x \neq y$ we have

$$\langle x - y, f(y) \rangle \geq 0 \Rightarrow \langle x - y, f(x) \rangle > 0 \quad (.1)$$

For a tractable criterion for a unique Nash equilibrium, we use the following proposition Hadjisavvas et al. (2006, P. 580, Proposition 13.8):

Proposition 1. *A game with payoff functions U_1 and U_2 and strategies σ_1, σ_2 defined on a convex set K has a unique Nash equilibrium if the function $(d_{\sigma_1}U_1, d_{\sigma_2}U_2)$ is strictly pseudomonotone as a function of (σ_1, σ_2) .*

Defining $f_1 = -d_{\tau_c}F_c |_{\bar{\tau}_c=\tau_c}$ and $f_2 = -d_{\tau_p}F_p |_{\bar{\tau}_p=\tau_p}$, to show that the Nash equilibrium Equation (11) is unique, it suffices to show that the function $g = (f_1, f_2)$ is strictly pseudomonotone. For each pair $a = (x_0, x_1) \in [0, 1]^2$ and $d = (y_0, y_1) \in \mathbb{R}^2$ define the set

$$I_{ad} = \{t \in \mathbb{R} : (x_0 + ty_0, x_1 + ty_1) \in [0, 1]^2\} \quad (.2)$$

By Hadjisavvas et al. (2006, p. 95), a function $f : [0, 1]^2 \rightarrow \mathbb{R}^2$ is strictly pseudomonotone if and only if the function

$$G(t) = \langle g((x_0 + ty_0, x_1 + ty_1)), (y_0, y_1) \rangle \quad (.3)$$

is strictly pseudomonotone for $t \in I_{ad}$ for all pairs (a, d) , see (Equation (.2)). Hence to establish pseudomonotonicity we must consider the function in Equation (.3) in our context. To define this, we need to establish how an expression for g in Equation (.3). Recall that:

$$\begin{aligned} f_1(\bar{\tau}_c, \bar{\tau}_p) &= - \left(\varepsilon \frac{a_c^2 \beta_c R \bar{\tau}_c}{(\beta_c R \bar{\tau}_c + a_c)^2} \right. \\ &\quad \left. - \frac{a_p P \bar{\tau}_p}{\beta_p C \bar{\tau}_c \bar{\tau}_p + F_p} \right) \\ f_2(\bar{\tau}_c, \bar{\tau}_p) &= -\varepsilon \frac{a_p^2 \beta_p C \bar{\tau}_c}{(\beta_p C \bar{\tau}_c \bar{\tau}_p + F_p)^2} + \xi \bar{\tau}_p \end{aligned} \quad (.4)$$

Fixing a pair $a \in [0, 1]^2$, $d \in \mathbb{R}^2$, and a corresponding set I_{ad} , we get a function $g(t) : I_{ad} \rightarrow \mathbb{R}^2$ using the definition in Equation (.4):

$$\begin{aligned}
g(t) &= (f_1(x_0 + ty_0), f_2(x_1 + ty_1)) \\
&= \left(- \left(\frac{a_c^2 \beta_c R(x_0 + ty_0)}{(\beta_c R(x_0 + ty_0) + a_c)^2} \right. \right. \\
&\quad \left. \left. \frac{a_p P(x_1 + ty_1)}{\beta_p C(x_0 + ty_0)(x_1 + ty_1) + F_p} \right), \right. \\
&\quad \left. - \varepsilon \frac{a_p^2 \beta_p C(x_0 + ty_0)}{(\beta_p C(x_0 + ty_0)(x_1 + ty_1) + F_p)^2} + \xi(x_1 + ty_1) \right)
\end{aligned} \tag{.5}$$

This allows us to find an expression for $G(t)$ as in Equation (.3):

$$\begin{aligned}
G(t) &= \langle g(t), (y_0, y_1) \rangle \\
&= - \left(\frac{a_c^2 \beta_c R y_0(x_1 + ty_1)}{(\beta_c R(x_0 + ty_0) + a_c)^2} \right. \\
&\quad \left. - \frac{a_p P y_0(x_1 + ty_1)}{\beta_p C(x_0 + ty_0)(x_1 + ty_1) + F_p} \right) \\
&\quad - \left(\frac{a_p^2 \beta_p C(x_0 + ty_0) y_1}{(\beta_p C(x_0 + ty_0)(x_1 + ty_1) + F_p)^2} - \xi(x_1 + ty_1) y_1 \right)
\end{aligned} \tag{.6}$$

To simplify the analysis and streamline the notation, we define the constants:

$$\begin{aligned}
k_0 &= \varepsilon a_c^2 \beta_c R \\
k_1 &= \beta_c R \\
k_2 &= a_c \\
k_3 &= a_p x_1 P \\
k_4 &= \beta_p C \\
k_5 &= a_p \\
k_6 &= \varepsilon a_p^2 \beta_p C \\
k_7 &= \xi
\end{aligned} \tag{.7}$$

In this notation, the expression for $G(t)$ simplifies slightly

$$\begin{aligned}
G(t) &= -y_0 \frac{k_0(x_1 + ty_1)}{(k_1(x_0 + ty_0) + k_2)^2} \\
&+ y_0 \frac{k_3(x_1 + ty_1)}{(k_4(x_0 + ty_0)(x_1 + ty_1) + k_5)} \\
&- y_1 \frac{k_6(x_0 + ty_0)}{(k_4y_1(x_0 + ty_0)(x_1 + ty_1) + k_5)^2} + (x_0 + ty_0)k_8 \\
&= y_1 k_8(x_0 + tx_1) + y_0 \frac{k_3(x_1 + ty_1)}{(k_4(x_0 + ty_0) + k_5)} \\
&- y_0 \frac{k_0}{(k_1(x_0 + ty_0) + k_2)^2} \\
&- y_1 \frac{k_6(x_0 + ty_0)}{(k_7(x_0 + ty_0)(x_1 + ty_1) + k_5)^2}
\end{aligned} \tag{.8}$$

By Karamardian et al. (1993, Theorem 2.2(iii)), the function $G(t)$ is strictly pseudomonotone if it has a unique zero and $G(x) > 0$ implies that $G(y) > 0$ when $y > x$. Consider the positive and negative terms in G , separately Equation (.8). Denoting them by G_+, G_- we get:

$$\begin{aligned}
G_+(t) &= y_1 k_8(x_0 + tx_1) \\
&+ y_0 \frac{k_3(x_1 + ty_1)}{(k_4(x_0 + ty_0) + k_5)} \\
G_-(t) &= y_0 \frac{k_0}{(k_1(x_0 + ty_0) + k_2)^2} \\
&+ y_1 \frac{k_6(x_0 + ty_0)}{(k_7(x_0 + ty_0)(x_1 + ty_1) + k_5)^2}
\end{aligned} \tag{.9}$$

Clearly both have monotone first-derivatives, as they are both convex. Due to the linear growth term in G_+ , the derivative of G_+ will always asymptotically dominate the derivative of G_- , hence the value of G_+ will continue to exceed to exceed that of G_- once they have crossed. Hence the function has at most one zero. This characteristic of the derivatives also gives the sign-preservation, as once the positive linear term dominates the function $G(t)$ is always positive. Hence the function $G(t)$ is strictly pseudomonotone.

Appendix B: Metabolic model

Recall that m_c, m_p denotes the mass of a consumer and a predator respectively and the relationship between predator and consumer masses $m_p = sm_c$. As noted in the methods section, we assume that the clearance rates β_c, β_p , maximal consumption rates a_c, a_p and metabolism μ_c, μ_p scale with the mass by a factor of 0.75. With this in mind, we can write the equations describing

the population dynamics with metabolic scaling fully:

$$\begin{aligned}
\dot{R} &= \lambda(\bar{R} - R) - \frac{bm_c^{3/4}\alpha m_c^{3/4}\tau_c CR}{bm_C^{3/4}\tau_C R + \alpha m_c^{3/4}} \\
\dot{C} &= C \left(\varepsilon \frac{bm_c^{3/4}\alpha m_c^{3/4}\tau_C R}{bm_c^{3/4}\tau_c R + \alpha m_c^{3/4}} \right. \\
&\quad \left. - \frac{b(sm_1)^{3/4}\alpha(sm_1)^{3/4}\tau_c\tau_p P}{b(sm_1)^{3/4}\tau_c\tau_p C + \alpha(sm_c)^{3/4}} - v\alpha m_c^{3/4} \right) \\
\dot{P} &= P \left(\varepsilon \frac{b(sm_c)^{3/4}\alpha(sm_c)^{3/4}\tau_c\tau_p P}{b(sm_c)^{3/4}\tau_c\tau_p C + \alpha(sm_c)^{3/4}} - v\alpha(sm_c)^{3/4} - \xi_p\tau_p^2 \right)
\end{aligned}$$

In order to simplify the expression, we rephrase the above in terms of the half-saturation, β_i/a_i :

$$\begin{aligned}
\dot{R} &= \lambda(\bar{R} - R) - \frac{\alpha m_c^{3/4}\tau_c CR}{\tau_c R + \alpha/b} \\
\dot{C} &= C \left(\varepsilon \frac{\alpha m_c^{3/4}\tau_c R}{\tau_c R + \alpha/b} - \frac{\alpha(sm_c)^{3/4}\tau_c\tau_p P}{\tau_c\tau_p C + \alpha/b} - v\alpha m_c^{3/4} \right) \\
\dot{P} &= P \left(\varepsilon \frac{\alpha(sm_c)^{3/4}\tau_c\tau_p C}{\tau_c\tau_p P + \alpha/b} - v\alpha(sm_c)^{3/4} - \xi_p\tau_p^2 \right)
\end{aligned}$$

To further simplify the expression, we change into consumer-specific units of mass m_s where $m_s = 1m_C$, which allows the final expression of our population-dynamical as:

$$\begin{aligned}
\dot{R} &= \lambda(\bar{R} - R) - \frac{\alpha\tau_c CR}{\tau_c R + \alpha/b} \\
\dot{C} &= C \left(\varepsilon \frac{\alpha\tau_c R}{\tau_c R + \alpha/b} - \frac{\alpha s^{3/4}\tau_c\tau_p P}{\tau_p\tau_c C + \alpha/b} - v\alpha \right) \\
\dot{P} &= P \left(\varepsilon \frac{\alpha s^{3/4}\tau_c\tau_p P}{\tau_c\tau_p C + \alpha/b} - v\alpha s^{3/4} - \xi_p\tau_p^2 \right)
\end{aligned}$$

PAPER C

Population games with
instantaneous behavior and
the Rosenzweig-MacArthur
model

Population games with instantaneous behavior and the Rosenzweig-MacArthur model

Emil F. Frølich · Uffe H. Thygesen

Received: date / Accepted: date

Emil F. Frølich
Technical University of Denmark
Department of Applied Mathematics and Computer Science - DTU Compute
Building 303B, Matematiktorvet, Kgs. Lyngby
Tel.: +45-26142497
E-mail: jaem@dtu.dk

Uffe H. Thygesen
Technical University of Denmark
Department of Applied Mathematics and Computer Science - DTU Compute
Building 303B, Matematiktorvet, Kgs. Lyngby

Abstract How to determine the spatial distribution and population dynamics of animals are some of the key questions in ecology. These two have been coupled before, but there is no general method for determining spatial distributions based on instantaneous behavior coupled with population dynamics. We propose modeling interacting populations with instantaneous habitat choice through mean-field games. By using the framework of variational inequalities, we are able to determine existence and uniqueness for habitat distributions of interacting populations, in both continuous and discrete habitats. With some additional restrictions, we are also able to show existence and uniqueness of fixed-points of the population dynamics along with spatial distributions. We illustrate our theoretical results by studying a Rosenzweig-MacArthur model where predators and consumers inhabit a continuous habitat. This study is conducted both theoretically and numerically. Analyzing the emergent dynamics is possible as viewing the system from the vantage point of variational inequalities allows for applying efficient numerical methods. The generality of our theoretical approach opens up for studying complex ecosystems, e.g. the impact of enrichment on spatial distributions in marine ecosystems.

Keywords game theory, population dynamics, habitat choice, population game

1 Introduction

Game theory is a natural tool to model the behavior of animals, who must respond to the behavior of other animals as well as complex and rapidly shifting environments. A classical application of game-theory is patch-choice models, where the ideal free distribution emerges to explain spatial distributions of populations (Cressman et al. 2004). A game theoretical approach has been fruitful in studying habitat choice in simple ecosystems under the assumption of static populations or simplifying the habitat to a few discrete patches, (Cressman and Krivan 2010; Valdovinos et al. 2010). Real-life habitat choice consists of animals choosing where to forage in a continuous landscape, with varying intra-specific competition and external risk factors. Building models that can handle these challenges would represent a significant step forward in understanding natural systems (Morris 2003).

A population game is a system of interacting populations where each individual chooses the best strategy at every instant. Typically, this is the strategy that maximizes individual fitness. That is, population games generalize the ideal free distribution (Cressman et al. 2004). The single-species ideal free distribution is characterized by evolutionary stability, but stability in the multi-species case is more complex (Krivan et al. 2008). In the multi-species case evolutionary stability is not immediate when each animal optimizes their fitness. We refer to the ideal free distribution without stability assumptions as the simple ideal free distribution. When including behavior in population models using game-theory a common simplification is to assume that at least one payoff is linear in the choice of strategy (Krivan 1997). Linear models are sufficient to explain simple predator-prey dynamics with optimal behavior, (Krivan 2007), but non-linear effects in natural systems are substantial (Gross et al. 2009).

A general model for population games based on fitness is set out in (Vincent and Brown 2005) where optimal behavior is introduced by every population maximizing

the per capita growth at every instant. This implicitly assumes monomorphic populations, where all individuals intrinsically act as one (Malone et al. 2020; Stump and Chesson 2017). The assumption of monomorphic populations is the typical approach to population games with instantaneous migrations (Křivan 2013; Vincent and Brown 2005), but it is well-known that this does not generalize the ideal free distribution and dramatically increases the per capita gain (Křivan et al. 2008). We propose a modification of the approach from (Vincent and Brown 2005) in the vein of (Cressman and Křivan 2010), based on individual optimization in the context of habitat selection. Rather than assuming a population where all individuals act in lockstep, we allow each animal to act independently with its risk-reward calculus affected by the population mean behavior (Fretwell 1969; Smith 1982; Cressman and Křivan 2010). Then the game at every instant becomes a mean field game with multiple types, which leads to the simple ideal free distribution if the animals are optimizing their fitness.

We model instantaneous movement, but the underlying reality is that animals migrate between adjacent patches, e.g. through advection-diffusion dynamics (Cantrell et al. 2010). If population dynamics are sufficiently slow, then the migration dynamics which lead to the simple ideal free distribution are those which are evolutionarily stable (Averill et al. 2012; Cantrell et al. 2010), and even very basic migration dynamics lead to the simple ideal free distribution (Avgar et al. 2020). As such, populations at a population-dynamical equilibrium can be expected to follow a distribution where each individual has optimal fitness (Cantrell et al. 2007; Cressman and Křivan 2010), which in this case is zero. When the population dynamics and migratory time-scales are sufficiently decoupled, the migration dynamics which lead to the simple ideal free distribution are also evolutionarily stable (Cantrell et al. 2020; Cressman and Křivan 2006), even when predators do not directly optimize their own fitness (Avgar et al. 2020). Therefore a wide range of natural systems can be modeled by coupling population dynamics to optimal patch distribution. Currently there is no general approach to do so, but we introduce an approach based on mean-field games and optimization.

We essentially unite the two parallel tracks which mean-field games have followed since their inception. One track is in mathematical biology through the ideal free distribution and habitat selection games (Fretwell 1969; Parker 1978; Cressman et al. 2004; Křivan et al. 2008; Cressman and Křivan 2010; Broom and Rychtár 2013), and the other in mathematical optimization based directly on anonymous actors (Lasry and Lions 2007; Aumann 1964; Blanchet and Carlier 2016). The main focus in the game-theoretically focused ecological work has been studying specific families of games in depth Broom and Rychtár (2013), while the focus in mathematical optimization has been in establishing uniqueness and existence of Nash equilibria through the toolbox of variational inequalities (Karamardian 1969; Gabay 1980; Nabetani et al. 2011).

Using the theory of variational inequalities, we show that population games based on individual optimization have a unique equilibrium under very mild assumptions. Our approach allows us to handle both continuous and discrete strategy spaces, but more technical assumptions are required for existence in the continuous setting. The simple ideal free distribution emerges as a special case of our approach, providing a compelling argument for the mean-field approach. By working with variational inequalities, we can generalize the classical definition of a multi-species evolutionary stable state to the continuous setting (Cressman et al.

2001). We demonstrate our approach by applying it to a Rosenzweig-MacArthur system with intraspecific predator competition in continuous space modeling a marine ecosystem. We modify the system so both predators and consumers have instantaneous optimal behavior based on maximizing the individual growth rate. We show that the Rosenzweig-MacArthur system with optimal behavior satisfies the criteria for existence and uniqueness of equilibria as a population game, and perform numerical experiments to see the effect of the carrying capacity and competition on the system.

In addition to our theoretical advances, we implement a simple and efficient numerical method of finding Nash equilibria and equilibria of population games. The numerical method is applied to the behaviorally modified Rosenzweig-MacArthur system. We examine the population dynamics through a phase portrait, where they appear to be asymptotically stable. We study the population levels and spatial distribution at equilibrium as a function of the carrying capacity and intraspecific predator competition. With optimal behavior, increased competition causes a drastic change in behavioral patterns for consumers and predators and an increase in consumer populations with a very low impact on predator populations. Increasing carrying capacity causes both predator and consumer populations to increase, while consumers move towards more cautious behavior.

The paper is organized as follows: We start with the general setting. After building the general setting, we introduce the machinery of variational inequalities in the context of game theory. Here we show the general uniqueness and existence results. We proceed to study the concrete Rosenzweig-MacArthur model, showing existence and uniqueness of the Nash equilibrium and population equilibrium. We analyze the results, and discuss the implications of both numerical and theoretical results.

2 Population games based on habitat choice

We build the general setting piece-by-piece, from the environment to the foraging strategies. First we define the environment, then we introduce the mean-field setting, as it is necessary to handle the strategy of an entire population. With this in place, we can give an exact definition of a population game in our sense. Once we have laid the building blocks for our setting, we show that mean-field games generalize the ideal free distribution.

We envision a setting with M different unstructured populations of animals co-existing in an environment, each with biomass N_i . We only model behavior as patch choice, excluding e.g. mating behavior. The distribution of population i in the environment is described by $\bar{\sigma}_i$. More rigorously, we assume that the environment is a probability space (X, μ) . Modeling the environment as a probability space allows us to model habitats which are continuous, discrete and mixtures thereof in the same context. As an example, bats forage over a continuous area while the caves where they rest are discrete and disconnected (Collet 2019). We model that the populations N_i , $i \in \{1, \dots, M\}$ are large compared to a single individual. This allows us to consider the population as continuous, consisting of infinitely many individuals. We assume that the population dynamics depend both on the distributions and the population sizes:

$$\dot{N}_i = N_i f_i((N_j \bar{\sigma}_j)_{j=1}^M) \quad (1)$$

That is, we consider population dynamics which can be described by a Kolmogorov model.

We suppose that the migration dynamics happen on a faster time-scale than the population dynamics, as is seen with e.g. vertical migrations in marine ecosystems (Iwasa 1982). This slow-fast dynamic allows us to model the migrations as instantaneous, with each individual picking the optimal foraging ground at every instant (Křivan 2013; Cressman and Křivan 2006).

We assume that every animal has an area where it forages at every instant. For an animal of type i this is described by a probability distribution σ_i over the environment X . We require that the distribution σ_i is absolutely continuous with respect to the measure μ . In an abuse of notation, we will denote this density by σ . We denote the space of probability densities over X with respect to μ by P_μ . We suppress X for notational brevity. By requiring absolute continuity with respect to the base measure we remove degenerate Nash equilibria e.g. Dirac-type distributions in a continuous setting, avoiding for example all gazelles stacked exactly at a single point in space. We hereby generalize both the continuous and discrete approach to habitat selection (Fretwell 1969; Broom and Rychtár 2013; Thygesen and Patterson 2018).

2.1 Foraging strategies and mean-field

In habitat choice games an animal faces the essential choice of where to forage, weighing risk and reward. Hence the density σ_i describing where it forages is a strategic choice. As we assume instantaneous migrations and perfect information, an animal of type i faces the foraging choices of all other inhabitants. Modeling the influence of the foraging choices necessitates the introduction of the mean-field strategy, $\bar{\sigma}_j$ for type j . The mean-field strategy $\bar{\sigma}_j$ is the average strategy of all individuals of type j . As a consequence, we can describe the foraging presence from type j at a point $x \in X$ by $N_j \bar{\sigma}_j(x)$.

The choice of optimal foraging strategy σ_i^* for an animal of type i is a trade-off based on the presence of competitors, predators and prey. When considering animal populations, finding the optimal behavior for all individuals simultaneously quickly becomes infeasible. For this reason, we need to simplify the problem. This is where mean-field games come into play. The fundamental idea behind a mean-field game is that in a sufficiently large population, the decision of a single individual has no discernible impact on the average behavior of the population. In this case we can decouple the behavior of an individual and the mean behavior of the population, and assume that an individual plays against the average behavior of the population. That is, an individual plays the field (Smith 1982). The fundamental assumption in the mean-field game that we consider is that the populations consist of infinitely many individuals acting instantaneously and independently so the choice of a single individual does not change the mean-field strategy (Aumann 1964)

The mean density of competitors, predators and prey at a point x is described by $N_j \bar{\sigma}_j(x)$. We capture this trade-off for each individual in a payoff function $U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M)$. The payoff U_i we have in mind is the instantaneous growth of an individual, i.e. individual fitness. This is given by the difference between the

instantaneous per capita reproduction and mortality for an individual in Equation (1). When using the individual fitness as payoff, the Nash equilibria we find should be the same as simple ideal free distributions.

Given that each type j is distributed according to $\bar{\sigma}_j$, the goal of a single animal of type i is finding the optimal strategy σ_i^* by playing the field at each instant such that

$$\sigma_i^* \in \operatorname{argmax}_{\sigma_i \in P_\mu} U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M) \quad (2)$$

Whether such a Nash equilibrium exists is well established when no additional regularity is imposed on the probability distributions (Glicksberg 1952), we will tackle the general problem of existence later. At the Nash equilibrium of a mean-field game every individual of type i follows the same strategy σ_i^* , (Lasry and Lions 2007; Aumann 1964). Heuristically, this is due to interchangeability as if any individual of type i gains by deviating from σ_i^* , any one of them would also gain from making the same deviation, hence doing so. Therefore if all individuals follow the optimal strategy, they follow the same strategy. This allows us to go from the individual-level optimization to the Nash equilibrium in Equation (2).

Using N to denote the Nash equilibrium, a mean-field equilibrium $\bar{\sigma}_i^N$ is a solution to the equation:

$$\bar{\sigma}_i^N = \left(\operatorname{argmax}_{\sigma_i \in P_\mu} U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1, j \neq i}^M, N_i \bar{\sigma}_i^N) \right) \quad (3)$$

A solution is guaranteed to exist by the results of Glicksberg (1952). Hence a Nash equilibrium of a game with M interacting populations is a solution to the system of equations:

$$\begin{aligned} \bar{\sigma}_1^N &= \left(\operatorname{argmax}_{\sigma_1 \in P_\mu} U_1(\sigma_1, (N_j \bar{\sigma}_j^N)_{j=1}^M) \right) \\ &\quad \vdots \\ \bar{\sigma}_M^N &= \left(\operatorname{argmax}_{\sigma_M \in P_\mu} U_M(\sigma_M, (N_j \bar{\sigma}_j^N)_{j=1}^M) \right) \end{aligned} \quad (4)$$

This system of equations looks intractable, but in the next section we will see that in many cases it can actually be solved using the toolbox of variational inequalities. Introducing Equation (4) allows us to define a population game exactly.

Definition 1 A population game consists of M unstructured populations with each population having a biomass of size N_i with dynamics given by Equation (1). Each individual of type i has a payoff function $U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M)$. Migrations are instantaneous, and at every instant the populations are distributed according to the mean-field Nash equilibrium Equation (4), $\bar{\sigma}_i^N$.

The canonical example of Definition 1 is the case where the payoff functions U_i are given by the individual fitness. The Nash equilibrium Equation (4) becomes a situation where all individuals of each type have the same fitness and do not gain from deviating Equation (4), i.e. the simple ideal free distribution (Fretwell 1969). We repeat the caveat that this version of the ideal free distribution does not incorporate any stability criteria (Křivan et al. 2008). For this reason we refrain from using the terminology "the ideal free distribution" and instead refer to Equation (4) as the Nash equilibrium of a mean-field game or the simple ideal

free distribution. We will give a definition of the multi-species ideal free distribution once we have introduced the entire framework of variational inequalities and their coupling with Nash equilibria.

Though we focus on population games with the individual fitness as payoff function, an appeal of the mean-field approach is that it allows general payoff functions. As an example, the impact of cooperation in a spatially extended game can be investigated by using a mean-field approach (Antonov et al. 2021).

3 Nash equilibria and variational inequalities

Calculating Nash equilibria, Equation (4) is generally a hard problem. A fruitful approach to calculating Nash equilibria is via the theory of complementarity problems and variational inequalities (Karamardian 1969; Nabetani et al. 2011). We unite the approach of variational inequalities and mean-field games which allows us to characterize a situation that guarantees uniqueness and existence of Nash equilibria in population games (Definition 1), and the existence of fixed-points of these games.

As in Section 2, our habitat is a probability space (X, μ) . We have M different animal types coexisting with individual payoff-functions U_i . The simplest example our framework needs to handle is that of a single type with population N inhabiting X with following a distribution with density σ . The pointwise encounter rate of an individual following the strategy σ with the entire population also following the strategy σ is $N\sigma(x)^2$. The expected total encounter for an individual with its conspecifics is then

$$N \int_X \sigma^2 d\mu \quad (5)$$

and this quantity must be finite. This motivates that the appropriate setting for our work is the space $L^2(X)$.

Definition 2 Define the real Hilbert space $H = L^2(X)$, where X is a probability space. Define $H_+ \subset H$ as the a.e. positive functions in H .

3.1 From Karush-Kuhn-Tucker to complementarity

In order to find the Nash equilibrium at every instant in a population game, we need to solve Equation (4). We recall the setup of the M -player mean field game, now restricted to H . Assume we have M different types of animals, with payoff functions U_i , and strategies σ_i , with corresponding mean-field strategies $\bar{\sigma}_i$. Before we proceed, we need to recall a simple version of the Karush-Kuhn-Tucker (KKT) conditions that we need. We denote the identity operator on H by 1_H . For the full version of the KKT conditions, see e.g. Deimling (2010).

Theorem 1 *A minimum x^* of a Gateaux differentiable function f in $P_{2,\mu} \subset L^2(X)$ satisfies the necessary condition that there exists an element $\nu \in H^+$ and a scalar $\lambda \in \mathbb{R}$ such that:*

$$\begin{aligned} f(x^*) + \nu &= 1_H \lambda \\ \langle x^*, \nu \rangle &= 0 \end{aligned} \quad (6)$$

The condition $\langle x^*, \nu \rangle = 0$ is described as the complementary slackness conditions, and the requirements that $x^* \geq 0$ and $\int x^* d\mu = 1$ are the primal conditions. The variable λ is a Lagrange multiplier, and ν is typically referred to as a slack variable.

The Nash equilibrium of the game specified by the family (U_i) corresponds to finding a system σ_i^* satisfying the KKT conditions simultaneously for every U_i , with $\bar{\sigma} = \sigma$ as in Equation (3). The total criterion for a Nash equilibrium of a mean-field game Equation (4) is:

$$\begin{aligned} \nabla_{\sigma_i} U_i((\sigma_j)_{j=1}^M) |_{\sigma_i=\bar{\sigma}_i} + \nu_i - \lambda_i \cdot 1_H &= 0 \\ \langle \sigma_i, \nu_i \rangle &= 0 \\ \nu_i \in H_+, \sigma_i &\in H_+ \\ \int_X \sigma_i d\mu(x) - 1 &= 0 \end{aligned} \tag{7}$$

Remark that the last two conditions are equivalent to $\sigma \in P_\mu \cap H$. This motivates the definition:

Definition 3 Assume we have a probability space (X, μ) . Consider the space of square-integrable functions $H = L^2(X, \mu)$ and space P_μ of probability densities over X . Define the space $P_{2,\mu} = H \cap P_\mu$ consisting of square-integrable probability densities.

Solving the system in Equation (7) is highly non-trivial, but it turns out that reinterpreting the problem is helpful. Finding Nash equilibria by interpreting the problem as a complementarity problem is one of the the original solutions to the hardness of finding Nash equilibria (Karamardian 1969). It turns out that the set of equations in Equation (7) is very close to being a complementarity problem, but first we need to introduce the notion (Hadjisavvas et al. 2006, p. 507).

Definition 4 Let H be a real Hilbert space, and $K \subset H$ be a closed convex cone. Define $K^* = \{x \in H : \langle x, y \rangle \geq 0, \forall y \in K\}$. Assume $T : K \rightarrow H$. The complementarity problem $CP(T, K)$ is the problem of finding an element x such that

$$\begin{aligned} \langle x, Tx \rangle &= 0 \\ Tx \in K^*, \quad x &\in K \end{aligned} \tag{8}$$

In Definition 4 we recover the notion of a linear complementarity problem if T is affine.

With Definition 4 we can write Equation (7) as an equivalent family of complementarity problems. Introduce $K = H_+ \oplus \mathbb{R}$, with $K^* = H_+ \oplus \{0\}$ and define

$$T(\sigma_i, \lambda_i) = (-\nabla_{\sigma_i} U_i + \lambda_i \cdot 1_H |_{\sigma_i=\bar{\sigma}_i}, 0) \tag{9}$$

Then the equations in Equation (7) can be recast as finding $(\sigma_i, \lambda_i) \in K$ such that:

$$\begin{aligned} \langle T(\sigma_i, \lambda_i), (\sigma_i, \lambda_i) \rangle &= 0 \\ T(\sigma_i, \lambda_i) &\in K^* \end{aligned} \tag{10}$$

Which, when writing out the definition of T , becomes:

$$\begin{aligned} \langle -\nabla_{\sigma_i} U_i |_{\sigma_i=\bar{\sigma}_i} + \lambda_i \cdot 1_H, \sigma_i \rangle + \langle 0, \lambda_i \rangle &= 0 \\ (-\nabla_{\sigma_i} U_i |_{\sigma_i=\bar{\sigma}_i} + \lambda_i \cdot 1_H), 0 &\in K^* \end{aligned} \quad (11)$$

There are dedicated tools available allowing for fast numerical resolution of complementarity problems in finite dimensions (Acary et al. 2019; Dirkse and Ferris 1995), which can be applied after suitable discretization of the problem. There is still the problem of establishing existence and uniqueness of the solution to this complementarity problem, which is generally hard, (Hadjisavvas et al. 2006).

3.2 Results on variational inequalities

Before we can proceed with the main theme of the article, we recount some results on existence and uniqueness of variational inequalities, which also show their general utility in optimization. We define a variational inequality:

Definition 5 Let H be a real Hilbert space and $K \subset H$ be a non-empty convex subset of H . Let $T : K \rightarrow H$. The variational inequality $VI(T, K)$ is the following system for $x \neq y$:

$$x \in K, \langle y - x, Tx \rangle \geq 0, \quad \forall y \in K \quad (12)$$

The relationship between variational inequalities and complementarity problems is captured in (Hadjisavvas et al. 2006, Proposition 12.1):

Proposition 1 Let $K \subset H$ be a convex cone, and $T : K \rightarrow H$. Then the variational inequality $VI(T, K)$ is equivalent to the complementarity problem $CP(T, K)$.

The solutions to a variational inequality are not generally unique, but with certain restrictions on T the solutions become unique.

Definition 6 The function $T : K \rightarrow H$ is strictly pseudomonotone if for every pair $x \neq y$ we have

$$\langle x - y, T(y) \rangle \geq 0 \Rightarrow \langle x - y, T(x) \rangle > 0 \quad (13)$$

Likewise, the function T is pseudomonotone if for every pair $x \neq y$ we have:

$$\langle x - y, T(y) \rangle \geq 0 \Rightarrow \langle x - y, T(x) \rangle \geq 0 \quad (14)$$

Which enables the uniqueness result:

Theorem 2 (Lemma 12.3, p. 516, (Hadjisavvas et al. 2006)) Let $K \subset H$ be a non-empty subset of H . If T is a strictly pseudomonotone function, then the problem $VI(T, K)$ has at most one solution.

Strict pseudomonotonicity is related to strict monotonicity, in that every strictly monotone function is also strictly pseudomonotone. A natural question is how strictly pseudomonotone arise, and they arise from a corresponding generalization of strict convexity.

Definition 7 Let $\Omega \subset H$ be an open subset of H , and let $f : \Omega \rightarrow \mathbb{R}$ be Gateaux-differentiable. The function f is strictly pseudoconvex if

$$\langle y - x, (\nabla f)(x) \rangle \geq 0 \Rightarrow f(y) > f(x) \quad (15)$$

Where a strictly convex function has a strictly monotone derivative, a variant holds for strictly pseudoconvex functions which have strictly pseudomonotone derivatives. Hence minimizing a differentiable strictly pseudoconvex f function over a convex set K is equivalent to solving the variational inequality (Hadjisavvas et al. 2006, P. 521)

$$x \in K, \langle (\nabla f)(x), x - y \rangle \geq 0, \forall y \in K \quad (16)$$

Having given a criterion for uniqueness, the next question is whether a solution exists at all. The existence of solutions to a variational inequality given by a pseudomonotone function can be determined by a simple criterion (Maugeri and Raciti 2009, Theorem 3.4), which we abridge:

Theorem 3 Let K be a closed convex set and $A : K \rightarrow H$ a pseudo-monotone map which is continuous on finite dimensional subspaces of H . A variational inequality $\langle A(x), y - x \rangle$ has a solution if and only if There exists a point $u_0 \in K$ such that the set

$$\{v \in K : \langle A(v), v - u_0 \rangle < 0\} \quad (17)$$

is bounded. This provides us with a testable criterion for whether a variational inequality admits a solution.

Remark 1 Boundedness of K , or more precisely weak compactness, also ensures that $VI(T, K)$ has a solution in K (Hadjisavvas et al. 2006, Theorem 12.1, P. 510). This also ensures existence of solutions to variational inequalities in the finite-dimensional case.

Intuitively, the criterion in Theorem 3 states that as long as there a direction where $A(v)$ becomes positive eventually, there exists a solution to the variational inequality in K . Or, on a more formal level, what the criterion says is that instead of K being weakly compact, it is sufficient that $\langle A(v), v - u_0 \rangle$ changes sign on weakly compact set. In practice this criterion should always be satisfied in a population game, as a negative density dependence should eventually outweigh any gain from clumping as an infinite concentration should not be advantageous.

Though strictly pseudomonotone functions initially arise as gradients of strictly pseudoconvex functions, they can be much more general. Checking whether a function is strictly pseudomonotone from the definitions can also be hard in practice, hence we state another characterization of strict pseudomonotonicity for differentiable functions.

Lemma 1 Let K be a convex subset of H . A function $f : K \rightarrow \mathbb{R}$ is strictly pseudomonotone if the following implication holds for any $x, h \in K$:

$$\langle f(x), h \rangle = 0 \Rightarrow \langle (\nabla_x f(x))h, h \rangle > 0 \quad (18)$$

A proof can be found in (Hadjisavvas et al. 2006, Proposition 2.8, p.96)

3.3 The Nash equilibrium as a variational inequality

We have recast the problem of finding a Nash equilibrium to a complementarity problem, which allows for numerical resolution. To establish existence and uniqueness, we need to use the relationship between complementarity problems and variational inequalities. We will show that in case the payoff-functions U_i are sufficiently nice, the machinery of variational inequalities can be applied to show existence and uniqueness of the Nash equilibrium.

We can now turn the problem finding a Nash equilibrium into a variational inequality. Consider the problem as stated in Equation (10). This is a complementarity problem over the convex cone $H_+ \oplus \mathbb{R}$. Hence it is equivalent to a variational inequality over the same convex cone with T as in Equation (10) by Proposition 1. The equivalent variational inequality becomes that of finding a pair σ_i, λ_i such that:

$$\langle T(\sigma_i, \lambda_i), (\sigma'_i - \sigma_i, \lambda'_i - \lambda_i) \rangle \geq 0, \quad \forall (\sigma'_i, \lambda'_i) \in K, (\sigma'_i, \lambda'_i) \neq (\sigma_i, \lambda_i) \quad (19)$$

Recalling the definition of T , $T = (-\nabla_{\sigma_i} U_i |_{\sigma_i=\bar{\sigma}_i} - \lambda_i, 0)$, we see the second coordinate is identically zero. Hence solving Equation (19) is equivalent to solving

$$\begin{aligned} \langle -\nabla_{\sigma_i} U_i |_{\sigma_i=\bar{\sigma}_i} - \lambda_i, \sigma'_i - \sigma_i \rangle &\geq 0 \quad \forall \sigma'_i \in K, \sigma'_i \neq \sigma_i \\ \langle -\nabla_{\sigma_i} U_i |_{\sigma_i=\bar{\sigma}_i}, \sigma'_i - \sigma_i \rangle - \langle \lambda_i, \sigma'_i - \sigma_i \rangle &\geq 0 \quad \forall \sigma'_i \in K, \sigma'_i \neq \sigma_i \end{aligned} \quad (20)$$

If we constrain the solution set to the convex set $P_{2,\mu}$ where it must lie due to the Lagrange multiplier, both σ_i and σ'_i integrate to 1, therefore the term $\langle \lambda_i, \sigma'_i - \sigma_i \rangle$ vanishes. Hence solving Equation (20) over K is equivalent to solving the variational inequality:

$$\langle -\nabla_{\sigma_i} U_i |_{\sigma_i=\bar{\sigma}_i}, \sigma'_i - \sigma_i \rangle \geq 0, \quad \forall \sigma'_i \in P_{2,\mu}, \sigma'_i \neq \sigma_i \quad (21)$$

We can now state the problem of finding the Nash equilibrium Equation (4) as finding the solution of a variational inequality.

Definition 8 (Nash equilibrium as variational inequality) Defining

$$dU = \begin{pmatrix} \nabla_{\sigma_1} U_1 |_{\sigma_1=\bar{\sigma}_1} \\ \vdots \\ \nabla_{\sigma_N} U_N |_{\sigma_N=\bar{\sigma}_N} \end{pmatrix} \quad (22)$$

the problem of determining the Nash equilibrium Equation (4) is the variational inequality of finding a vector $S = (\sigma_i)_{i=1}^M$ such that:

$$\langle -dU(S), W - S \rangle \geq 0 \quad \forall W \in (P_{2,\mu})^M, W \neq S \quad (23)$$

with $P_{2,\mu}$ as defined in Definition 3

With Definition 6 in hand, we can finally give sufficient criteria for existence and uniqueness of the Nash equilibrium of the game specified in Equation (4).

Theorem 4 Consider a game with M players with payoff functions U_i such that the total operator $-dU$ from Definition 8 is strictly pseudomonotone. Assume the strategies σ_i are in $P_{2,\mu}$. The game has a unique Nash equilibrium if $-dU$ as in Definition 8 satisfies the criterion in part (2) of Theorem 3 or H is finite dimensional.

Proof By Theorem 2 any Nash equilibrium will be unique since dU is strictly pseudomonotone. So if the solution exists, it is unique. By assumption Theorem 3 gives existence of a solution of $VI(dU, P_{2,\mu}^M)$ in case H is infinite dimensional. If H is finite-dimensional then $P_{2,\mu}^M$ is compact and there exists a solution by Remark 1. \square

With Theorem 4, we can show that there exist unique fixed points of population games where dU is strictly pseudomonotone and the vector fields specifying the population dynamics are sufficiently regular.

Theorem 5 *We have a population game as Definition 1 with M populations of size N_i , payoff functions $U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M)$ and dynamics given by $f_i((N_j \bar{\sigma}_j)_{j=1}^M)$:*

$$\dot{N}_i = N_i f_i \quad (24)$$

Assume that the set of stationary points of the population dynamics is uniformly bounded in $(\sigma_i)_{i=1}^M$, and that the stationary points can be described by a continuous function $\Phi : P_{2,\mu}^M \rightarrow \mathbb{R}_+^M$. Let $-dU = (\nabla_{\sigma_i} U_i |_{\sigma_i = \bar{\sigma}_i})$ be strictly pseudomonotone and satisfy the criterion of Theorem 3. Then the population game has a fixed point. If further the system f_i defines a pseudomonotone operator $F : \mathbb{R}_+^M \rightarrow \mathbb{R}_+^M$ with $F = (f_1, \dots, f_M)$, the fixed-point is unique.

Proof The game specified by the family $(U_i)_{i=1}^M$ defines a variational inequality problem over $P_{2,\mu}^M$ with operator $-dU$. This variational inequality has a unique solution for each $x \in \mathbb{R}_+^M$, due to the existence and uniqueness of the solution by Theorem 4. This solution defines a continuous function from \mathbb{R}_+^M , denoted G , where $G : \mathbb{R}_+^M \rightarrow P_{2,\mu}^M$, (Barbagallo and Cojocaru 2009, Theorem 4.2).

Finding a fixed point of the dynamical system along with a Nash equilibrium then corresponds to finding a fixed point of the mapping $\Phi \circ G : \mathbb{R}_+^M \rightarrow \mathbb{R}_+^M$. Since the set of stationary points is assumed bounded, G has compact range, and $\Phi \circ G$ has compact image. Therefore $\Phi \circ G : \mathbb{R}_+^M \rightarrow \mathbb{R}_+^M$ has a fixed point (x_1^*, \dots, x_m^*) by Schauder's fixed point theorem (Granas and Dugundji 2003, Theorem 3.2, p. 119).

We can conclude that a fixed-point exists, hence a combined Nash and population equilibrium.

To show uniqueness, we need to shift perspectives. We are searching for zeros of the system f_i , i.e. solutions of the variational inequality $VI(F, \mathbb{R}_+^M)$ constrained by the fact that the system of σ_i constitute a Nash equilibrium, i.e. they need to solve the variational inequality $VI(-dU, P_{2,\mu}^M)$. This is an example of a so-called bi-level variational inequality. As we have already established existence, the strict pseudomonotonicity of $-dU$ and pseudomonotonicity of F give us uniqueness of the solution (Chen et al. 2014). This shows the desired result. \square

3.4 The ideal free distribution

Having introduced the framework of variational inequalities allows us to connect with the ideal free distribution. As noted in the introduction, the ideal free distribution is classically defined as emerging from playing the field in single-species habitat

selection games (Fretwell 1969). As such, the ideal free distribution is informally characterized by no individual gaining anything from moving from their spot in a habitat selection game. This definition, while perfectly suitable for single-species games is insufficient for the multi-species case. A stability requirement should also be introduced so a small deviation from the ideal free distribution will not change the overall distribution and such that best-response dynamics converge to the ideal free distribution (Křivan et al. 2008). The ideal free distribution can also be expanded to incorporate population dynamics (Cressman and Křivan 2010), but we refrain from going in this direction here as it would bring us too far afield. As in Section 2 we consider M populations with mean-field strategies $(\bar{\sigma}_i)_{i=1}^M$, individual strategies $(\sigma_i)_{i=1}^M$ and individual payoff functions U_i . We assume that we have a population game with a total operator $-dU$ Definition 8, with components $-dU_i$.

We generalize the definition of (Křivan et al. 2008) and go with a rather restrictive definition of the multi-species ideal free distribution which ensures stability. It is typically posed as a result that the ideal free distribution is an evolutionarily stable strategy (ESS), but we take it as a part of the definition. We introduce the notion of evolutionary stable strategies based on the definition on evolutionary stable states using variational inequalities (Migot and Cojocaru 2021). For simplicity, we do not take weakly evolutionary stable strategies into account but concern ourselves with the strict case. In (Cressman et al. 2004) the notion of an M -species evolutionarily stable strategy is introduced, which is equivalent to the ideal free distribution defined in terms of best responses, Křivan et al. (2008, Section 3.3).

Definition 9 A set of strategies $(\bar{\sigma}^N)_i)_{i=1}^M$ in an M -species population game is an evolutionarily stable strategy if invaders following the slightly perturbed strategies $(\sigma'_i)_{i=1}^M$ do not have an advantage against the resident population. In our notation, implies that for at least one i , we have $U_i(\sigma'_i, (\bar{\sigma}_j)_{j=1}^M) < U_i(\bar{\sigma}_i, (\bar{\sigma}_j)_{j=1}^M)$.

We can now relate strict pseudomonotonicity and evolutionary stable strategies, which motivates that strict pseudomonotonicity is the correct notion to look for in population games, apart from the uniqueness properties.

Theorem 6 *Given a population game with payoff functions $(U_i)_{i=1}^M$ with total operator $-dU$, if each component $-dU_i$ is strictly pseudomonotone, the Nash equilibrium $(\bar{\sigma}_i^N)_{i=1}^M$ is an evolutionarily stable strategy.*

Proof We wish to show that $U_i(\sigma'_i, (\bar{\sigma}_j)_{j=1}^M) < U_i(\bar{\sigma}_i, (\bar{\sigma}_j)_{j=1}^M)$. As the in assumption in Definition 9 is that σ'_i is a slight perturbation of $\bar{\sigma}_i$, we can equivalently show

$$\langle \bar{\sigma}_i^N - \sigma'_i, -dU_i((\bar{\sigma}_j)_{j=1}^M) \rangle > 0 \quad (25)$$

As we assume each $-dU_i$ is strictly pseudomonotone and that $\bar{\sigma}_i^N$ is the Nash equilibrium for the game defined by $U_i(\sigma, \bar{\sigma})$, by definition of pseudomonotonicity any strategy ω different from $\bar{\sigma}_i^N$ satisfies the inequality:

$$\langle -dU_i(\bar{\sigma}_i), \omega - \bar{\sigma}_i \rangle > 0 \quad (26)$$

which is exactly the criterion for evolutionary stability of the strategy $\bar{\sigma}_i$.

This allows us to define an M -species ideal free distribution.

Definition 10 A Nash equilibrium $(\bar{\sigma}_i^N)_{i=1}^M$ of an M -species population game with payoff-functions U_i given by the individual fitness is an M -species ideal free distribution if the Nash equilibrium $(\bar{\sigma}_i^N)_{i=1}^M$ is an evolutionarily stable strategy.

This allows us to state the result which motivates that strict pseudomonotonicity is the correct notion to look for in population games, apart from the uniqueness properties.

Corollary 1 *If $-dU$ and each component $-dU_i$ are strictly pseudomonotone, the Nash equilibrium $(\bar{\sigma}_i^N)_{i=1}^M$ in a population game is unique and an ideal free distribution.*

Proof The uniqueness of the Nash equilibrium follows from the strict pseudomonotonicity of $-dU_i$. As we assume each $-dU_i$ is strictly pseudomonotone the Nash equilibrium also constitutes an ESS by Theorem 6.

The strict pseudomonotonicity in Corollary 1 is also sufficient for asymptotic convergence of the replicator dynamics to the Nash equilibrium (Migot and Cojocaru 2021), providing additional motivation for the choice of strict pseudomonotonicity as the defining characteristic in population games. Our definition of an evolutionarily stable strategy is closely related to that of an evolutionarily stable state (Migot and Cojocaru 2021). If all components $-dU_i$ are strictly pseudomonotone as in Corollary 1 and not just a single one or a few, the resulting ESS is even stable in the sense that it can invade other states (Apaloo et al. 2009).

Having established the general results for population games based on habitat choice with instantaneous migrations and introduced the connection to the ideal free distribution, we are ready to apply the theory to a Rosenzweig-MacArthur system with fast adaptive behavior.

4 Revisiting the Rosenzweig-MacArthur model

We consider a predator-prey system modeled as a Rosenzweig-MacArthur system where each individual consumer and predator seeks to maximize its growth at every instant, in the vein of (Krivan and Cressman 2009). We represent consumer, respectively predator, per capita growth by G_c and G_p . Likewise, we represent the per capita mortality by M_c and M_p . We denote the growth and mortality rates of an individual by the superscript ind . Defining the per capita dynamics $f_c = G_c - M_c$ and $f_p = G_p - M_p$, we can write the dynamical system for the population dynamics as:

$$\begin{aligned} \dot{N}_c &= N_c f_c \\ \dot{N}_p &= N_p f_p \end{aligned} \tag{27}$$

The payoff functions for an individual consumer and predator are given by the individual growth rates U_c, U_p , and they are:

$$\begin{aligned} U_c(\sigma_c, N_c \bar{\sigma}_c, N_p \bar{\sigma}_p) &= G_c^{ind} - M_c^{ind} \\ U_p(\sigma_p, N_c \bar{\sigma}_c, N_p \bar{\sigma}_p) &= G_p^{ind} - M_p^{ind} \end{aligned} \tag{28}$$

We consider a system with zooplankton as consumers (N_c) and forage fish as predators (N_p) in the water column, modeled as the interval $[0, 100]$, with 0 as the top of the water column and 100 as the bottom. The choice of strategy is the depth at which to forage. Both forage fish and zooplankton have large populations, so it is reasonable to model this system as a mean-field game. We denote the mean strategies of the predator and consumer populations by $\bar{\sigma}_c$, and $\bar{\sigma}_p$. The productive zone of the water column, i.e. where zoo-plankton can find food, is near the top where sunlight allows phytoplankton to grow. Forage fish are visual predators, so their predation success is greatest near the top of the water column (Schadegg and Herberholz 2017). We model an arctic summer where there is constant sunlight which allows us to ignore the influence of the day-night cycle. Both zooplankton and foraging fish populations in the arctic are mainly driven by the summer (Astthorsson and Gislason 2003; Mueter et al. 2016).

As zooplankton are olfactory foragers, we model that their growth rate β_c is constant throughout the water column but the carrying capacity varies. We assume the zooplankton are not limited either by maximal consumption or handling (Kiørboe 2011), which coupled with the varying capacity leads to a logistic model for their growth. Summarizing, we assume that the maximal potential growth for a consumer from a location depends both on the absolute carrying capacity and how many consumers are already occupying the spot. We model the carrying capacity as $K_0 + K\varphi$ where K_0 is the minimal carrying capacity, K is the varying capacity and φ is a probability density function. The per capita growth rate of a consumer becomes:

$$G_c(N_c, \bar{\sigma}_c) = \beta_c \left\langle \bar{\sigma}_c, 1 - N_c \frac{\bar{\sigma}_c}{K\varphi + K_0} \right\rangle \quad (29)$$

The mortality of the consumers is directly related to the growth of the predators, so we define the growth of the predators and then come back to the mortality of the consumers. Predator-prey interactions are fundamentally governed by the clearance or catch rate β_p which describes the change in encounter rate from an increase in consumer or predator concentration. The encounter rate incorporates the light-dependent nature of forage fish, while incorporating that there is still a minimal chance of catching prey without light. Concretely, we define:

$$\beta_p = \beta_l + \beta_0$$

where β_l varies locally and β_0 is the minimal clearance rate. We define the maximal consumption rate for a predator F_p as the reciprocal of the handling time of a predator H_p :

$$F_p = \frac{1}{H_p} \quad (30)$$

The choice of maximal consumption rate as a parameter rather than handling time reflects that marine animals are rarely limited by handling (Schadegg and Herberholz 2017). We assume the maximal predator consumption rate is H_p , and the predators have a conversion efficiency of ε . Consumption events are assumed local, so the expected encounter rate between predators and prey is $N_c N_p \langle \beta_p \bar{\sigma}_p, \bar{\sigma}_c \rangle$. We assume that predators have a Type II functional response, and their consumption is limited by prey-capture and digestion rather than handling, which causes

a non-linearity in the functional response as a function of the strategy (Kiørboe et al. 2018). This gives a per capita predator growth rate G_p :

$$G_p(N_p, \bar{\sigma}_p, N_c, \bar{\sigma}_c) = \varepsilon \frac{F_p \langle \beta_p N_c \bar{\sigma}_c, \bar{\sigma}_p \rangle}{F_p + \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle N_c} \quad (31)$$

Having defined the growth rate of the predators allows us to define the per capita consumer mortality $M_c = \frac{N_p}{\varepsilon N_c} G_p$. Predator losses stems both from a metabolic loss μ_p and mortality from intraspecific predator competition, which we assume leads to a quadratic loss for predators as there is no satiation. We assume that predators losses from competition are greatest in the area where they are best specialized for hunting, since this is where they are best able to confront their con-specifics. Introducing a competition parameter c , the per capita predator mortality M_p is:

$$M_p(N_p, \bar{\sigma}_p) = c \langle \bar{\sigma}_p, N_p \beta_p \bar{\sigma}_p \rangle + \mu_p \quad (32)$$

Hence the population dynamics in eq. (27) are a modified Rosenzweig-MacArthur system, where behavior of both consumer and predator populations has been incorporated. Having considered the population dynamics, we now proceed to the individual level.

4.1 The instantaneous game

Following the exposition in Section 2 we model predator and consumer movement as instantaneous. We assume that each predator and consumer seeks to maximize their instantaneous growth at every instant. As we have switched to focusing on the individuals, we have to distinguish between the strategy of an individual and the mean-field strategy of the population. Denote the strategies of a focal consumer and predator by σ_c and σ_p respectively. The growth of the focal individual depends on the mean-field strategies of both predators and consumers, and can be arrived at by analysing the expressions for G_c, M_c and G_p, M_p carefully, noting which terms depend upon individual choice and which are dependent on the mean-field strategy.

The growth G_c^{ind} of an individual consumer depends on the choices of the consumer, while the available food depends on the spatial distribution of the entire population. Hence the growth of an individual consumer is:

$$G_c^{ind} = \beta_c \left\langle \sigma_c, 1 - N_c \frac{\bar{\sigma}_c}{K\varphi + K_0} \right\rangle \quad (33)$$

The loss from predation (M_c) for an individual consumer is more complex. The risk of encountering a predator depends on the strategy of the focal consumer and the overall predator distribution, while the satiation of the predator depends on how many total consumers it encounters, hence the mean of the population behavior. Therefore the individual mortality of a consumer M_c^{ind} becomes

$$M_c^{ind} = \frac{F_p \langle \beta_p \sigma_c, \bar{\sigma}_p \rangle N_p}{F_p + N_c \langle \beta_p \bar{\sigma}_c, \bar{\sigma}_p \rangle} \quad (34)$$

Going to a focal predator, the growth G_p^{ind} of an individual predator has the same expression as the per capita growth, since the satiation of an individual predator has does not depend on the behavior of the other predators.

$$G_p^{ind} = \varepsilon \frac{F_p \langle \beta_p \bar{\sigma}_c, \sigma_p \rangle N_c}{F_p + \langle \beta_p \bar{\sigma}_c, \sigma_p \rangle N_c} \quad (35)$$

The individual predator mortality M_p^{ind} depends on both the strategy of the individual predator and the distribution of the entire predator population.

$$M_p^{ind} = c \langle \sigma_p, N_p \beta_p \bar{\sigma}_p \rangle + \mu_p \quad (36)$$

4.2 Existence and uniqueness of Nash and population equilibria

In order to establish existence and uniqueness of the Nash equilibrium we show that the variational inequality defined by $-dU$ is strictly pseudomonotone and admits a solution. We start by showing that there is a unique Nash equilibrium for the cases where the predator and consumer respectively have constant behavior, i.e. $\sigma_i = 1$, $i \in \{c, p\}$. First we need a small lemma to simplify the calculations.

Lemma 2 *A function $g : P_{2,\mu} \rightarrow H$ is pseudomonotone if and only if $g + \lambda$ is pseudomonotone for any $\lambda \in \mathbb{R}$.*

Proof Consider $\langle g(x) + \lambda, x - y \rangle = \langle g(x), x - y \rangle + \lambda \int x d\mu - \lambda \int y d\mu$. Using that $\int y d\mu = \int x d\mu = 1$, we arrive at $\langle g(x), x - y \rangle$. Hence the pseudomonotonicity of g and $g + \lambda$ are equivalent.

Proposition 2 *For every pair of non-zero abundances N_c, N_p we have: There is a unique mean-field Nash equilibrium in the Rosenzweig-MacArthur system where the consumers have adaptive behavior and predators have constant behavior $\sigma_p = 1$. Likewise, there is a unique Nash equilibrium in the Rosenzweig-MacArthur system where the predators have optimal behavior and the consumers have constant behavior $\sigma_c = 1$.*

Proof To show the uniqueness of the Nash equilibrium when the consumers have optimal behavior, consider $dU_c = \nabla_{\sigma_c} U_c |_{\sigma_c = \bar{\sigma}_c}$. Without loss of generality, we may assume $\bar{\sigma}_p = 1$ as the difference may be absorbed in β_p . By Lemma 2 it suffices to show that $f = -dU_c + 1$ is strictly pseudomonotone. To de-clutter the calculations we set $\beta_c = 1$ in the following calculations, but the necessary changes for an arbitrary value are straightforward. For Lemma 1 assume $\langle f((\bar{\sigma}_c)), h \rangle = 0$, then

$$\begin{aligned} \langle f(x), h \rangle &= 0 \\ \left\langle \sigma_c \frac{N_c}{K\varphi + K_0}, h \right\rangle + \frac{N_p F_p \langle \beta_p, h \rangle}{F_p + N_c \langle \beta_p, \bar{\sigma}_c \rangle} - \langle 1, h \rangle + \langle 1, h \rangle &= 0 \end{aligned} \quad (37)$$

Hence

$$\left\langle \sigma_c \frac{N_c}{K\varphi + K_0}, h \right\rangle = - \frac{N_p F_p \langle \beta_p, h \rangle}{F_p + N_c \langle \beta_p, \bar{\sigma}_c \rangle} \quad (38)$$

Introducing $\langle x |$ as the functional defined from x , consider

$$H((\bar{\sigma}_c, h) = \langle (\nabla f)((\bar{\sigma}_c, \sigma_p)) h, h \rangle$$

, where $\langle f(\bar{\sigma}_c), h \rangle = 0$. We calculate ∇f :

$$\nabla f = \left(\frac{N_c}{K\varphi + K_0} - \frac{F_p N_c \langle \beta_p | \langle \beta_p | \rangle}{(F_p + N_c \langle \beta_p, \bar{\sigma}_c \rangle)^2} \right) \quad (39)$$

So

$$H(\bar{\sigma}_c, h) = \left\langle \frac{N_c}{K\varphi + K_0} h, h \right\rangle - \left\langle \frac{F_p N_c N_p \langle \beta_p, h \rangle \beta_p}{(F_p + N_c \langle \beta_p, \bar{\sigma}_c \rangle)^2} h, h \right\rangle \quad (40)$$

Inserting Equation (38) in Equation (40), we arrive at

$$H(\bar{\sigma}_c, h) = \left\langle \frac{N_c}{K\varphi + K_0} h, h \right\rangle + \frac{N_c}{N_p F_p} \left(\left\langle \bar{\sigma}_c \frac{N_c}{K\varphi + K_0}, h \right\rangle \right)^2 \quad (41)$$

As $\frac{N_c}{K\varphi + K_0}$ is strictly positive, we conclude that $H(\bar{\sigma}_c, h) > 0$. Therefore f is strictly pseudomonotone by Lemma 1. The situation for the predators is even simpler, since $-dU_p$ is strictly monotone, hence strictly pseudomonotone, so the Nash equilibrium is unique. The existence of the Nash equilibria follows from the proof of existence in Proposition 3.

Remark 2 In Proposition 2 we considered the single-species game where the constant behavior was a uniform distribution. The proofs for constant behavior different from the uniform distribution are the same, but are heavier in notation.

Having shown that each of the underlying mean-field games has a unique Nash equilibrium, we can consider the total game.

Proposition 3 *The game defined by U_c and U_p has a unique Nash equilibrium for every non-zero pair N_c, N_p . Further, this Nash equilibrium constitutes an ideal free distribution.*

Proof By Remark 2 and Proposition 2, any Nash equilibrium of this game is an ideal free distribution as both single-species game are strictly pseudomonotone by Corollary 1. Again, to simplify the notational load in the calculations we set $\beta_c = 1$, but the changes to accommodate an arbitrary value are straight-forward. To show existence of a Nash equilibrium, we need to show that the variational inequality defined by the function

$$dU = \begin{pmatrix} -\nabla_{\sigma_c} U_c |_{\sigma_c = \bar{\sigma}_c} \\ -\nabla_{\sigma_p} U_p |_{\sigma_p = \bar{\sigma}_p} \end{pmatrix} \quad (42)$$

satisfies the criteria of Theorem 3 and is strictly pseudomonotone. To reduce notational clutter we write σ_c in place of $\bar{\sigma}_c$ and σ_p in place of $\bar{\sigma}_p$ through the remainder of the proof. To show that there exists a solution, start by noting that for all $S \in H^2$, $S \mapsto -dU(S)$ is Lipschitz continuous, hence continuous on finite-dimensional subspaces, fulfilling the first criterion of Theorem 3. For the second criterion, consider

$$\langle -dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle \quad (43)$$

We relegate the calculations to the appendix Appendix A.1, but we conclude

$$\langle -dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle \geq C_1 \|\sigma_c\|_2^2 + C_2 \|\sigma_p\|_2^2 - W(\sigma_c, \sigma_p) \quad (44)$$

where W is uniformly bounded on $P_{2,\mu}^2$, and C_1, C_2 strictly positive. Recall that constraining the problem to $P_{2,\mu}$ is equivalent to $\|\sigma_c\|_1 = 1, \|\sigma_p\| = 1$. Hence

Equation (44) tends to infinity as $\|(\sigma_c, \sigma_p)\|_2$ tends to infinity. Therefore Equation (43) is only negative on a bounded subset of $P_{2,\mu}^2$, showing existence of a solution to the variational inequality defined by the function Equation (42) by Theorem 3.

To show strict pseudomonotonicity, we again apply Lemma 1. Assume that

$$\langle -dU((\sigma_c, \sigma_p)), (h_1, h_2) \rangle = 0 \quad (45)$$

Re-arranging gives:

$$\frac{\varepsilon F_p N_c \langle \beta_p \sigma_c, h_2 \rangle}{(F_p + N_c \langle \beta_p \sigma_c, \sigma_p \rangle)^2} = c \langle \beta_p \sigma_p, h_2 \rangle N_p + \left\langle \frac{\sigma_c}{K_0 + K\varphi}, h_1 \right\rangle + \frac{F_p N_p \langle \beta_p \sigma_p, h_1 \rangle}{(F_p + N_c \langle \beta_p \sigma_c, \sigma_p \rangle)} \quad (46)$$

Introducing $\langle x |$ as the functional defined by the inner product with x , we calculate:

$$H(x) = (\nabla - dU)(x) = \begin{bmatrix} \frac{N_c}{K} - \frac{F_p N_c N_p \langle \beta_p \sigma_p | \langle \beta_p \sigma_p |}{(F_p + N_c \langle \sigma_c, \beta_p \sigma_p \rangle)^2} & \frac{F_p^2 N_p \langle \beta_p \sigma_p |}{(F_p + N_c \langle \beta_p \sigma_c, \sigma_p \rangle)^2} \\ \frac{\varepsilon N_c F_p^2 (N_c \langle \beta_p \sigma_p | \beta_p - \langle \beta_p \sigma_p | F_p)}{(F_p + N_c \langle \beta_p \sigma_c, \sigma_p \rangle)^3} & \frac{\varepsilon N_c^2 F_p^2 \langle \beta_p \sigma_c | \langle \beta_p \sigma_c |}{(F_p + N_c \langle \beta_p \sigma_c, \sigma_p \rangle)^3} + c N_p \langle \beta_p | \end{bmatrix} \quad (47)$$

We need to show that $\langle H(x)h, h \rangle > 0$. We immediately see that the negative contribution from the lower-left corner is cancelled by the upper-right corner. Inserting the relationship Equation (46) in the term from the lower right right corner in $\langle H(x)h, h \rangle$ allows cancellation of the negative terms from the upper left corner in $\langle H(x)h, h \rangle$. This shows the desired result. \square

Remark 3 From the proof of existence in Proposition 3, we can extract that a negative density dependence described by a quadratic form is enough for existence of a Nash equilibrium in a population as long as all other terms have sub-quadratic growth.

As we are interested in the fixed-points of the population dynamics Equation (27), we show that a fixed-point of the population dynamics exists and is unique.

Theorem 7 *The population game Equation (27) has a unique co-existence fixed point.*

Proof The stationary-point mapping of the behaviorally modified Rosenzweig-MacArthur system is clearly continuous as a function of σ_c, σ_p . Due to the metabolic terms and logistic terms the set of fixed-points of is uniformly bounded in $\bar{\sigma}_c, \bar{\sigma}_p$, and non-empty for sufficiently large K . By Proposition 3 the Nash equilibrium exists and is unique for every N_c, N_p . The operator $(-f_c, -f_p)$ can be shown to be pseudomonotone in an entirely analogous fashion as $(-dU_c, -dU_p)$, and we omit the calculations. Therefore, by Theorem 5 any coexistence equilibrium for the population game is unique and this will exist for K sufficiently large. Hence the equilibrium is unique as desired. \square

4.3 Parameters

We parametrize the model according to Kleibers' law (Yodzis and Innes 1992), hence that clearance rates, metabolic loss and the maximal consumption rate all scale with the mass to the power of 0.75. We decompose the depth-dependent predator clearance rate into a constant and a depth-dependent function $D(x)$. Denoting the consumer mass by m_c and the predator mass by m_p , the parameters of the model are given by:

$$\begin{aligned} F_p &= \alpha m_p^{0.75} \\ \beta_l(x) &= b m_p^{0.75} D(x) \\ \beta_c &= b m_c^{0.75} \\ \mu_p &= \gamma m_p^{0.75} \end{aligned} \quad (48)$$

We model light decay $I(x)$ throughout the water column as $I(x) = \exp(-kx)$, hence the depth-dependent carrying capacity as following the light-curve:

$$\varphi(x) = \exp(-kx) \quad (49)$$

And the depth-dependent predator clearance rate as being specialized in hunting near the top of the water-column:

$$D(x) = \exp(-k/m \cdot x^2) \quad (50)$$

The scaling parameters for the model are taken from (Andersen 2019, Table 2), except for the zooplankton mass which is from (Kjørboe 2011).

Name	Value	Meaning
m_c	0.01 g	Consumer mass
m_p	10 g	Predator mass
α	$1.25 \text{ g}^{1/4}/\text{month}$	Scaling of consumption rate
b	$27.5 \text{ g}^{1/4} \text{ m}^3/\text{month}$	Scaling of clearance rate
γ	0.2	Ratio between max growth and respiration
K_0	$10^{-4} \text{ g m}^3 \cdot \text{month}$	Minimal carrying capacity
$\beta_{p,0}$	$10^{-4} \text{ m}^3/\text{month}$	Minimal predator clearance rate
μ_p	$0.35 \text{ g}/(\text{m}^3 \cdot \text{month})$	Predator metabolic rate
F_p	$7 \text{ g}/(\text{m}^3 \cdot \text{month})$	Predator maximum growth rate
ε	0.1	Trophic efficiency
k	0.05 m^{-1}	Light attenuation
κ	$\frac{1}{10} \text{ m}^2$	Decay of predation success

5 Numerical approach and results

5.1 Numerical implementation

In order to find Nash equilibria and fix-points of the behaviorally modified Rosenzweig-MacArthur system Section 4, we use the formulation of Equation (10). We discretize space uniformly, using the trapezoidal rule to evaluate the integrals. By using the trapezoidal rule, we keep a banded sparsity pattern in the coupling of

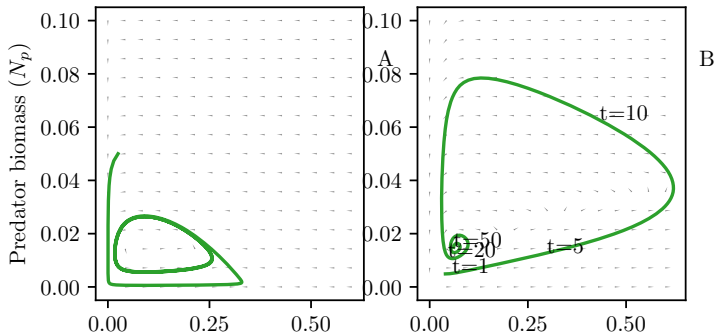
the locations. The equations Equation (27) and the functions $-dU_c, -dU_p$ are formulated via the symbolic language CasADi (Andersson et al. 2019), where we then solve the complementarity problem as a feasibility problem using IPOPT (Wächter and Biegler 2006) using the HSL subroutines for linear algebra (HSL 2007). We verified the numerical results by also solving the problem with a non-linear complementarity routine from the open-source package SICONOS (Acary et al. 2019).

The numerical approach for finding Nash equilibria and fixed points is extremely fast, and should scale to much larger problems. It allows for determination of fixed-points of the dynamics in less than 1 second with several hundred grid points. Simulating the population dynamics is, in contrast, a comparatively slow affair since we simulate the population dynamics using a forward Euler method.

5.2 Population dynamics

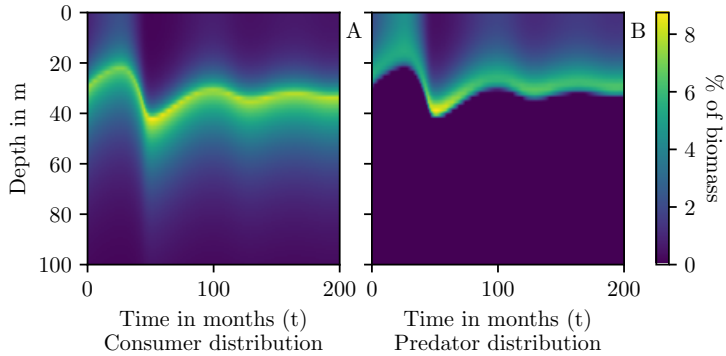
With a numerical approach in place, we can perform numerical experiments to study the population dynamics and the impact of carrying capacity (K) and intraspecific predator competition (c) on the distributions and populations at equilibrium on the model in Section 4.

Fig. 1 Phase portrait of the Rosenzweig-MacArthur system without optimal behavior ($\sigma_c = 1, \sigma_p = 1$), (A) and with optimal behavior (B) at carrying capacity of $K = 40$ and a competition of $c = 0$. The green lines show a system trajectory.



The direction of the flow with optimal behavior (Section 5.2(B)) is consistent with the usual Rosenzweig-MacArthur system (Section 5.2(A)). The phase portrait reveals that the system dynamics have been stabilized. Looking at the sample trajectory, the system has been damped. The stable dynamics stand in contrast to the Rosenzweig-MacArthur model with constant behavior ($\sigma_p = \sigma_c = 1$) where the point of the Hopf bifurcation has been passed (Rosenzweig 1971), leading to limit cycles.

Fig. 2 Transient strategies of consumers (A) and predators (B) at carrying capacity of $K = 40$ and a competition of $c = 0$ corresponding to the phase portrait Section 5.2.



Both consumer and predator strategies change rapidly at the start of the time-interval, before stabilizing towards the equilibrium values. It appears that the consumers are more present in the most productive area when the predator population is lower, which is not that surprising.

5.3 Population at equilibrium

Fig. 3 Panel (A) shows population levels of consumers (blue) and predators (red) at equilibrium with changing carrying capacity (K). Panel (B) again shows the population levels, but with varying intraspecific predator competition (C).

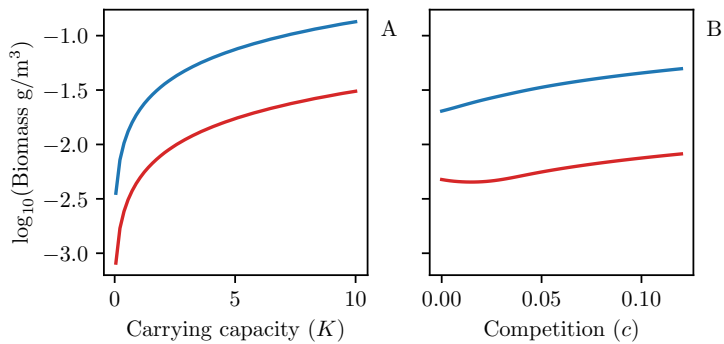


Figure 3 reveals how the population levels of consumers and predators change at equilibrium with varying carrying capacity (Figure 3(A)) and intraspecific predator competition (Figure 3(B)).

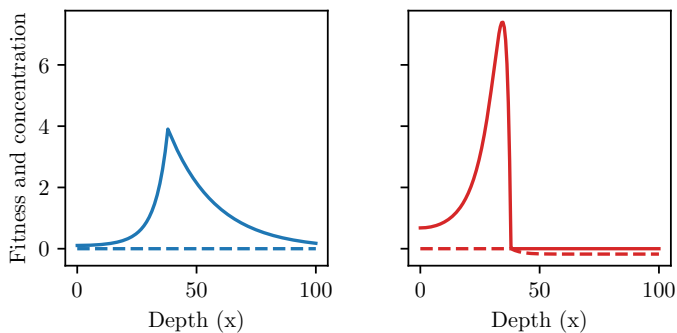
A higher carrying capacity causes higher populations of both consumers and predators populations at equilibrium (Figure 3). The increase in both populations is probably because the behavioral choice allows the consumers to avoid the risk of predation, while achieving the same fitness.

Varying the intraspecific predator competition causes an increase in the population of predators (Figure 3(C, red)) until a point where the population stabilizes (Figure 3($c \approx 1/3$)). The population of consumers continues to increase (Figure 3(C, blue)) throughout.

5.4 Spatial distributions

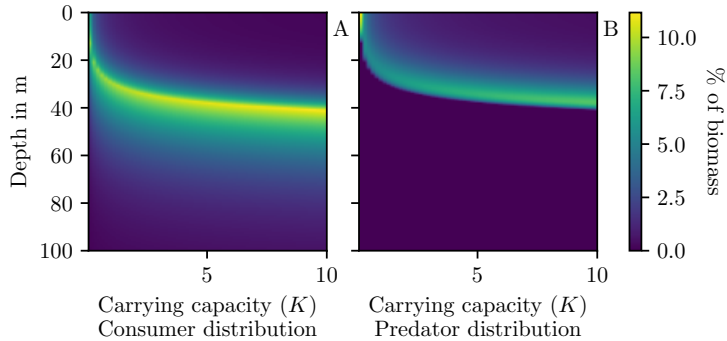
We start by investigating the spatial distribution of consumers and predators compared to their spatially varying fitness ($-dU_c$, $-dU_p$).

Fig. 4 Spatial distribution (full lines) and fitness (dashed lines) of consumers (A) and predators (B) at the equilibrium with carrying capacity $K = 3$.



Both consumers and predator distributions have a constant fitness of zero in the area with coexistence, where the fitness of the predators changes when their concentration is zero. In this we recognize the emergence of the ideal free distribution.

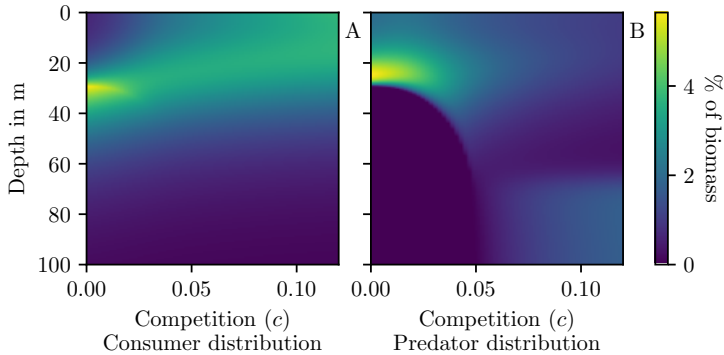
Fig. 5 Spatial distribution of consumers (*A*) and predators (*B*) at the equilibrium with increasing carrying capacity (K).



At low carrying capacity consumers are relatively spread out in the most optimal part of the habitat (0-0.3), while predators are concentrated near the most optimal part (0). As the carrying capacity increases, the distribution of consumers becomes more concentrated, distributed around a peak of 0.4. The peak slowly moves downward with increasing carrying capacity. The consumers can be found throughout the habitat, even at the points of lowest productivity.

Predators go from being concentrated to very spread out, but surprisingly the peak of the predator distribution is just above the peak of the consumer distribution. There are no predators below the band of highly concentrated consumers. This is quite surprising since they have a non-zero encounter rate everywhere. The predator and consumer distributions follow each other as the carrying capacity increases, and appear to approach a stable asymptote.

Fig. 6 Distribution of consumers (*A*) and predators (*B*) at equilibrium under changing predator competition (*c*).



When there is no intraspecific predator competition consumers are highly concentrated at about 0.4, while the predator distributions spreads from 0.4 to 0. The distribution of predators spreads out as we increase competition, before concentrating in the safest zone (1) again. The foraging benefits from clustering on the consumers is outweighed by the risk of encountering other predators. The movement of predators is echoed by the consumers. The consumers spread out and gradually migrate to the most productive area (0). The spreading out of the consumer population though the predator population is concentrated far away is caused by the intraspecific competition between consumers, akin to the ideal free distribution. It appears that both consumer and predator densities are converging to asymptotic densities.

6 Discussion and conclusion

We study population games through the introduction of mean-field games, which generalize the ideal free distribution (Fretwell 1969) to multi-species settings, albeit without the dynamical considerations of the multi-species ideal-free distribution (Cressman and Křivan 2010). We establish existence and uniqueness of Nash equilibria for a large class of population games using variational inequalities. In particular, we are able to handle a wide class of payoff functions with unique extrema and continuous strategy spaces. Having determined existence and uniqueness of Nash equilibrium for the instantaneous game, we showed the existence and uniqueness of fixed-points for suitably nice population games. This provides a simple criterion for population games, extending theorems based on specific models (Cressman and Křivan 2010; Sandholm 2010). As such, our work provides a multi-species generalization of the work on two-species ideal free distributions, (Cressman and Křivan 2010; Cressman et al. 2004) and provides a generalization of the criteria for a unique equilibrium in a habitat selection game (Cressman and Křivan 2006, Appendix B).

We demonstrate the utility of our results by applying them to study a Rosenzweig-MacArthur system with fast optimal behavior. We establish existence and uniqueness of Nash equilibria, both for only consumers or predators and when both have optimal behavior. The method of proof is computational, and hence can almost certainly be extended to larger more complex ecosystems where the Nash equilibrium appears unique but has not been shown to be unique Pinti et al. (2019). This shows that our general results open up the study of population games from a general mathematical viewpoint than has otherwise been the case, (Cressman and Krivan 2010; Krivan 2013; Krivan and Cressman 2009; Broom and Rychtár 2013).

After showing existence and uniqueness, we analyzed the modified Rosenzweig-MacArthur game numerically by discretizing space. Adding optimal individual behavior appears to eliminate the paradox of enrichment (Rosenzweig 1971), which is a common consequence of optimal behavior in ecosystem models (Abrams 2010). We were unable to find a Lyapunov function to provide a theoretical justification (Krivan and Cressman 2009). In the sensitivity analysis we saw that the intraspecific predator competition did not noticeably affect the predator population levels, while elevating the consumer population levels, which was surprising (Abrams 2010). The increase in carrying capacity increased both predator and prey levels, as is usually the case in models with optimal behavior (Valdovinos et al. 2010). The numerical analysis also showed the emergence of an interesting pattern of consumer predator co-existence, with an ideal-free distribution emerging in the areas without any predators. In our numerical experiments we saw that changing the predator competition had a powerful indirect on both distribution and population of prey. The ecological interest of these results is supported by corresponding effects appearing when movement is not instantaneous and information is limited (Flaxman et al. 2011).

Our definition of an evolutionarily stable strategy (ESS) follows (Cressman et al. 2001), but generalized to function spaces. This definition allows for verification of whether a Nash equilibrium is an ESS, without taking population dynamics into account (Cressman and Krivan 2010). Though the definition does directly draw on population dynamics, whether a Nash equilibrium constitutes an ESS can be tested by studying the population dynamics (Grunert et al. 2021). This method of attack may reveal greater insights on the coupling of the population dynamics and the inner game, but is computationally heavy.

The key assumption in our modeling approach is the of instantaneous optimal behavior. Instantaneous optimal behavior in a transient population is reasonable model if there is a decoupling between behavioral and population-dynamical time-scales. If this decoupling is not present, then the populations cannot be expected to follow the simple ideal free distribution at transient states (Abrams et al. 2007; Lou et al. 2014). The evolutionary stability of strategies leading to the simple ideal free distribution can break down, for instance when migrations driven by diffusion (Cantrell et al. 2010), or the resources and interactions are too irregular (Averill et al. 2012). As such, the model of instantaneous optimal behavior must be used with care, but is particularly suited for studying populations at steady-state (Cantrell et al. 2020, 2010, 2012a,b) or populations with separate behavioral and population-dynamical time-scales (Cressman and Krivan 2006; Krivan 2013).

Though the instantaneous ideal free distribution may serve to stabilize the dynamics, this is not always the case when the population dynamics and migration dynamics cannot be modeled on separate time-scales. When the simple ideal free

distribution emerges through an explicit advection-diffusion model in a two-species setting, the simple ideal free distribution can serve to destabilize the population dynamics with a slightly sub-optimal strategy leading to stable population dynamical regime (Zelenchuk and Tsybulin 2021). Showing stability in systems with optimal behavior like the behaviorally modified Rosenzweig-MacArthur system is a hard analytical problem (Krivan and Cressman 2009). It seems a general approach could be drawing on the rapidly developing theory of dynamical variational inequalities (Adly 2018; Brogliato and Tanwani 2020; Tang et al. 2020) or studying dynamical systems associated to bi-level variational inequalities (Anh and Hai 2021). This could also provide a general theory of why optimal behavior generally enhances stability (Valdovinos et al. 2010). It appears that using these tools could be a promising future direction of research.

We have not touched on the topic of differential games, where the optimization is not instantaneous but takes e.g. the entire life-history into account. Variational inequalities can be applied to differential games, (Pang and Stewart 2008), so this seems like a tantalizing next step. This could also provide a logical coupling with advection-diffusion dynamics to study e.g. habitats which are periodic in time (Cantrell et al. 2021).

By introducing mean-field games and studying them through variational inequalities, we show that it is possible to model the distribution of coexisting animal populations where all seek to optimize their foraging in models with strong time-scale separation or at the fixed-point. This enables accurate modeling of the spatial distribution of animals along with their populations, which moves us closer to the ultimate goal of being able to model the spatial distribution of animals exactly (Morris 2003).

Declarations

Funding

This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

Code availability

All code for reproducing the results of this project is available on github https://github.com/jemff/MFG_Static.

Conflict of interest

The authors declare that they have no conflict of interest.

Authors' contributions

E.F.F. designed the study. E.F.F. realized the model design E.F.F. coded the model and chose the numerical approach. E.F.F. analyzed the results along with U.H.T.. E.F.F. wrote the paper. All authors read and approved the final version.

Data availability

All data can be generated using the files `2d_sensitivity.py` and `phase_wrapper.py` at https://github.com/jemff/MFG_Static.

References

- Abrams PA (2010) Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology* 24(1):7–17
- Abrams PA, Cressman R, Krivan V (2007) The role of behavioral dynamics in determining the patch distributions of interacting species. *The American Naturalist* 169(4):505–518
- Acary V, Bonnefon O, Brémond M, Huber O, Pérignon F, Sinclair S (2019) An introduction to siconos. PhD thesis, INRIA
- Adly S (2018) A variational approach to nonsmooth dynamics: applications in unilateral mechanics and electronics. Springer
- Andersen KH (2019) Fish ecology, evolution, and exploitation. In: *Fish Ecology, Evolution, and Exploitation*, Princeton University Press
- Andersson JAE, Gillis J, Horn G, Rawlings JB, Diehl M (2019) CasADi – A software framework for nonlinear optimization and optimal control. *Mathematical Programming Computation* 11(1):1–36, DOI 10.1007/s12532-018-0139-4
- Anh PK, Hai TN (2021) Dynamical system for solving bilevel variational inequalities. *Journal of Global Optimization* 80(4):945–963
- Antonov D, Burovski E, Shchur L (2021) Mean-field interactions in evolutionary spatial games. *Physical Review Research* 3(3):L032072
- Apaloo J, Brown JS, Vincent TL (2009) Evolutionary game theory: Ess, convergence stability, and nis. *Evolutionary Ecology Research* 11(4):489–515
- Astthorsson OS, Gislason A (2003) Seasonal variations in abundance, development and vertical distribution of calanus finmarchicus, c. hyperboreus and c. glacialis in the east icelandic current. *Journal of Plankton Research* 25(7):843–854
- Aumann RJ (1964) Markets with a continuum of traders. *Econometrica: Journal of the Econometric Society* pp 39–50
- Averill I, Lou Y, Munther D (2012) On several conjectures from evolution of dispersal. *Journal of Biological Dynamics* 6(2):117–130
- Avgar T, Betini GS, Fryxell JM (2020) Habitat selection patterns are density dependent under the ideal free distribution. *Journal of Animal Ecology* 89(12):2777–2787
- Barbagallo A, Cojocaru MG (2009) Continuity of solutions for parametric variational inequalities in banach space. *Journal of Mathematical Analysis and Applications* 351(2):707–720
- Blanchet A, Carlier G (2016) Optimal transport and cournot-nash equilibria. *Mathematics of Operations Research* 41(1):125–145
- Brogliato B, Tanwani A (2020) Dynamical systems coupled with monotone set-valued operators: Formalisms, applications, well-posedness, and stability. *Siam Review* 62(1):3–129
- Broom M, Rychtár J (2013) *Game-theoretical models in biology*. CRC Press
- Cantrell RS, Cosner C, Deangelis DL, Padron V (2007) The ideal free distribution as an evolutionarily stable strategy. *Journal of Biological Dynamics* 1(3):249–271
- Cantrell RS, Cosner C, Lou Y (2010) Evolution of dispersal and the ideal free distribution. *Mathematical Biosciences & Engineering* 7(1):17
- Cantrell RS, Cosner C, Lou Y (2012a) Evolutionary stability of ideal free dispersal strategies in patchy environments. *Journal of Mathematical Biology* 65(5):943–965
- Cantrell RS, Cosner C, Lou Y, Ryan D (2012b) Evolutionary stability of ideal free dispersal strategies: a nonlocal dispersal model. *Can Appl Math Q* 20(1):15–38
- Cantrell RS, Cosner C, Lewis MA, Lou Y (2020) Evolution of dispersal in spatial population models with multiple timescales. *Journal of mathematical biology* 80(1):3–37
- Cantrell RS, Cosner C, Lam KY (2021) Ideal free dispersal under general spatial heterogeneity and time periodicity. *SIAM journal on applied mathematics* 81(3):789–813
- Chen Jw, Wan Z, Zou YZ (2014) Bilevel invex equilibrium problems with applications. *Optimization Letters* 8(2):447–461
- Collet S (2019) *Algorithmic game theory applied to networks and populations*. PhD thesis, Université de Paris

- Cressman R, Krivan V (2006) Migration dynamics for the ideal free distribution. *The American Naturalist* 168(3):384–397
- Cressman R, Krivan V (2010) The ideal free distribution as an evolutionarily stable state in density-dependent population games. *Oikos* 119(8):1231–1242
- Cressman R, Garay J, Hofbauer J (2001) Evolutionary stability concepts for n -species frequency-dependent interactions. *Journal of Theoretical Biology* 211(1):1–10
- Cressman R, Krivan V, Garay J (2004) Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *The American Naturalist* 164(4):473–489
- Deimling K (2010) *Nonlinear functional analysis*. Courier Corporation
- Dirkse SP, Ferris MC (1995) The path solver: a nonmonotone stabilization scheme for mixed complementarity problems. *Optimization methods and software* 5(2):123–156
- Flaxman SM, Lou Y, Meyer FG (2011) Evolutionary ecology of movement by predators and prey. *Theoretical Ecology* 4(2):255–267
- Fretwell SD (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica* 19(1):45–52
- Gabay D (1980) On the uniqueness and stability of nash-equilibria in noncooperative games. *Applied Stochastic Control in Econometrics and Management Science*
- Glicksberg IL (1952) A further generalization of the kakutani fixed point theorem, with application to nash equilibrium points. *Proceedings of the American Mathematical Society* 3(1):170–174
- Granas A, Dugundji J (2003) Elementary fixed point theorems. In: *Fixed Point Theory*, Springer, pp 9–84
- Gross T, Rudolf L, Levin SA, Dieckmann U (2009) Generalized models reveal stabilizing factors in food webs. *Science* 325(5941):747–750
- Grunert K, Holden H, Jakobsen ER, Stenseth NC (2021) Evolutionarily stable strategies in stable and periodically fluctuating populations: The rosenzweig–macarthur predator–prey model. *Proceedings of the National Academy of Sciences* 118(4):e2017463118
- Hadjisavvas N, Komlósi S, Schaible SS (2006) *Handbook of generalized convexity and generalized monotonicity*, vol 76. Springer Science & Business Media
- HSL A (2007) A collection of fortran codes for large-scale scientific computation. See <http://www.hsl.rl.ac.uk>
- Iwasa Y (1982) Vertical migration of zooplankton: a game between predator and prey. *The American Naturalist* 120(2):171–180
- Karamardian S (1969) The nonlinear complementarity problem with applications, part 2. *Journal of Optimization Theory and Applications* 4(3):167–181
- Kjørboe T (2011) How zooplankton feed: mechanisms, traits and trade-offs. *Biological reviews* 86(2):311–339
- Kjørboe T, Saiz E, Tiselius P, Andersen KH (2018) Adaptive feeding behavior and functional responses in zooplankton. *Limnology and Oceanography* 63(1):308–321
- Krivan V (1997) Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. *The American Naturalist* 149(1):164–178
- Krivan V (2007) The lotka–volterra predator–prey model with foraging–predation risk trade-offs. *The American Naturalist* 170(5):771–782
- Krivan V (2013) Behavioral refuges and predator–prey coexistence. *Journal of Theoretical Biology* 339:112–121
- Krivan V, Cressman R (2009) On evolutionary stability in predator–prey models with fast behavioural dynamics. *Evolutionary Ecology Research* 11(2):227–251
- Krivan V, Cressman R, Schneider C (2008) The ideal free distribution: a review and synthesis of the game-theoretic perspective. *Theoretical population biology* 73(3):403–425
- Lasry JM, Lions PL (2007) Mean field games. *Japanese journal of mathematics* 2(1):229–260
- Lou Y, Tao Y, Winkler M (2014) Approaching the ideal free distribution in two-species competition models with fitness-dependent dispersal. *SIAM Journal on Mathematical Analysis* 46(2):1228–1262
- Malone MA, Halloway AH, Brown JS (2020) The ecology of fear and inverted biomass pyramids. *Oikos* 129(6):787–798
- Maugeri A, Raciti F (2009) On existence theorems for monotone and nonmonotone variational inequalities. *J Convex Anal* 16(3–4):899–911
- Migot T, Cojocaru MG (2021) On minty-variational inequalities and evolutionary stable states of generalized monotone games. *Operations Research Letters* 49(1):96–100

- Morris DW (2003) Shadows of predation: habitat-selecting consumers eclipse competition between coexisting prey. *Evolutionary Ecology* 17(4):393–422
- Mueter FJ, Nahrgang J, John Nelson R, Berge J (2016) The ecology of gadid fishes in the circumpolar arctic with a special emphasis on the polar cod (*boreogadus saida*)
- Nabetani K, Tseng P, Fukushima M (2011) Parametrized variational inequality approaches to generalized nash equilibrium problems with shared constraints. *Computational Optimization and Applications* 48(3):423–452
- Pang JS, Stewart DE (2008) Differential variational inequalities. *Mathematical programming* 113(2):345–424
- Parker GA (1978) Searching for mates. *Behavioural ecology: an evolutionary approach* 1:214–244
- Pinti J, Kjørboe T, Thygesen UH, Visser AW (2019) Trophic interactions drive the emergence of diel vertical migration patterns: a game-theoretic model of copepod communities. *Proceedings of the Royal Society B* 286(1911):20191645
- Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* pp 385–387
- Sandholm WH (2010) *Population games and evolutionary dynamics*. MIT press
- Schadegg AC, Herberholz J (2017) Satiation level affects anti-predatory decisions in foraging juvenile crayfish. *Journal of Comparative Physiology A* 203(3):223–232
- Smith JM (1982) *Evolution and the Theory of Games*. Cambridge university press
- Stump SM, Chesson P (2017) How optimally foraging predators promote prey coexistence in a variable environment. *Theoretical Population Biology* 114:40–58
- Tang GJ, Cen J, Nguyen VT, Zeng S (2020) Differential variational–hemivariational inequalities: existence, uniqueness, stability, and convergence. *Journal of Fixed Point Theory and Applications* 22(4):1–30
- Thygesen U, Patterson T (2018) Oceanic diel vertical migrations arising from a predator-prey game. *Theoretical Ecology* 12(1):17–29
- Valdovinos FS, Ramos-Jiliberto R, Garay-Narváez L, Urbani P, Dunne JA (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology letters* 13(12):1546–1559
- Vincent TL, Brown JS (2005) *Evolutionary game theory, natural selection, and Darwinian dynamics*. Cambridge University Press
- Wächter A, Biegler LT (2006) On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. *Mathematical programming* 106(1):25–57
- Yodzis P, Innes S (1992) Body size and consumer-resource dynamics. *The American Naturalist* 139(6):1151–1175
- Zelenchuk P, Tsybulin V (2021) The ideal free distribution in a predator–prey model with multifactor taxis. *Biophysics* 66(3):464–471

A Calculations

A.1 Existence

We complete the omitted calculations from the main text. Initially,

$$\begin{aligned}
\langle -dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle &= \left\langle \frac{N_c \sigma_c}{K_0 + K\varphi} - 1, \sigma_c - 1 \right\rangle \\
&\quad + \left\langle \frac{F_p N_p \beta_p \sigma_p}{F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle}, \sigma_c - 1 \right\rangle \\
&\quad - \left\langle \frac{\varepsilon F_p^2 N_c \beta_p \sigma_c}{(F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle)^2}, \sigma_p - 1 \right\rangle \\
&\quad + \langle N_p c \beta_p \sigma_p, \sigma_p - 1 \rangle
\end{aligned} \tag{51}$$

Using that $\langle 1, \sigma \rangle = 1$, we can write out Equation (51) and gather the positive and negative terms

$$\begin{aligned}
\langle -dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle &= \\
&\quad \left\langle \frac{N_c \sigma_c}{K_0 + K\varphi}, \sigma_c \right\rangle + \langle N_p c \beta_p \sigma_p, \sigma_p \rangle \\
&\quad + \left\langle \frac{F_p N_p \beta_p \sigma_p}{F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle}, \sigma_c \right\rangle - \left\langle \frac{\varepsilon F_p^2 N_c \beta_p \sigma_c}{(F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle)^2}, \sigma_p \right\rangle \\
&\quad - \|N_p c \beta_p \sigma_p\|_1 - \left\| \frac{N_c \sigma_c}{K_0 + K\varphi} \right\|_1 - \left\| \frac{N_p F_p \beta_p \sigma_p}{F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle} \right\|_1 \\
&\quad - \left\| \frac{\varepsilon F_p^2 N_c \beta_p \sigma_c}{(F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle)^2} \right\|_1
\end{aligned} \tag{52}$$

To handle Equation (52), we consider the individual terms. We start by considering the terms:

$$\begin{aligned}
&\left\langle \frac{F_p N_p \beta_p \sigma_p}{F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle}, \sigma_c \right\rangle, \\
&\left\langle \frac{\varepsilon F_p^2 N_c \beta_p \sigma_c}{(F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle)^2}, \sigma_p \right\rangle
\end{aligned} \tag{53}$$

We see both terms in Equation (53) are uniformly bounded in (σ_c, σ_p) over $P_{2,\mu}^2$, hence so is their difference $W_0(\sigma_c, \sigma_p)$. Defining $C_1 = \frac{1}{K_0 + K \text{ess sup } \varphi}$ and $C_2 = c \text{ess inf } \beta_p$ we can rewrite Equation (52) as:

$$\begin{aligned}
\langle -dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle &\geq C_1 \|\sigma_c\|_2^2 + C_2 \|\sigma_p\|_2^2 \\
&\quad - \|c \beta_p \sigma_p\|_1 - \left\| \frac{\sigma_c}{K_0 + K\varphi} \right\|_1 - \left\| \frac{F_p N_p \beta_p \sigma_p}{F_p + N_c \langle \beta_p \sigma_p, \sigma_c \rangle} \right\|_1 \\
&\quad - \left\| \frac{F_p^2 N_c \beta_p \sigma_c}{(F_p + \langle \beta_p \sigma_p, \sigma_c \rangle)^2} \right\|_1 + W_0(\sigma_c, \sigma_p)
\end{aligned} \tag{54}$$

Since $\|\sigma_i\|_1 = 1, i \in \{c, p\}$, all terms involving $\|\cdot\|_1$ in Equation (52) are uniformly bounded, and can be gathered with W_0 in a single uniformly bounded function W . Hence we end with:

$$\langle -dU(\sigma_c, \sigma_p), (\sigma_c - 1, \sigma_p - 1) \rangle \geq C_1 \|\sigma_c\|_2^2 + C_2 \|\sigma_p\|_2^2 - W(\sigma_c, \sigma_p) \tag{55}$$

PAPER D

Coupling population dynamics and diel migration patterns

Highlights

Copuling population dynamics and diel migration patterns *

Emil F. Frølich

- The diel migration is shown to be linked to productivity
- We couple mean-field games and population dynamics
- The ideal free distribution emerges from a mean-field game

Copuling population dynamics and diel migration patterns

Emil F. Frølich^a

^a*DTU Compute, Building 324, Richard Petersens Plads, Kgs. Lyngby, 2800, , Denmark*

Abstract

The diel vertical migration is one of the main drivers of population dynamics in the ocean. Population dynamical models of the ocean typically do not incorporate the behavioral aspects of the migration. We demonstrate a model with coupled population dynamics and behavior with the diel vertical migration emerging. We study the population dynamics and behavioral dynamics of a predator-prey system. We impose a cost of motion for both consumers and prey, and model each individual as following an Ito stochastic differential equation. We study the fixed-points of the ecosystem. Our modeling shows that as we increase the basal resource load, the strength of the diel vertical migration increases, as well as maximal velocity. In addition, a bimodal pattern emerges both for predators and consumers. The increase in the magnitude of the diel vertical migration causes a change in the allocation of copepod resources.

Keywords:

diel vertical migration, mean-field games, predator-prey, ideal free distribution

1. Introduction

The diel vertical migration is an inescapable fact of ocean life, constituting the largest migration of animals on the planet. Though the diel vertical migration is driven by behavior, models of ocean population dynamics typically include the diel vertical migration as a mechanistic phenomenon (van Denderen et al., 2021), if at all (Andersen, 2019). When the diel vertical migration is included, it is often included by simply dividing a 24-hour period into two phases, a day and a night phase (Iwasa, 1982). The introduction of vertical migrations driven behavioral choices in this binary division has a major impact on ecosystem function (Pinti et al., 2021). The division of the day into just a day-night cycle has a major weakness, that is ocean population dynamics to a large degree are driven by the interactions at dusk and dawn (Benoit-Bird and McManus, 2014). A binary simplification of the day can not catch this dynamic of dusk

*This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

and dawn, so a finer division of the day could be expected to explain more of the impact of behavior.

The diel vertical migration is a prime candidate for a phenomenon to model as a game Pinti et al. (2019), but incorporating both continuous space and time is non-trivial, but has been modeled (Thygesen and Patterson, 2018). A general approach incorporating population dynamics in the approach of (Thygesen and Patterson, 2018) exists (Frölich and Thygesen, 2022). This approach has the assumption that assumes animals choose their optimal location at each instant in time, moving instantaneously. This requires that behavior is much faster than population dynamics and that movement happens at approximately the same time-scale for the different types of animals (Cressman and Krivan, 2006). Neither of these assumptions are necessarily satisfied in an aquatic setting with sufficiently big differences in sizes (Thygesen et al., 2016). The simplifying assumption that predators and prey do not plan their decisions over a longer time-horizons but move at every instant also contrasts observations (Schadegg and Herberholz, 2017). A final element which has been left unaccounted for in models of the diel vertical migration is the effect of non-linearity in shaping behavior in predator-prey interactions (Thygesen and Mazuryn, 2022). In particular, predator-prey interactions have generally been modeled as governed by Type I functional responses, with notable exceptions in the case of a day in two parts (Pinti et al., 2019).

Drawing the above together, there is a need for a robust approach to model the diel vertical migration incorporating both population dynamics and emergent behavior. When very large populations interact and the payoff for an individual depends on the overall distribution of the populations, the method of mean-field games can be used (Lasry and Lions, 2007). As the populations involved in the diel vertical migrations are large (Mariani et al., 2016) the interactions can be modeled as a mean-field game (Thygesen and Mazuryn, 2022; Mazuryn and Thygesen, 2022). As the diel vertical migration drives ocean population dynamics, (Benoit-Bird and McManus, 2014) understanding the interplay between the diel vertical migration and population dynamics is key to a greater understanding of ocean population dynamics. Using a model based on individual behavior also allows an explicit study of resource allocation of copepods, as theoretical models and empirical measurements of copepod energy budgets are rarely in agreement (Vlymen, 1970; Svetlichny et al., 2000). Hence a model which can uncover these relationships is a desirable goal.

In this paper, we study a predator-prey system where both the predator and prey populations are modeled through the mean-field game framework introduced by (Lasry and Lions, 2007). This lets us model the diel vertical migration as an emergent phenomenon from behavior, allowing us to study the interplay between the fixed-point population levels and behavior. Having the diel vertical migration emerge organically allows us to understand how individual trade-offs and behavior change with a varying resource load, and the effect on population dynamics. Specifically, we study how the population equilibrium changes with changing resource load, and how the resource allocation of an individual changes. We find that a changing carrying capacity can explain the

myriad patterns observed in the diel vertical migrations, and that the allocation of resources of phytoplankton to movement is dependent on the carrying capacity.

2. Methods

We consider a tri-tropic marine ecosystem with a resource N_r , a consumer population N_c and a predator population N_p . We model a marine ecosystem with phytoplankton as resource, copepods as the consumers and forage fish as predators. We assume the resources are well-mixed and have the same distribution r_p in the water column at all times. The distribution of the copepod population is $\bar{\sigma}_c$ and the distribution of the forage fish population is $\bar{\sigma}_p$. These two distributions vary in time.

2.1. Individual and population movement

We model the movement of an individual copepod (c) or forage fish (p) by an Itô stochastic differential equation with constant noise intensity κ

$$dX_t^i = v_t^i dt + \kappa dB_t \quad (1)$$

We assume that the functional responses of both copepods and forage fish can be described by a Type II model. We presume that individuals of type i have maximal growth rates F_i and clearance rates β_i $i \in \{c, p\}$. We assume that consumers and predators have conversion efficiencies ε_i , $i \in \{c, p\}$. The specific growth rate of a consumer at position x is

$$G_c(x, t, N_r) = \varepsilon_c \frac{F_c N_r \beta_c r_p(x)}{F_c + \beta_c N_r(x)} \quad (2)$$

Phytoplankton growth is modeled by as a chemostat, denoting the expectation value by $E(\cdot)$ the mortality M_r of the phytoplankton population is:

$$M_r = \frac{1}{\varepsilon_c} E(G_c) \quad (3)$$

The mortality M_c of a consumer at a point x depends on the number of predators at x . The number of predators depends both on the total predator population and the distribution of the predator population $\bar{\sigma}_p$. The other factor is the satiation of the predators, which depends on the distribution of the consumers. This gives a specific consumer mortality:

$$M_c(x, t, N_r, N_c, N_p) = \frac{F_p \bar{\sigma}_p(x, t) \beta_p(x, t) N_p}{F_p + N_c \bar{\sigma}_p(x, t) \bar{\sigma}_c(x, t)} \quad (4)$$

An individual can control their swimming velocity. Moving expends energy as it induces drag. Drag is proportional to the square of the velocity,

$$\nu_c(x, t) = \frac{\gamma_c}{2} v^2(x, t) \quad (5)$$

This leads an individual consumer to seek the strategy v_c^t which maximizes the expected value over 24 hours of

$$J_c(x, t, N_p, N_c, N_r) = G_c - M_c - \nu_c \quad (6)$$

That is, an individual consumer seeks the velocity which maximizes their expected fitness:

$$EF_c(v, \bar{\sigma}_c, \bar{\sigma}_p) = E \left(\int_0^{24} J(x, t) dt \right) \quad (7)$$

Analogously, the specific growth rate of a predator G_p depends on the number of consumers N_c and their distribution $\bar{\sigma}_c$ and is

$$G_p(x, t, N_c) = \frac{F_p N_c \beta_p(x, t) \bar{\sigma}_c}{F_p + N_c \beta_p(x, t) \bar{\sigma}_c} \quad (8)$$

We now switch our focus to the forage fish. The vertical migration of forage fish is dependent on swimbladder dynamics. Using a swimbladder is more energy efficient than swimming, but creates complex relationship between energy and speed (Strand et al., 2005). For this reason we simply model the scaling as scaling with the drag. The loss from drag ν_p is

$$\nu_p(x, t) = \frac{\gamma_p}{2} v_p^2(x, t) \quad (9)$$

Defining $J_p(x, t) = G_p(x, t, N_c) - \nu_p(x, t)$, a predator seeks to maximize:

$$EF_p = E \left(\int_0^{24} G_p - \nu_p dt \right) \quad (10)$$

The optimal strategy for a predator a consumer at each point in space and time (x, t) can be found by solving a Hamilton-Jacobi-Bellman (HJB) equation. Remark that we have simplified the mortality, by assuming the mortality contributes with an energy loss. Solving the HJB equations simultaneously then leads to a solution of the differential game, without taking the mean-field phenomena into account. The HJB equation describing the optimal value for a consumer V_c and a predator V_p , is

$$-\frac{\partial v_i^t}{\partial t} = \sup_v \left(J_i(x, t) + v_i^t \nabla_x v_i^t + \frac{\kappa}{2} \frac{\partial^2 v_i^t}{\partial x^2} \right) \quad i = \{c, p\} \quad (11)$$

The optimal value of v_i^t , $i = \{c, p\}$ is then

$$v_i^t = \frac{1}{\gamma_i} \nabla_x v_i^t \quad (12)$$

i.e. the optimal strategy for both consumers and predators is to climb along the gradient of the value function at a rate inversely proportional to the scale of the cost of motion.

We now have the equations to find an optimal strategy for an individual, given the overall distributions of the populations. This is where the mean field approach of Lasry and Lions (2007) comes into play. Given that each individual follows the optimal strategy, the distributions of predator and prey each evolve according to the Fokker-Planck equation.

$$\frac{\partial \bar{\sigma}_i}{\partial t} = -\nabla_x(v_i^t \bar{\sigma}_i) + \frac{\partial^2 \bar{\sigma}_i}{\partial x^2} \quad (13)$$

2.2. Population dynamics

The growth of each population is given by the expected fitness of an individual minus their metabolic rate μ_i , $i \in \{c, p\}$ multiplied by the total population size. Note the metabolic rate was not included in the fitness functional, as the metabolic rate does not depend on behavior in contrast to the losses from mortality and movement. The population dynamics can therefore be described by the equations in Equation (14).

$$\begin{aligned} \dot{N}_r &= \lambda(\bar{R} - N_r) - M_r \\ \dot{N}_c &= N_c(E(J_c) - \mu_c) \\ \dot{N}_p &= N_p(E(J_p) - \mu_p) \end{aligned} \quad (14)$$

We consider the population-dynamical equilibrium on a 24-hour scale. This imposes the additional set of constraints:

$$\begin{aligned} \int_0^{24} \dot{N}_r dt &= 0 \\ \int_0^{24} \dot{N}_c dt &= 0 \\ \int_0^{24} \dot{N}_p dt &= 0 \end{aligned} \quad (15)$$

Solving Equation (14) and Equation (15) together let us find a periodic population-dynamical equilibrium.

2.3. Environment and encounters

We model an ecosystem in a water column, where the dominating factors are the light intensity throughout the day and the resources available for the copepods. Copepods are olfactory predators, so their clearance rate β_c is constant throughout the water column. We presume that light attenuates through the water column by e^{-kz} where z describes the depth from the surface. As forage fish are visual predators, their clearance rate β_p depends on the light-levels I , with a small term β_0 capturing other modes of sensing food and direct encounters. We model the predation rate as a function of light decay as in (Pinti et al., 2021), leading to Equation (16)

$$\beta_{p,c} = \frac{I}{1 + \exp(kz)} + \beta_0 \quad (16)$$

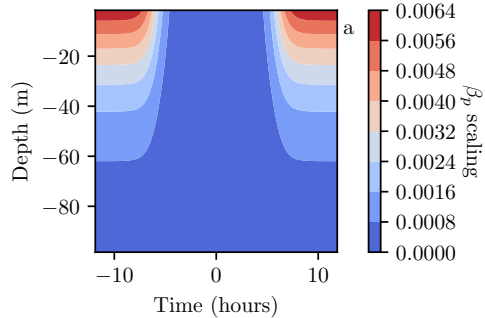


Figure 1: The daily variation in clearance rate for the predators.

As the optical system is satiated beyond some threshold (Thygesen and Patterson, 2018), we model the variation in clearance rate I in Equation (16) caused by the day night cycle as a periodic function varying from 0 to 1 smoothly, keeping the values 0 and 1 constant throughout the night and day respectively, leading to the daily variation in clearance rates seen in Figure 1. We model the distribution of phytoplankton r_p as constant in space and time, with a rate of decline c and a fixed mixed layer depth of x_{mld} Section 2.3 as in (Thygesen and Mazuryk, 2022).

$$r_p = \frac{1}{1 + c(\exp(x - x_{mld}))} \quad (17)$$

2.4. Parameters

Metabolic function, clearance rate and maximal consumption rate in an aquatic ecosystem typically all scale according to Kleibers law, scaling by the mass of an individual to the power of 0.75, (Yodzis and Innes, 1992). The metabolic rate and maximal consumption rate are typically related by $F_i = 10\mu_i$. Using the values in (Andersen, 2019, Table 2.2), and (Thygesen and Mazuryk, 2022) we arrive at the following parameters.

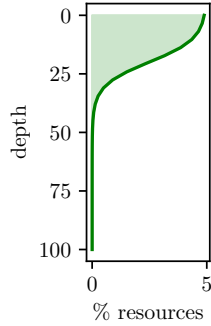


Figure 2: The distribution of the basal resource.

Meaning	Symbol	Value
Copepod mass	m_c	0.05 g
Forage fish mass	m_p	20 g
Consumer clearance	β_c	33 m ³ /year
Minimum clearance	β_0	1.5 m ³ /year
Predator clearance	β_p	3120 m ³ /year
Maximal consumer consumption	F_c	2 g/year
Maximal predator consumption	F_p	190 g/year
Consumer conversion rate	ε_c	0.26
Predator conversion rate	ε_p	0.46
Carrying capacity	\bar{R}	Varies
Renewal rate	λ	1 /year
Consumer metabolic rate	μ_c	0.2 g/year
Predator metabolic rate	μ_p	3.1 g/year
Consumer drag	γ_c	$10^{-6} \cdot 1/6$ Jh/m ²
Predator drag	γ_p	$10^{-5} \cdot 1/6$ Jh/m ²
Light dispersal	k	0.05/m
Noise	κ	1 m ² /h
Mixed layer depth	x_{mld}	20 m
Resource gradient	c	0.2/m

Our model ecosystem is the north sea, which has an average depth of 100m, allowing comparison with the case study in (Frølich and Thygesen, 2022).

2.5. Numerical approach

Our numerical approach is based on the concept of grid-refinement. We discretize the differential operators according to a second-order scheme, and discretize the integration according to the finite element method. We start by solving the system at low spatial and temporal resolution (4x12) using

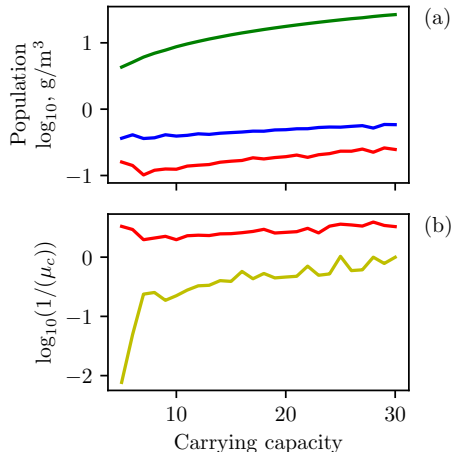


Figure 3: (a) Daily average of resource (green), consumer (blue) and predator (red) population levels as a function of carrying capacity at steady-state. (b) Energy budget of a consumer as a function of carrying capacity, mortality compared to metabolism M_c/μ_c (red) and swimming costs in comparison to metabolism, v_c/μ_c (yellow)

CasADi (Andersson et al., 2019) to deliver exact derivatives to the interior-point solver IPOPT (Wächter and Biegler, 2006). In order to improve both speed and convergence of the interior point solver, we use the HSL numerical libraries (HSL, 2007). Having solved the system at low spatial and temporal resolution, we gradually increase the resolution. We do this by interpolating a guess to a solution the system at step $n + 1$ based on step n . This is done using the interpolation tools in SciPy, `interp2d` and `interp1d`.

3. Results

Increasing the carrying capacity of the basal resource has essentially no effect on the higher trophic levels Figure 3 (a, blue red), but causes a marked increase in the resource population (a, green). At the finer scale, the increase in carrying capacity by a factor of ten causes an approximate doubling of the consumer population, and also an increase in the predator population.

We see that the energy expenditure to predation remains approximately constant Figure 3(b, red), while the energy allocated to movement increases and then plateaus Figure 3(b, yellow). Hence the total expected consumption must rise to a plateau, and then level off. At low carrying capacities basal metabolism accounts for two-thirds of energy consumption Figure 3(b), decreasing to a bit less than 25% at the maximal carrying capacity.

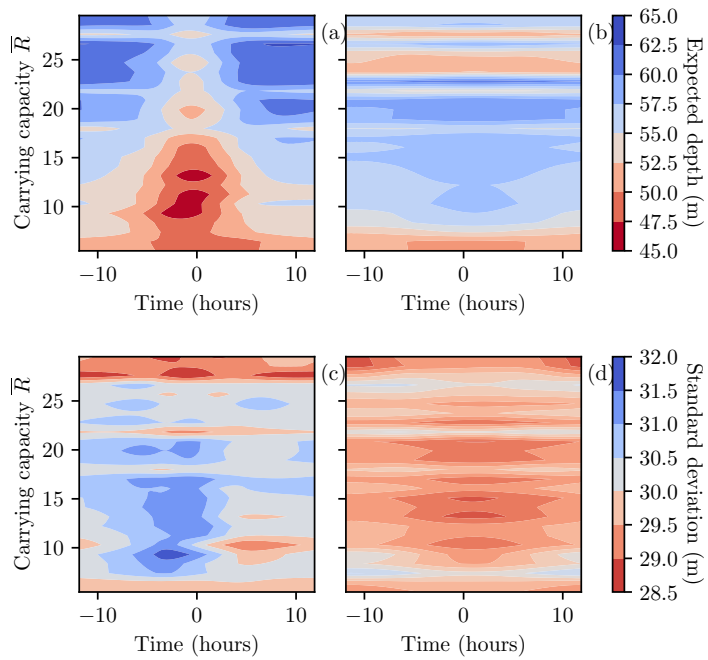


Figure 4: Average location across the day with varying capacity for a consumer (a) and predator (b) and standard deviation of location of consumers (c) and predators (d)

In the Figure 4 (a) we see the emergence of the diel vertical migration of copepods as the carrying capacity increases. With a greater carrying capacity comes a larger energy budget, allowing an individual consumer to migrate up and down to increase their survivability. This is also reflected in the standard deviation of their distribution Figure 4 (c), which is highest during the migration down, adding safety, and lowest during the migration up. For the predators the situation is quite different Figure 4(b). Predators are spread throughout the water column with approximately the same depth throughout the day Figure 4(b), albeit with a vertical migration for low carrying capacities capacity (Figure 4(b, 5-8), then moving to a reverse migration at medium to high carrying capacities Figure 4(d, 20-25). The distributions, are however, essentially unchanged throughout the day.

We see the emergence of three distinct migration patterns for the consumers. At low resource levels, the consumers have a bimodal distribution, but are essentially distributed across the water column Figure 5 (a). At medium resource levels, the consumer population has bifurcated Figure 5 (b). There is a part of the population which is always concentrated at the top,, while the part of the consumer population which is concentrated at the bottom conducts a larger vertical migration Figure 5(b) . If we then proceed to the high-resource case Figure 5 (c), the situation is again completely changed. Now we have a unimodal consumer distribution, this time concentrated at the bottom with a migration towards the top of the water column. What we see is a behavioral emergence of a layer below the surface so the maximal zoo-plankton concentration is not at the top but at a point below the top. The situation for the predators is less interesting, with a standard vertical migration emerging from at low carrying capacities Figure 5 (d) switching to a reverse migration Figure 5(e, f) carrying capacities. A much greater change occurs in the modality, with a bimodal distribution at a low carrying capacity Figure 5 (d), switching to a unimodal one at medium and high carrying capacity Figure 5(e, f). We note that as a general trend, particularly noticeable in Figure 5(b) is that the zoo-plankton migrate down before sunrise (6), anticipating the changing environment. This difference in modes can also be seen in the standard deviation of their distribution Figure 4(d) As could be expected from the migration patterns, the speed of the predators across varying resources is approximately constant Figure 6 (d,e,f), while the consumers drastically increase their speed Figure 6(a) to Figure 6(b) and increase the range and time where they swim fast Figure 6(c). As such the changes in movement patterns are two-fold, with more mobile zooplankton across a larger range both in space and time. This ties into the expected energy consumption, which does not change essentially from Figure 6(b) to Figure 6(c) for the consumers, see Figure 3(b). This is due to the concentration at the bottom, so though the swimming speeds are high a consumer does not expect to encounter these swimming speeds.

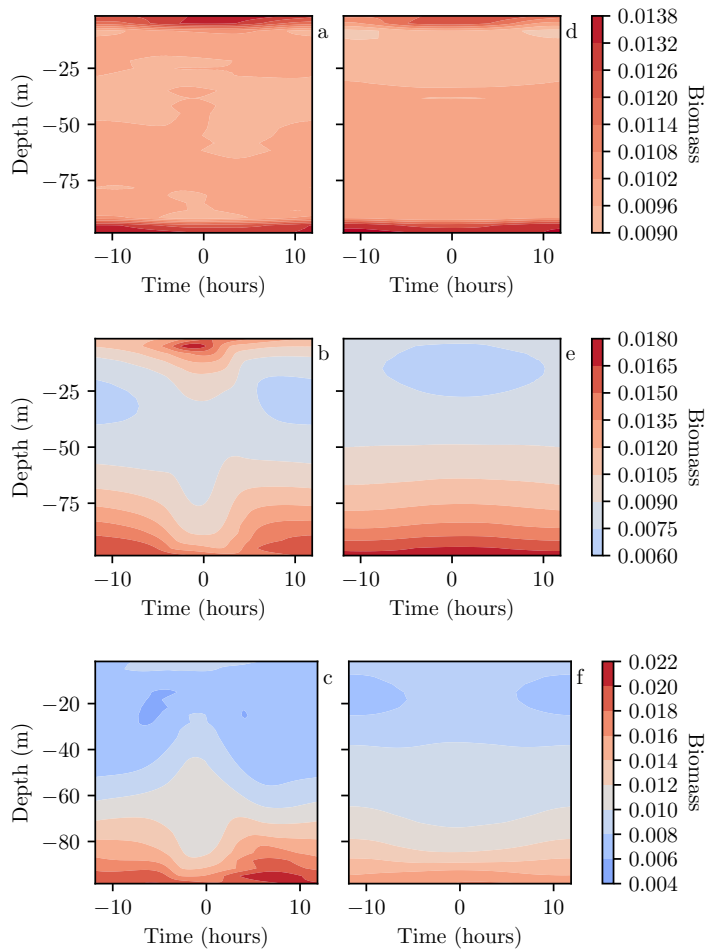


Figure 5: Distribution of consumers (a, b, c) and predators (d, e, f) at low (a,d), medium (b,e), and high (c,f) resource levels.

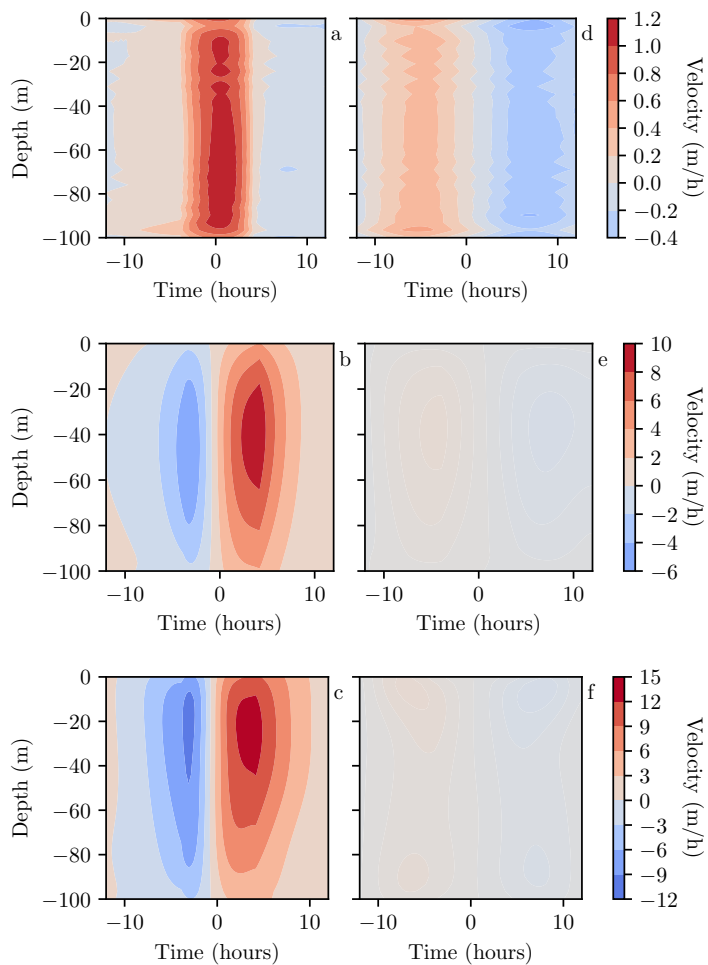


Figure 6: Speed of consumers (a, c) and predators (b, d) at low (5, a, b) and high resource levels (50, b, e)

4. Discussion

At the behavioral level, our results show that the diel vertical migration of copepods and forage fish can be understood as an emergent behavioral strategy in response to bottom-up forcing. We see the emergence of different modalities at different levels of basal productivity, with bimodal distributions and unimodal distributions appearing depending on the resource load. The energy budget of an individual copepod changes drastically as the carrying capacity rises, with active energy usage increasing relative to metabolism. At the same time, the mortality risk falls, as the behavioral adaptation in swimming faster allows for greater risk aversion.

In our system where forage fish are at no risk of predation, their optimal behavior at population equilibrium is essentially to stand still in the water column. At the population level, our results reiterate the point that the ecosystem enrichment hypothesis is insufficient to explain the effect of enrichment. In particular, we see that the primary grazers increase in population while the predators decline.

4.1. Population-level phenomena

We find both bimodal and unimodal distributions of zooplankton at population equilibrium. Bimodal distributions emerge at medium productivities, corresponding to e.g. the start of fall in agreement with observations (Hattori, 1989). The two kinds of unimodal migration in our model, concentrated either at the top or bottom, represent respectively high and low productivity, and could be tested empirically to see migration modes (Hays et al., 2001; Bayly, 1986). Thus our model provides a direct coupling between productivity and behavior, serving to explain empirical observations of the variation in zooplankton behavior with respect to seasons and latitudes (Hattori, 1989).

The result that forage fish do not migrate to any serious degree is quite surprising. This contradicts findings when behavior is assumed instantaneous (Thygesen and Patterson, 2018; Frølich and Thygesen, 2022). This difference may be occasioned by the stable population levels in our model, so our results show that bottom-up pressure is not always sufficient to drive a migratory pattern for predators. In reality, forage fish are themselves subject to massive predation pressure and their migration is also influenced by this. An interesting side-effect is that this results vindicates modeling the threat of predation by a light-dependent mortality field (Thygesen and Mazuryn, 2022) to model a simple predator-prey system.

The impact on population levels is in tune with what is usually found in models of optimal behavior, with all trophic levels increasing due to optimal behavior (Valdovinos et al., 2010).

4.2. Individual impacts

The optimal strategy is following the gradient of an optimal value function, which reflects the underlying structure in the ocean. That copepods follow such a strategy is plausible, as copepods follow the physical gradients associated with

ocean structure, i.e. light and productivity (Woodson et al., 2005). These are exactly the two features which determine the value function. As such, our model provides a behavioral explanation for both individual phenonema and large-scale movements. The expected energetic requirements of swimming compared to metabolism that we find range from 5% to 70%. This is an extremely wide range, and matches the measured energy expenditure of swimming copepods which lies in a range of 10-60% of metabolism (Svetlichny et al., 2000; Epp and Lewis, 1984). This illustrates that behavioral models provides realistic predictions for energy expenditure, improving on purely fluid-dynamical approaches (Vlymen, 1970; Visser, 2007).

4.3. Game theory and model

The optimal movement strategy we find is the evolutionarily stable strategy migration strategy in a constant environment (Cantrell et al., 2012), of constantly moving towards better fitness. As we investigate the Nash equilibrium at a population dynamical equilibrium the expected payoff for each individual of each type is the same for every path, namely zero. Hence the emergent distributions in our model constitute an ideal free distribution (Cantrell et al., 2021), and the strategies are evolutionarily stable, (Cantrell and Cosner, 2018). This is illustrated by the emergent migration patterns where we see a diving down before daybreak, i.e. a use of non-local temporal information. This is one of the hallmarks of a temporally periodic ideal free distribution, (Cantrell et al., 2021), and a key point of difference from the standard ideal free distribution (Parker, 1978). The emergence of the ideal free distribution supports further investigation of ecosystem models incorporating both mean-field games and population dynamics, as being distributed according to the ideal free distribution is one of the chief features of realistic models of population distribution (Cressman and Krivan, 2010).

4.4. Conclusion

In conclusion, our results show that it is possible to solve multi-species population games in continuous space and time, taking both population dynamics and behavior into account. We show that mean-field games have a natural place in studying population games with population dynamics. In this work we considered a simple predator-prey model with continuous space and time, but there is no reason to believe complex ecosystems could not be studied with the same approach. This expands the ecosystems where behavior and population dynamics can naturally be coupled, and paves the way to incorporating optimal behavior in large-scale population models e.g. for fisheries management.

Declarations

Funding

This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

Code availability

All code for reproducing the results of this project is available on github https://github.com/jemff/predator_preymodel_NE.

Conflict of interest

The authors of Copuling population dynamics and diel migration patterns declare that they have no conflict of interest.

Authors' contributions

E.F.F. designed the study. E.F.F. realized the model design. E.F.F. coded the model and chose the numerical approaches. E.F.F. analyzed the results. E.F.F. wrote the paper.

Data availability

All data can be generated using the file `dvm_data_gen.py` from https://github.com/jemff/multi_species_water

References

- Andersen, K.H., 2019. Fish ecology, evolution, and exploitation, in: *Fish Ecology, Evolution, and Exploitation*. Princeton University Press.
- Andersson, J.A.E., Gillis, J., Horn, G., Rawlings, J.B., Diehl, M., 2019. CasADi – A software framework for nonlinear optimization and optimal control. *Mathematical Programming Computation* 11, 1–36. doi:10.1007/s12532-018-0139-4.
- Bayly, I., 1986. Aspects of diel vertical migration in zooplankton, and its enigma variations, in: *Limnology in Australia*. Springer, pp. 349–368.
- Benoit-Bird, K.J., McManus, M.A., 2014. A critical time window for organismal interactions in a pelagic ecosystem. *PLoS One* 9, e97763.
- Cantrell, R.S., Cosner, C., 2018. Evolutionary stability of ideal free dispersal under spatial heterogeneity and time periodicity. *Mathematical biosciences* 305, 71–76.
- Cantrell, R.S., Cosner, C., Lam, K.Y., 2021. Ideal free dispersal under general spatial heterogeneity and time periodicity. *SIAM journal on applied mathematics* 81, 789–813.
- Cantrell, R.S., Cosner, C., Lou, Y., Ryan, D., 2012. Evolutionary stability of ideal free dispersal strategies: a nonlocal dispersal model. *Can. Appl. Math. Q.* 20, 15–38.
- Cressman, R., Krivan, V., 2006. Migration dynamics for the ideal free distribution. *The American Naturalist* 168, 384–397.

- Cressman, R., Krivan, V., 2010. The ideal free distribution as an evolutionarily stable state in density-dependent population games. *Oikos* 119, 1231–1242.
- van Denderen, P.D., Petrik, C.M., Stock, C.A., Andersen, K.H., 2021. Emergent global biogeography of marine fish food webs. *Global Ecology and Biogeography* 30, 1822–1834.
- Epp, R.W., Lewis, W.M., 1984. Cost and speed of locomotion for rotifers. *Oecologia* 61, 289–292.
- Frölich, E.F., Thygesen, U.H., 2022. Solving multispecies population games in continuous space and time. *Theoretical Population Biology* 146, 36–45.
- Hattori, H., 1989. Bimodal vertical distribution and diel migration of the copepods *metridia pacifica*, *m. okhotensis* and *pleuromamma scutullata* in the western north pacific ocean. *Marine Biology* 103, 39–50.
- Hays, G., Kennedy, H., Frost, B., 2001. Individual variability in diel vertical migration of a marine copepod: why some individuals remain at depth when others migrate. *Limnology and Oceanography* 46, 2050–2054.
- HSL, A., 2007. A collection of fortran codes for large-scale scientific computation. See <http://www.hsl.rl.ac.uk>.
- Iwasa, Y., 1982. Vertical migration of zooplankton: a game between predator and prey. *The American Naturalist* 120, 171–180.
- Lasry, J.M., Lions, P.L., 2007. Mean field games. *Japanese journal of mathematics* 2, 229–260.
- Mariani, P., Krivan, V., MacKenzie, B.R., Mullon, C., 2016. The migration game in habitat network: the case of tuna. *Theoretical ecology* 9, 219–232.
- Mazuryn, M., Thygesen, U., 2022. Mean field games for diel vertical migration with diffusion. Under review.
- Parker, G.A., 1978. Searching for mates. *Behavioural ecology: an evolutionary approach* 1, 214–244.
- Pinti, J., Andersen, K.H., Visser, A.W., 2021. Co-adaptive behavior of interacting populations in a habitat selection game significantly impacts ecosystem functions. *Journal of Theoretical Biology* 523, 110663.
- Pinti, J., Kjørboe, T., Thygesen, U.H., Visser, A.W., 2019. Trophic interactions drive the emergence of diel vertical migration patterns: a game-theoretic model of copepod communities. *Proceedings of the Royal Society B* 286, 20191645.
- Schadegg, A.C., Herberholz, J., 2017. Satiation level affects anti-predatory decisions in foraging juvenile crayfish. *Journal of Comparative Physiology A* 203, 223–232.

- Strand, E., Jørgensen, C., Huse, G., 2005. Modelling buoyancy regulation in fishes with swimbladders: bioenergetics and behaviour. *Ecological Modelling* 185, 309–327.
- Svetlichny, L., Hubareva, E., Erkan, F., Gucu, A., 2000. Physiological and behavioral aspects of calanus euxinus females (copepoda: Calanoida) during vertical migration across temperature and oxygen gradients. *Marine Biology* 137, 963–971.
- Thygesen, U., Patterson, T., 2018. Oceanic diel vertical migrations arising from a predator-prey game. *Theoretical Ecology* 12, 17–29.
- Thygesen, U.H., Mazuryn, M., 2022. Ideal free flows of optimal foragers: Vertical migrations in the ocean. *Theoretical Ecology* , 1–12.
- Thygesen, U.H., Sommer, L., Evans, K., Patterson, T.A., 2016. Dynamic optimal foraging theory explains vertical migrations of bigeye tuna. *Ecology* 97, 1852–1861.
- Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P., Dunne, J.A., 2010. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology letters* 13, 1546–1559.
- Visser, A.W., 2007. Motility of zooplankton: fitness, foraging and predation. *Journal of Plankton research* 29, 447–461.
- Vlymen, W.J., 1970. Energy expenditure of swimming copepods. *Limnology and Oceanography* 15, 348–356.
- Wächter, A., Biegler, L.T., 2006. On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. *Mathematical programming* 106, 25–57.
- Woodson, C., Webster, D., Weissburg, M., Yen, J., 2005. Response of copepods to physical gradients associated with structure in the ocean. *Limnology and Oceanography* 50, 1552–1564.
- Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. *The American Naturalist* 139, 1151–1175.

PAPER E

Optimal behavior in a shelf ecosystem

Optimal behavior in a shelf ecosystem ^{*}

Emil F. Frølich^b

^a*DTU Compute, Building 324, Richard Petersens Plads, Kgs. Lyngby, 2800, , Denmark*

Highlights

Optimal behavior in a shelf ecosystem

Emil F. Frølich

- The diel migration is linked to both benthic and pelagic productivity
- A reverse diel migration of zooplankton emerges at high productivity
- Benthic productivity serves to enhance phytoplankton productivity

^{*}This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

Optimal behavior in a shelf ecosystem

Emil F. Frølich^b

^b*DTU Compute, Building 324, Richard Petersens Plads, Kgs. Lyngby, 2800, , Denmark*

Abstract

Shelf ecosystems support 90% of the worlds fisheries, and having good models of shelf ecosystems is essential for ensuring that we have sustainable fisheries. Models of shelf ecosystems rarely take behavior into account other than mechanistically, though behavior essentially governs the population dynamics. We study a model of a shelf-ecosystem with six different trophic levels, where four of them have optimal behavior. We implement the optimal through a mean-field a game. This allows us to show the vertical migration of zooplankton as dependent on phytoplankton productivity, and find reverse vertical migrations. In addition we show that both and phytoplankton productivity negatively impacts large pelagic fish, but benefit large demersal fish.

Keywords:

shelf eco-system, mean-field games, food-web, population dynamics

1. Introduction

Shelf ecosystems are some of the most productive ecosystems, responsible for over 90% of global fisheries (Pauly et al., 2002). Hence a proper understanding of the complexities of shelf eco-systems is essential for global fisheries management. The structure of shelf ecosystems can be described by a simple food-web, incorporating both benthic and phytoplankton productivity. These support a food-web consisting of both zooplankton, forage fish, large pelagic fish and large demersal fish. This food-web has many indirect effects, with an increase in benthic production having been shown to decrease large pelagic populations (Petrik et al., 2019; van Denderen et al., 2018).

One of the main drivers of population dynamics is behavior, and models of shelf eco-systems typically do not include behavior (Petrik et al., 2019), or only do so mechanistically (van Denderen et al., 2021). In the ocean the major important behavioral pattern is the diel vertical migration, which is usually characterized by prey seeking to avoid predation by swimming to safe areas. Incorporating the diel vertical migration in population models is expected to

*This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

improve their predictive power, as most trophic interactions happen at dawn and dusk (Benoit-Bird and McManus, 2014), driven by the migration. Due to its simple nature, incorporating the diel vertical migration (DVM) by dividing the day into two and imposing migratory patterns seems promising. This approach, however, is not supported by data. The strength and nature of diel migration patterns is highly dependent on the individual risk of predation (Stockwell et al., 2010; Scheuerell and Schindler, 2003). In a complex ecosystem, reverse diel migrations where zooplankton migrate up during the day are known to emerge as a function of predator density, (Kahilainen et al., 2009). This due to the day becoming safe, as their main predators are also under the threat of predation. As such, a wide variety of complex migration patterns can arise depending on the state of the ecosystem. A model of a shelf ecosystem where population dynamics are coupled to an emergent diel migration could provide a framework where e.g. the transition of the state of shelf ecosystem from overfishing could be studied, as in the case of north-west Atlantic cod (Choi et al., 2004).

The diel vertical migration is an example of a habitat choice decision, one of the places where game theory has been most successful in theoretical ecology. Habitat selection games are typically modeled as playing the field, where each individual plays against the behavior of the entire population (Smith, 1982). The diel vertical migration in can be shown to arise from a game between predators and prey, in complex ecosystems such as a shelf system (Pinti et al., 2021). In this study the day-night cycle was divided into two parts. A weakness of simply dividing the day into two zones is that this causes the critical feeding windows of dawn and dusk to disappear, but as noted is to a large degree these which drive population dynamics of the upper trophic layers of the ocean (Benoit-Bird and McManus, 2014). Models with a continuous time resolution, can, however, catch this dynamic (Thygesen and Patterson, 2018). This approach has been advanced and expanded, incorporating both randomness in behavior and behavioral decisions taken over a longer time-horizon through the development of mean-field games (Lasry and Lions, 2007). Mean-field games represent a powerful addition to the toolbox of theoretical ecology, allowing for the resolution of population games without resorting to adaptive dynamics. This leads directly to the next point, namely coupling population dynamics and behavior. Optimal behavior has a large effect on population dynamics in simple models (Abrams, 2010), but there are no models coupling an emergent vertical migration in a complex ecosystem with a population dynamics.

We propose a model of a food web in a shelf ecosystem which allows us to study the coupling of population dynamics and behavior in a realistic ecosystem. This is done by modeling the individual behavior of each population group as a mean-field game. We couple the mean-field game to a population dynamical model, studying the size of the populations at the fixed-points of the population dynamics. This allows us to couple diel migration patterns, population levels, and productivity in a shelf ecosystem.

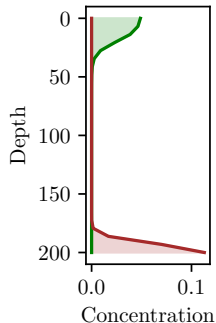


Figure 1: The distribution of phytoplankton (green, r_r), and benthic resources (brown, r_b)

2. Methods

Our model has two basic components: A population dynamical and a behavioral component. Our food-web is a simple shelf ecosystem at a depth of 200m, as in (van Denderen et al., 2021). The food web consists of two different sources of primary production. Phytoplankton N_r growing at the top of the water column with a growth λ_r and maximal population \bar{R} , and a benthic production N_b with a growth rate of λ and maximal population \bar{B} . The benthic resource follows a distribution r_b with width w and the phytoplankton is distributed according to r_r , with a mixed layer depth of x_{mld} and a decline of c , see Figure 1 and ??.

$$\begin{aligned} r_r &= \frac{1}{1 + \exp(c(x - x_{mld}))} \\ r_b &= \exp(-(x - 200)/w^2) \end{aligned} \tag{1}$$

Going upwards in the food web, the phytoplankton is consumed by zooplankton N_z , who are then consumed by forage fish N_f . Forage fish are consumed by large pelagic fish N_p and large demersal fish N_d . Apart from forage fish, large demersal fish also consume the benthic production. The interactions governing the population dynamics are summarized by the food-web in Section 2. This leads directly to the behavioral component of the model. Zooplankton seek a behavioral pattern so they can maximize their consumption of phytoplankton while avoiding being eaten by forage fish. This can be avoided by migrating to the bottom, where they cannot be seen. Forage fish have the same drive, but with the caveat that their predators the large demersals are also motivated to stay at the bottom to consume benthic production. This leads directly to the behavioral pattern of the large demersals, who must choose whether to consume

Model food-web in a shelf ecosystem

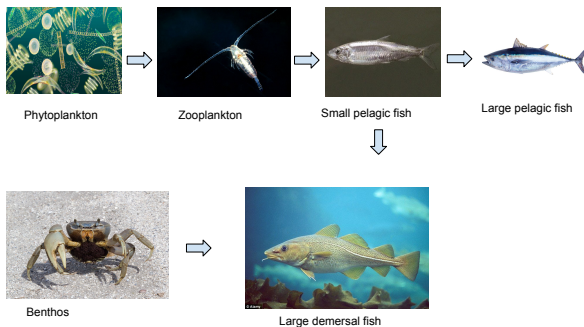


Figure 2: An unstructured food-web in a shelf eco-system

benthic resources or swim in search of forage fish. Finally the large pelagics seek to eat the forage fish.

2.1. Behavioral dynamics

As in the ideal free distribution (Fretwell, 1969) we assume that each individual seeks to maximize their fitness. As the ocean is a time-varying environment, with light changing throughout the day, we cannot use the ideal free distribution as this assumes a static environment and that individuals move instantaneously. We assume that the movement of an individual can be modeled by an Ito stochastic differential equation.

$$dX_t^i = v_i^t dt + \sigma dB_t \quad (2)$$

Equation (2) captures that the movement of an individual is governed both by active advection and noise. Instead, our model is that each individual seeks to maximize their total fitness over a day. The fitness can be broken down into four components. A growth G_i , a mortality term M_i , the energy lost to locomtion ν_i and metabolism μ_i . These are determined by their location in the water column x_i and their velocity v_i^t . In addition, individual growth and mortality depend on the distribution of food sources, predators and conspecifics. That is, each individual maximizes a utility function depending on its vertical position x_i , that of its conspecifics $N_i \bar{\sigma}_i$, the distribution of the other animals $N_j \bar{\sigma}_j$ as well as the velocity v_i^t . At each instant, the growth of an individual is

$$J_i = G_i(x_i, (N_j \bar{\sigma}_j)_{j=1}^4) - M_i(x_i, (N_j \bar{\sigma}_j)_{j=1}^4) \quad (3)$$

We assume that the populations of each type is large, so the actions of an individual do not have an effect on the overall population distribution. With this in mind, each individual of type i maximizes

$$F_{i,ind} = E \left(\int_0^{24} J_i - \nu_i dt \right) \quad (4)$$

We can now specify the concrete growth and mortality rates, depending on the maximal consumption rates C_i , clearance rates β_i and conversion efficiencies ε_i . Remark that large demersals have two different clearance rates. The first is β_d which depends on light-levels and determines encounters with forage fish, the second is β_{db} which determines clearance of the benthos. In addition to these parameters, the growth and mortality depend on the ecosystem state, i.e. the population levels and distributions. We start from the bottom of the food-web, by specifying the growth and mortality of zooplankton.

$$\begin{aligned} G_z &= \varepsilon_z N_r C_z \beta_z d_r / (C_z + N_r \beta_z d_r) \\ M_z &= \frac{N_f \bar{\sigma}_f \beta_f}{c_f + N_z \beta_f \bar{\sigma}_z \bar{\sigma}_f} \end{aligned} \quad (5)$$

The growth and mortality of forage fish is the most complex, as they are preyed upon both by large demersals and large demersals

$$\begin{aligned} G_f &= \varepsilon_f C_f N_z \frac{\beta_f \bar{\sigma}_z}{(C_f + \beta_f N_z \bar{\sigma}_z)} \\ M_f &= \frac{N_p \bar{\sigma}_p C_p \beta_p}{(C_p + \bar{\sigma}_f \beta_p N_f)} \\ &\quad + \frac{N_d \bar{\sigma}_d \beta_d}{(C_d + \beta_d \bar{\sigma}_f N_f + \beta_{db} N_b d_b)} \end{aligned} \quad (6)$$

The large pelagics and large demersals have no mortality from predation, and have growth functions:

$$\begin{aligned} G_p &= \varepsilon_p C_p \frac{N_f \bar{\sigma}_f \beta_p}{(C_p + \bar{\sigma}_f \beta_p N_f)} \\ G_d &= \varepsilon_d C_d \frac{N_f \bar{\sigma}_f \beta_d + N_b \beta_{db} d_b}{(C_d + \beta_d \bar{\sigma}_f N_f + N_b \beta_{db} d_b)} \end{aligned} \quad (7)$$

Though the energy expenditure of swimming of fish in a viscous fluid is proportional to the cube of the speed, we model it as proportional to the speed squared. This is done for the sake of modeling, as the smoothness of a quadratic function is more tractable than the absolute value. Hence the instantaneous energetic cost of movement for all types is

$$\nu_i = \frac{\gamma_i}{2} v_i^2 \quad i \in \{z, f, p, d\} \quad (8)$$

We assume that each individual optimal value, or fitness, is given by V_i . With V_i in hand, we can write up an expression for the instantaneous reward J_i following

Thygesen (2022)

$$J_i(t) = G_i - V_i M_i - \nu_i \quad (9)$$

Each individual then seeks to optimize their expected fitness F_i , given by integral of the expected value of J_i over an entire day.

$$F_i = E \left(\int_0^{24} J_i dt \right) \quad (10)$$

With the fitness measure settled, we can now write up the Hamilton-Jacobi-Bellman equation governing the optimal movement of an individual of type i with value function $V_i t$

$$-\frac{\partial V_i}{\partial t} = \sup_{v_i^t} \left(J_i(x, t) + v_i^t \nabla_x V_i + \frac{\kappa}{2} \frac{\partial^2 V_i}{\partial x^2} \right) \quad i \in \{z, f, p, d\} \quad (11)$$

As we assume the populations are large, the situation we are in is that of a mean-field game (Lasry and Lions, 2007). The Nash equilibrium of this game can be found by solving a coupled system of Hamilton-Jacobi-Bellman equations Equation (11) and Fokker-Planck equations Equation (12).

$$\frac{\partial \bar{\sigma}_i}{\partial t} = -\nabla_x (v_i^t \bar{\sigma}_i) + \frac{\partial^2 \bar{\sigma}_i}{\partial x^2} \quad i \in \{z, f, p, d\} \quad (12)$$

This is a slight simplification, as the equation should include source and death terms. These contributions are negligible over a daily horizon, hence we do not include them to ease the modeling.

2.2. Population dynamics

We have so far refrained from defining the mortality of the phytoplankton the benthic resource, M_r and M_b . The mortality at any instant is

$$\begin{aligned} M_r &= \frac{N_z}{\varepsilon_z} E(G_z) \\ M_b &= N_d E \left(C_d \frac{N_b \beta_{db} d_b}{(C_d + \beta_d \bar{\sigma}_f N_f + N_b \beta_{db} d_b)} \right) \end{aligned} \quad (13)$$

We assume both the benthic and phytoplankton resource can be described by a chemostat, so their population dynamics can be described by Equation (14)

$$\begin{aligned} \dot{N}_r &= \lambda_r (\bar{R} - N_r) - M_r \\ \dot{N}_b &= \lambda_b (\bar{B} - N_b) - M_b \end{aligned} \quad (14)$$

The population dynamics of each group of animals is governed by the average growth of all individuals in the group. As such, the population dynamics of group i are given by

$$\dot{N}_i = N_i E(G_i - M_i - \nu_i - \mu_i), \quad i \in \{z, f, p, d\} \quad (15)$$

We are interested in the population levels at the fixed-point, which in this case means a periodic solution. Hence we also require

$$\int_0^{24} \dot{N}_i dt = 0, \quad i \in \{z, f, p, d\} \quad (16)$$

The two equations Equation (15) and Equation (16) completely specify the population dynamics of zoo-plankton, forage fish, large pelagics and large demersals.

2.3. Parameters and resource distributions

We follow the parameter choices of FEISTY (Petrik et al., 2019; van Denderen et al., 2021). The parameters are represented in Section 2.3

Name	Symbol	Value
Copepod mass	m_z	0.05g
Forage fish mass	m_f	15g
Large pelagic mass	m_p	5000g
Large demersal mass	m_d	4000g
Copepod maximal consumption rate	c_z	2 g/year
Forage fish maximal consumption rate	c_f	152 g/year
Large pelagic maximal consumption	c_p	10059 g/year
Large demersal maximal consumption	c_d	11892 g/year
Clearance rate zooplankton	β_z	35 m ³ /year
Clearance rate forage fish	β_f	2515 m ³ /year
Clearance rate large pelagic	β_p	165981 m ³ /year
Clearance rate large demersal	β_d	82991 m ³ /year
Benthic clearance large demersal	β_{db}	41495 m ³ /year
Light attenuation coefficient	k	0.05/m
Noise	κ	1 m ² /h
Mixed layer depth	x_{mld}	20
Phytoplankton attenuation	c	0.2/m
Benthic layer width		
Copepod drag	γ_c	$\frac{1}{6}10^{-6}$ Jh
Forage fish drag	γ_f	$\frac{1}{6}10^{-5}$ Jh
Large pelagics drag	γ_p	$\frac{1}{6}10^{-4}$ Jh
Large demersals drag	γ_d	$\frac{1}{6}10^{-4}$ Jh

2.4. Numerical approach

Our ability to resolve the system and find optimal strategies and stable population levels simultaneously is based on the numerical scheme we use. We discretize both space and time according to a second-order scheme. We start by solving the system on a rough grid spatio-temporal resolution of 3×15 . We do this by using the package CasADi (Andersson et al., 2019), using the interior-point solver IPOPT (Wächter and Biegler, 2006) with the HSL linear algebra routines (HSL, 2007). At this low resolution of the grid, an exact Hessian can be computed and the system can be solved using this.

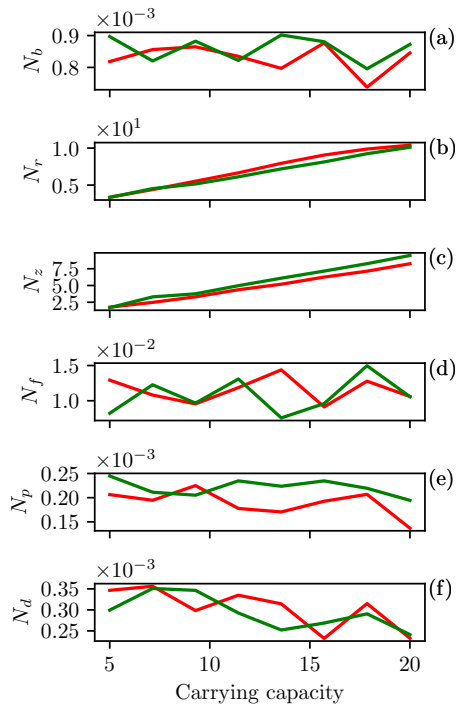


Figure 3: Population levels as a function of carrying capacity \bar{R} of phytoplankton (a), benthic resource (b), zooplankton (c), forage fish (d), large pelagics (e) and large demersals (f) at benthic carrying capacity \bar{B} levels of 0.01g (red), 0.1g (green)

Then we successively refine the space and time dimensions, using the solution at step $n - 1$ to as an initial guess for the solution at step n , where we use an inexact Hessian. This allows us to solve the system at a final resolution of 30×150 .

3. Results

Examining the population levels reveals several surprising effects. The first general effect is the increase in both zoo-plankton and phytoplankton populations Figure 3(a,c) from increasing the carrying capacity. Surprisingly, an increased benthic productivity causes the effect of phytoplankton productivity to increase Figure 3(a,b). At a both low and high benthic productivity the

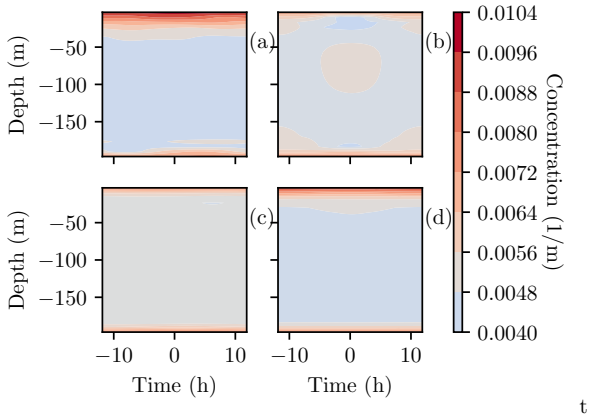


Figure 4: Migration of patterns of zooplankton (σ_z , a), forage fish (σ_f , b), large pelagics (σ_p , c), and large demersals (σ_d , d) at a carrying capacity of $\bar{R} = 5g$ and $\bar{B} = 0.01g$

population of forage fish is essentially unchanged by the change in productivity Figure 3(d, red, green). The situation for large pelagics is surprising. An increase in carrying capacity causes a decrease in large pelagic populations at both and low high benthic carrying capacities Figure 3(e, red, green). The population of large demersals and large pelagics are both surprisingly essentially unchanged when increasing the benthic productivity Figure 3(f, red, green). Together, these two lead to the conclusion that an increase in carrying capacity, either planktonic or benthic, favors mainly the zoo-plankton community.

The migration patterns in Figure 4 reflect the migration patterns in a shelf ecosystem with a low phytoplankton productivity and low benthic productivity. The zooplankton Figure 4 (a) have a bimodal distribution. The uppermost layer has a barely noticeable reverse diel vertical migration, where they concentrate at dusk. The mode at the bottom moves in counterpoint, migrating slightly up during the dawn. If we consider the forage fish Figure 4 (b), their patterns are more surprising. They concentrate near the surface at day, and slightly below the surface at night. Proceeding in the food web, the large pelagics also have a bimodal distribution. The large demersals have a small diel migration, with a group migrating up during the night and down in the day. There is also a population of large demersals which stays down during the entire day-night cycle.

The migration patterns in Figure 5 reflect the migration patterns in a shelf ecosystem with a medium phytoplankton productivity and low benthic productivity. The distribution of zooplankton Figure 5(a) has now changed to an essentially unimodal distribution, with a clear diel vertical migration, surprisingly concentrating during dusk. This is probably an anti-predation measure, as their

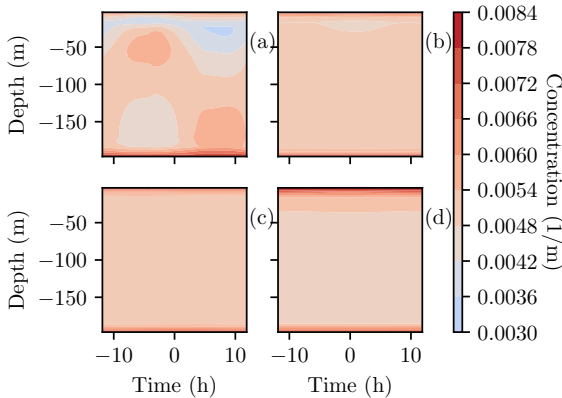


Figure 5: Migration of patterns of zooplankton (σ_z , a), forage fish (σ_f , b), large pelagics (σ_p , c), and large demersals (σ_d , d) at a carrying capacity of $\bar{R} = 13g$ and $\bar{B} = 0.01g$

predators are also vulnerable here. If we consider the forage fish Figure 5(b), their behavior has changed to an essentially uniform distribution with a small reverse migration. Proceeding in the food web, the large pelagics now have a unimodal distribution distributed evenly throughout the water column. The large demersals are quite distributed, but have a very minor reverse migration.

At high phytoplankton and low benthic productivity, a new pattern emerges. The migrations of zoo-plankton Figure 6 (a) has increased in scope and concentration. Forage fish lost all trace of a migration Figure 6 (b). Large pelagics and demersals have the same behavioral pattern as at medium productivity Figure 6(c,d).

Inspecting the migration patterns in Figure 7 we immediately spot a difference from the case with low benthic productivity Figure 4. Zooplankton Figure 7(a) are still bimodal in their distribution, while forage fish Figure 7(b) perform a small reverse vertical migration but have the lost concentration beneath the surface at midnight. Large pelagics have bimodal distributions as in the case with low productivity, and large demersals now have a bimodal distribution without migration, concentrated in the top Figure 7(c,d), Figure 4(c,d)

At medium productivity, zooplankton perform a reverse diel vertical migration, concentrating 50 meters below the surface Figure 7(a), and forage fish migrate to follow them Figure 7(b), concentrating on the zooplankton. The forage fish also gather beneath the surface at midnight, which serves to scare any copepods away Figure 7(b). The large pelagic population follows a uniform distribution in the water column. The large demersals have a bimodal distribution concentrated at the top of the water column, Figure 7(d), with a slight reverse vertical migration.

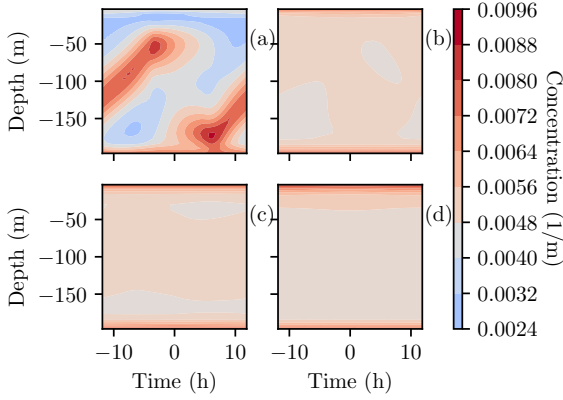


Figure 6: Migration of patterns of zooplankton (σ_z , a), forage fish (σ_f , b), large pelagics (σ_p , c), and large demersals (σ_d , d) at a carrying capacity of $\bar{R} = 20g$ and $\bar{B} = 0.01g$

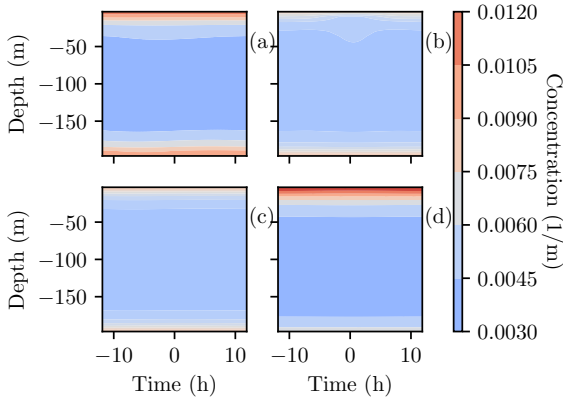


Figure 7: Migration of patterns of zooplankton (σ_z , a), forage fish (σ_f , b), large pelagics (σ_p , c), and large demersals (σ_d , d) at a carrying capacity of $\bar{R} = 5g$ and $\bar{B} = 0.1g$

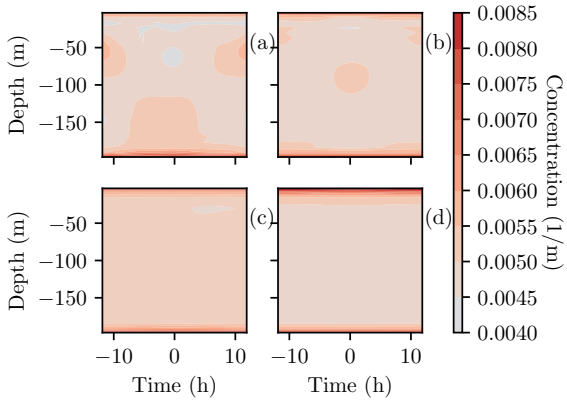


Figure 8: Migration of patterns of zooplankton (σ_z , a), forage fish (σ_f , b), large pelagics (σ_p , c), and large demersals (σ_d , d) at a carrying capacity of $\bar{R} = 13g$ and $\bar{B} = 0.1g$

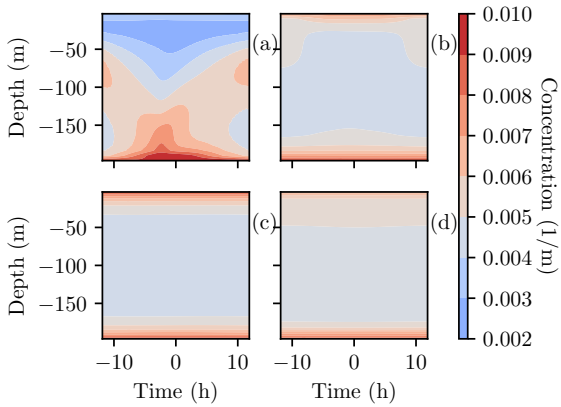


Figure 9: Migration of patterns of zooplankton (σ_z , a), forage fish (σ_f , b), large pelagics (σ_p , c), and large demersals (σ_d , d) at a carrying capacity of $\bar{R} = 13g$ and $\bar{B} = 0.1g$

At high productivity of both benthics and phytoplankton, zooplankton perform a reverse vertical migration, and forage fish perform a vertical migration Figure 9. At the same time, forage fish have a dilute concentration at the top of the water column during the day, just intersection the zooplankton layer Figure 9, (a,b). The large pelagics now have a clear bimodal distribution Figure 9(c) and the so do the large demersals, which are more spread out Figure 9(d)

4. Discussion and conclusion

The study shows the potential of incorporating complex behavior in realistic ecosystem models. By changing environmental conditions, complex behavior can emerge from simple individual choices, affecting population dynamics. Our results show that benthic productivity apparently has a large effect on populations, Our results show that surprisingly benthic and phytoplankton productivity have the same overall effect on ecosystems, causing an increase in phytoplankton and zooplankton. Meanwhile they cause a decline in large pelagic populations, and have little effect on forage fish populations beyond a certain point. Phytoplankton productivity negatively impacts large demersals, but this is to some degree counteracted by the positive effect of increased benthic productivity.

Both a normal and a reverse vertical migration of zooplankton emerges from the optimal behavioral patterns, while forage fish perform a limited reverse migration, and a normal diel migration at high productivity of both benthic and phytoplankton. Large pelagics and demersals have a tendency to either evenly or distribute or have bimodal distributions. Large demersals, do, however, have very slight reverse vertical migrations.

The population-level effects we find on the effect of benthic productivity corresponds to the FEISTY model without optimal behavior, (Petrik et al., 2019; van Denderen et al., 2021). The effect of phytoplankton productivity, is, however, novel. Whether this prediction of our model holds water can be tested by comparing the population levels in different shelf ecosystems. It would, however, serve to explain the very large Krill populations on the highly productive Antarctic shelf and the large demersal population, with a correspondingly low population of large pelagics and forage fish (Smith Jr et al., 2007).

The behavioral adaptation of an emergent diel vertical migration matches findings that the diel vertical migration is dependent on ecosystem productivity and predator counts (Stockwell et al., 2010; Kahilainen et al., 2009; Ohman, 1990), but the reverse migrations by the forage fish are unexpected (Scheuerell and Schindler, 2003; Bayly, 1986). We expected the emergence of a reverse migration of zooplankton at sufficiently high productivities due to high counts of forage fish (Kahilainen et al., 2009), and it was surprising that this was also the case when forage fish made the clearest normal vertical migration. Whether this is a general pattern of this model, or just a result of the specific parameters governing the migrations should be investigated further. The result that large pelagics are evenly distributed throughout the water column corresponds well

to reality, where pelagics are sparsely distributed but can speedily migrate to consume their prey (Thygesen et al., 2016).

Our model brings new results to the table of shelf-ecosystem modeling, and shows the promise of incorporating optimal behavior in realistic ecosystem models.

Declarations

Funding

This work was supported by the Centre for Ocean Life, a Villum Kann Rasmussen Centre of Excellence supported by the Villum Foundation.

Code availability

All code for reproducing the results of this project is available on github https://github.com/jemff/multi_species_water.

Conflict of interest

The authors declare that they have no conflict of interest.

Authors' contributions

E.F.F. designed the study. E.F.F. realized the model design. E.F.F. coded the model and chose the numerical approaches. E.F.F. analyzed the results. E.F.F. wrote the paper with contributions from all authors.

Data availability

All data can be generated using the file `4_spec_HJB.py` from the git repository https://github.com/jemff/multi_species_water.

References

- Abrams, P.A., 2010. Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology* 24, 7–17.
- Andersson, J.A.E., Gillis, J., Horn, G., Rawlings, J.B., Diehl, M., 2019. CasADi – A software framework for nonlinear optimization and optimal control. *Mathematical Programming Computation* 11, 1–36. doi:10.1007/s12532-018-0139-4.
- Bayly, I., 1986. Aspects of diel vertical migration in zooplankton, and its enigma variations, in: *Limnology in Australia*. Springer, pp. 349–368.
- Benoit-Bird, K.J., McManus, M.A., 2014. A critical time window for organismal interactions in a pelagic ecosystem. *PLoS One* 9, e97763.
- Choi, J.S., Frank, K.T., Leggett, W.C., Drinkwater, K., 2004. Transition to an alternate state in a continental shelf ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* 61, 505–510.

- van Denderen, P.D., Lindegren, M., MacKenzie, B.R., Watson, R.A., Andersen, K.H., 2018. Global patterns in marine predatory fish. *Nature ecology & evolution* 2, 65–70.
- van Denderen, P.D., Petrik, C.M., Stock, C.A., Andersen, K.H., 2021. Emergent global biogeography of marine fish food webs. *Global Ecology and Biogeography* 30, 1822–1834.
- Fretwell, S.D., 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica* 19, 45–52.
- HSL, A., 2007. A collection of fortran codes for large-scale scientific computation. See <http://www.hsl.rl.ac.uk>.
- Kahilainen, K., Malinen, T., Lehtonen, H., 2009. Polar light regime and piscivory govern diel vertical migrations of planktivorous fish and zooplankton in a subarctic lake. *Ecology of Freshwater Fish* 18, 481–490.
- Lasry, J.M., Lions, P.L., 2007. Mean field games. *Japanese journal of mathematics* 2, 229–260.
- Ohman, M.D., 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs* 60, 257–281.
- Pauly, D., Christensen, V., Gu enette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. *Nature* 418, 689–695.
- Petrik, C.M., Stock, C.A., Andersen, K.H., van Denderen, P.D., Watson, J.R., 2019. Bottom-up drivers of global patterns of demersal, forage, and pelagic fishes. *Progress in oceanography* 176, 102124.
- Pinti, J., Andersen, K.H., Visser, A.W., 2021. Co-adaptive behavior of interacting populations in a habitat selection game significantly impacts ecosystem functions. *Journal of Theoretical Biology* 523, 110663.
- Scheuerell, M.D., Schindler, D.E., 2003. Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology* 84, 1713–1720.
- Smith, J.M., 1982. *Evolution and the Theory of Games*. Cambridge university press.
- Smith Jr, W.O., Ainley, D.G., Cattaneo-Vietti, R., 2007. Trophic interactions within the ross sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362, 95–111.
- Stockwell, J.D., Hrabik, T.R., Jensen, O.P., Yule, D.L., Balge, M., 2010. Empirical evaluation of predator-driven diel vertical migration in lake superior. *Canadian Journal of Fisheries and Aquatic Sciences* 67, 473–485.

- Thygesen, U., Patterson, T., 2018. Oceanic diel vertical migrations arising from a predator-prey game. *Theoretical Ecology* 12, 17–29.
- Thygesen, U.H., 2022. Stochastic differential equations for science and engineering. Accepted for publication by CRC Press / Taylor and Francis.
- Thygesen, U.H., Sommer, L., Evans, K., Patterson, T.A., 2016. Dynamic optimal foraging theory explains vertical migrations of bigeye tuna. *Ecology* 97, 1852–1861.
- Wächter, A., Biegler, L.T., 2006. On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. *Mathematical programming* 106, 25–57.