

TAKING STOCK



FROM **PATTERN**
TO **PROCESS**

In modelling the
dynamics of
marine communities

Mark Rademaker

Propositions

1. Data-driven approaches should only be used as a precursor to formal scientific inference.
(this thesis)
2. Individual-level processes cannot be ignored even when examining large-scale patterns across species.
(this thesis)
3. Each ecology PhD should strive to engage with the philosophy in their Doctor of Philosophy.
4. Theoretical studies without an empirical base are as scientifically hollow as empirical studies without a theoretical base.
5. When in doubt about where your PhD is going, surf.
6. Humanity needs a new narrative to collaboratively tackle the global climate-biodiversity crises.
7. Bestowing Rights of Nature upon the Wadden Sea is the most effective means of ensuring accountability regarding human use of this ecosystem.
8. Soon only the wealthiest individuals with the largest environmental footprints will be able to afford viewing the increasingly rare wildlife of our world.

Propositions belonging to the thesis, entitled

Taking stock: From pattern to process in modelling the population dynamics of marine communities

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Thesis

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Chapter 1

General introduction

1.1 A brief history of marine population ecology

Beginnings

It was the first of animal life, it was the simplest of animal life, and it formed in the depths of the sea over half a billion years ago (Anderson et al., 2023; Betts et al., 2018; Smith & Szathmary, 1997). From these early beginnings, through eons of time, countless shapes, forms and modes of existence evolved and disappeared. Right up to our present times the marine environment continues to harbor some of the most abundant and productive populations of species on our planet. Populations upon which hundreds of millions of people depend for their nutrition and livelihoods (Selig et al., 2019; Kawarazuka & Béné, 2010; Teh & Sumaila, 2013). Therefore, it is perhaps unsurprising that populations of marine species have played a central role in human understanding of the natural world (Moyle & Moyle, 1991; Nellen & Dulčić, 2008), including, in the early 20th century, the newly emerging scientific discipline of population ecology (Egerton, 2015). Population ecology centers on how and why populations fluctuate over time (Egerton, 2015; Kingsland, 1986, 1995). Right from the start two different approaches were applied in attempt to answer these questions:

- (1) Statistically oriented studies relying on systematically collected data that I will refer to as **pattern** based approaches.
- (2) Mathematically oriented studies based on unifying general principles captured in a limited set of equations that I will refer to as **process** based approaches.

These approaches are exemplified by the seminal papers of Hjort (1914) and Volterra (1926), that both sought to understand observed fluctuations in fishery landings¹. Understanding fluctuations in fisheries was the natural starting point for marine population ecology in the 20th century, as fishing success dropped across the world, and people were forced to reconsider the famous notion expressed by Huxley in 1883 that “*Probably all the great sea fisheries are inexhaustible; that is to say, that nothing we do seriously affects the numbers of fish. Any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless.*” (Nielsen, 1976).

¹The Russian scientist Igor Baranov (1886-1964), sometimes called the ‘Grandfather of fisheries science’ is worth mentioning in this regard. Baranov was the first to publish a correlation between the size of fish stocks in a water body and the size of fish catches in his 1914 article ‘The theory of overfishing’ (Quinn, 2003; Baranov, 1976). Unfortunately for Baranov, he was heavily criticized by his contemporaries for his mathematical work and simplifying assumptions, and others would rise to more scientific prominence; although his contributions were later well recognized and documented (Quinn, 2003)

Seminal early papers

Johan Hjort (1869-1948) was a Norwegian government scientist interested in understanding the factors that might explain fluctuations in the landings of the Norwegian herring and cod fisheries that had been systematically monitored by the government since the 1860s. With his keen interest in scientific fieldwork out on the rough seas of the North Atlantic, he personified the classical ‘naturalist’ in ecology (Schwach, 2014). In his famous 1914 report, Hjort found a linear correlative relationship between fisheries catches and phytoplankton abundance. A finding that was to change the field of fisheries science. You may ask what made this relationship such an important scientific contribution.

In the decades preceding Hjort’s study, there was still a generally held notion of fish species having a certain ‘home’ in the world from which they would migrate across the globe (Sinclair & Smith, 2002, January). The exact origins of this theory remain unknown, but it was first systematically described for herring by the British surgeon James Solas Dodd in 1728, and expanded upon by the mayor of Hamburg Johan Anderson in 1746 (Anderson & Winckler, 1746; Wegner, 1993; Sinclair & Smith, 2002, January; Sinclair, 2009). The ‘home’ of herring was thought to be located under the northern polar ice sheet. The excess herring that could not be supported by conditions in the polar regions then migrated across the world’s oceans in search of food, escaping predators, and reproducing along the way, leading to variation in catches over time in different areas (Sinclair & Smith, 2002, January). This ‘migration thinking’ was first challenged by the German scientist Heincke in 1898, who showed that the ‘global’ herring stock was actually composed of several separate groups (Heincke, 1898; Goethel & Cadrin, 2021), a concept which we would nowadays refer to as populations. Crucially, Hjort used Heincke’s insight to formulate the theory that fluctuations in Norwegian fisheries catches were therefore not the consequence of global migration, but of differences between years in the number of eggs and larvae produced by regional populations that were able to survive and grow large enough to be caught by fisheries in subsequent years (Schwach, 2014).

The statistical correlation shown between adult fish catches and the abundance of phytoplankton provided convincing ‘proof’ that Hjort’s theory was pointing in the right direction because fish feed on plankton during the early larval stage. Hjort further strengthened his argument by using annual growth lines on fish scales to show that those fish born under abundant phytoplankton conditions could be identified as dominant in the catch for several years (Egerton, 2015). The paradigm shift was complete. Hjort’s findings lead to the recognition that survival of the larval stage was critical for observed ‘year-class fluctuations’ in fish; a term Hjort later replaced in 1945 with the now more familiar term of ‘recruitment’ (Kjesbu et al., 2021).

Hjort’s early research highlights the potential of statistical, pattern-based, approaches to understand fluctuations in fish populations. Other scientists independently addressed the same question using more mathematical, process-based, approaches. From my perspective, this school of thought is personified by the Italian mathematician and physicist Vito Volterra (1860-1940), and his independent discovery of the famous Lotka-Volterra

equations².

Volterra was a mathematical prodigy whose exceptional abilities allowed him to move from a largely fatherless childhood spent in poverty in the Jewish ghetto of Pisa on to obtaining a doctorate in mathematics at the city's university in 1882 at age 22 (Bacaër, 2011). He subsequently held university chairs as professor of mechanics in Pisa and Turin, before moving to Rome to become professor of mathematical physics in 1905 (the city in which he would later serve as senator of the Italian parliament). By this time, his reputation and fame as a mathematical genius had been well established in the scientific world. What put Volterra apart from other scientists from a present-day perspective was his rather modern 'interdisciplinary' focus on uniting the mathematical and social and biological sciences (Scott, 2018).

In 1925, Volterra started to gain interest in fish populations through a publication of his future-son-in-law Umberto D'Ancona that showed how the proportion of sharks and rays in fishery landings in the Adriatic Sea had increased during the period of World War One, when fishing intensity was lower (Scudo, 1971; D'Ancona, 1926). Inspired by this finding, Volterra drew up a pair of first-order non-linear differential equations (ODE's), one for the predator and one for the prey. Examining the properties of these equations Volterra was ultimately able to show that if fishing effort decreases, the 'extinction rate' of the predator population decreases. This would lead the average number of prey fish to decrease (as there are relatively more predators around to eat them), and the average number of predatory fish to increase, in line with the observations made by D'Ancona (Bacaër, 2011). Volterra's study on population fluctuations was groundbreaking because it was the first time a mathematical model matched reliable empirical data (Scudo, 1971). Furthermore, as a classically trained physicist and mathematician, Volterra was not the typical 'naturalist' in ecology but introduced, alongside the American scientist Alfred J. Lotka, a very different way of systematic thinking and analysis to ecological problems.

Advantages, drawbacks, and points of contention in the early work

The 'beauty' of mathematical models such as the Lotka-Volterra equations is that causality is implicit; one can know exactly what causes what by analyzing the equations, and thus form an understanding of the functioning of the population one is studying. In contrast, in the statistical approach Hjord used, scientists will have to provide convincing proof that certain factors cause population fluctuations through correlations, while there is always the chance that the effect is due to other alternative explanations. Especially considering the data from in-situ population studies come from an 'open world' laboratory where you cannot control for the myriad of biases seeping in, including in the way the data itself is collected. Mathematical models also come with an important drawback. In order to derive

²The other independent discoverer of these equations being the American scientist Alfred J Lotka (1880-1949), who upon his initial publication of his findings in bookform in 1920, failed to gain recognition from his peers and suffered great mental anxiety for this. He was later duly credited and cemented in history as one of the founding fathers of theoretical population ecology (Kingsland, 2015)

meaningful ecological inferences from the model, the equations should reflect the natural processes governing the system or population under study. This has led to strong critiques and pushbacks to the way mathematical models such as Volterra's were developed and used in population ecology, poignantly summarized by Watt in his 1962 review of the use of mathematics in population ecology: "*all the conclusions which Volterra draws out in a very thorough monograph are perfectly valid deductions from the assumptions he makes. However, the assumptions are not drawn from biological reality.*" (Watt, 1962).

The development of mathematical, process-based approaches has since focused on improving the biological realism of these models (although the original Lotka -Volterra models remain popular to this day). Similarly, statistical, pattern-based approaches sought to improve ways to account for other important biological factors that might explain population fluctuations, and the relationships that can be fitted by these models. After all, the world is rarely linear. Finally, the following decades would see the merging of statistical and mathematical thinking to understand population fluctuations.

Major modelling developments in marine population ecology

Many of the scientific methods currently used to examine population fluctuations in marine communities were developed by fisheries scientists in the period 1945 -1960. This period is marked by the merging of mathematical (**process**) and statistical (**pattern**) ways of thinking, into what I categorize as a third more '**hybrid**' approach. The developments were driven by a distinctly applied motivation: using models to achieve optimal exploitation and prevent overfishing of fish populations. In a hybrid-based population model, a generic mathematical equation is formulated to predict the number of individuals, or biomass, in a population at a future time step, based on the number of individuals at the current time step. This equation generally depends on several parameters such as fishing intensity, natural mortality, and reproductive output, that can be estimated at the population level based on survey data. The equation is solved for the next time step, and this process can be iteratively repeated to come to a prediction of the population at any future point of interest. Importantly, the equation as a whole, or functions within the equation, e.g. describing growth, can be fitted to data in statistically familiar fashion. This kind of approach can therefore also be used to estimate certain unknown parameter values for a population through statistical optimization algorithms. However, estimating model parameters from empirical data of the population under study does create interdependence between model assumptions and predicted dynamics that ideally should be independent of each other (de Roos & Persson, 2013a). In essence, in hybrid models the predicted stock biomass or recruitment at say, 100 years down the line given certain fishing intensity, is a population-level extrapolation or projection from initial conditions.

Given the ability to estimate population-level model parameters directly from fisheries data, this approach provided a new and useful way to quantitatively examine the effects of different fisheries management options, such as catch quota, on the dynamics of exploited fish stocks. The most influential scientists in developing this 'hybrid' approach in a marine context are William E. Ricker (1908-2001), Ray Beverton (1922 - 1955), and Sidney Holt

(1926 - 2019). Although not a marine scientist, a special place is also reserved for Patrick H. Leslie (1900-1974), who studying animal population fluctuations in the widest sense would develop an important 'equation-free' approach whose principles would be quickly adopted by fisheries science to make future stock projections.

In 1954, when scientific journal space was certainly less contested, Ricker published a lengthy 65-page paper entitled 'Stock-and Recruitment' that outlines his view of the general theory of population regulation in fish stocks (Ricker, 1954). The most famous equations in the paper (still in use today) are the 'Ricker-model' and the 'spawner-recruitment equation'. The Ricker-model is a basic variant of logistical population growth equation (discovered by Verhulst (1838)), that can be used to predict the total fish population size at a future time step given current population size, population growth, rate and the carrying capacity of the environment. The Ricker spawner-recruitment equation predicts the number of recruits entering a population based on the total number of reproducing adults. The derivation of the spawner-recruitment equation is slightly more involved than the Ricker-model, covering some ten equations, each with their own important limiting assumptions. For example, the basic assumptions that adult fish take on the role of 'cannibalistic' predators, and all other forms of mortality can be realistically summarized by a single constant parameter, are essential for the proofs provided in the article.

Three years after Ricker's influential paper, in 1957, two young scientists working at the Lowestoft Fishing Laboratory in the UK published a book that would modestly become known as 'the Bible' of fisheries science. In 'On the Dynamics of Exploited Fish populations' Raymond Beverton and Sidney Holt outline a range of methods for the quantitative analysis of fish population dynamics. The book build upon the methods introduced by Ricker, but extended this type of thinking to account for interactions between the populations of exploited species, spatial variation in populations, and the dynamics of fishing fleets (Beverton & Holt, 1957; Raicevich et al., 2021). Famous equations include the Beverton-Holt model equation to predict total population size and the yield per year-class equation. The Beverton-Holt model equation is in essence a slightly different formulation of the Ricker model, where the estimated population size one time step in the future is dependent on current population size, the net reproduction in the population (by the R_0 measure now familiar to most due to the covid pandemic), and the carrying capacity of the environment. The applicability to management of Beverton and Holts work shines through the yield per year-class equation. Here the total number of fish of a certain age class that can be expected to be caught can be predicted based on the fishing mortality, reproduction of the population, and the growth of a year class given natural and fishing mortality. The work of Beverton and Holt generalized the way in which fisheries management would determine optimum 'sustainable' harvesting strategies. Sidney Holt, in particular, remained an immensely influential figure in the debate around the impact of human exploitation on marine populations throughout his lifetime. Not only through his scientific work on fish populations, but also subsequent studies using population models to show how whaling practices were pushing entire species towards extinction. He later also publicly voiced critique on perhaps the most famous fisheries harvesting metric, The Maximum Sustainable Yield, as "*the worst idea in fisheries management*" and "*a way to*

institutionalize greed” (Holt, 2011; Raicevich et al., 2021).

Thus far, I discussed mathematical equations, that could be fitted in a statistical fashion to data, in order to predict changes in populations over time. But in 1945, the Scottish scientist P.H. Leslie working at the Bureau of Animal Population at Oxford University found a way to use another well-known mathematical tool, to examine population fluctuations. This powerful tool was matrix algebra. The Leslie matrix (Leslie, 1945) takes key demographic parameters of different age classes (reproduction, survival), and uses these to determine population growth up to a certain future time-point, and the relative size of each age-class to the overall population at that point in time. One interesting outcome is that the population growth predicted by a Leslie matrix is similar to that obtained using an exponential growth function (or ‘Malthusian’ growth (Malthus, 1798)). Using matrix algebra further meant that it was relatively straightforward, mathematically, to project future population or age class sizes based on current conditions. Adaptations of the Leslie matrices to deal with various types of population data remain one of the most popular tools in population ecology and demographic studies to date to understand population fluctuations. These approaches are nowadays gathered under the umbrella term Matrix Population Models (MPM’s) (Logofet & Salguero-Gómez, 2021a; Caswell, 2001a). Despite founding an entire modelling discipline, Leslie remained a somewhat elusive figure in the scientific world. A serious lung-condition at a young age made him prefer a quiet and secluded life, and he performed most of his work from home (Nature, 1972). Perhaps more incredible, Leslie was never formally trained as a mathematician or an ecologist; only making the switch to the Oxford Bureau of Animal Populations at the age of 35, after his health prevented him from finishing his medical studies (Nature, 1972).

Fundamental questions in population modelling

When we take a step back and examine the major modelling developments in marine population ecology discussed up to 1960, we see, perhaps unsurprisingly, a focus on the population level. We can use the Lotka-Volterra equations, the Ricker-model, or the Beverton-Holt model and Leslie matrices to examine how biological and non-biological factors affect population abundance, survival, growth, and reproduction. Even how the population abundance of one species affects the other. However, underlying this type of analysis is one very important assumption: that all individuals in a population can be represented by some ‘average’ type (de Roos & Persson, 2013a). Modelling population fluctuations based on these assumptions, is referred to as using a ‘phenomenological’ modelling philosophy. In phenomenological models there is no explicit specification of the mechanism by which biological and non-biological conditions affect life history processes such as growth and reproduction, but these are instead represented by average ‘rates’ at the population level (de Roos & Persson, 2013a).

Such phenomenological assumptions are present in all the mathematical, statistical, and hybrid approaches discussed thus far. Yet, at the same time, there is also an intuitive understanding that a population doesn’t undergo cellular growth, a population doesn’t

produce eggs or sperm for reproduction, and a population doesn't have food intake. Such life history processes take place at the individual organismal level and are limited by the energetic status of the (individual) organism (Kleiber, 1961). Only when energy intake exceeds energy expenditure in terms of metabolic demands can organisms grow and reproduce. When energy intake is too low, organisms will eventually starve. Each and every individual organism in a population will furthermore differ slightly in their metabolic rate, their growth, their reproduction, and other life history processes. The recognition of this variation between individuals and the 'uniqueness' of the life history of each individual organism arguably forms the most important principle underlying Darwin's theory of natural selection (Lewontin et al., 1974); strongly conflicting with the assumption of an 'average type'. Because variation in life history processes between individuals is so central to ecology and evolution, it is good to take stock and consider where the assumption of the 'average type' in the theory of population ecology originates.

The foundational scientists of theoretical population ecology such as Vito Volterra and Alfred J. Lotka had backgrounds in physics, mathematics, and chemistry. Unlike 'naturalist' ecologists such as Hjordt, they were not fascinated by spending large amounts of time outdoors carefully collecting information on their study species. In fact, the primary goal of Alfred J. Lotka was to found an entire new scientific field of 'physical biology', by which he meant "*the broad application of physical principles and methods in the contemplation of biological problems*" (Kingsland, 2015). Volterra's 'interdisciplinary' work can equally be seen as an attempt to integrate mathematical and physical principles in the biological, social, and economic sciences (Scott, 2018). The starting perspective for scientists such as Lotka and Volterra was therefore that the interaction between animals could be formulated in the same way as the interaction between particles. Subatomic particles such as electrons are identical and will behave in the same way, thus one can use an 'average type' to represent the response of an entire group or population of particles. In contrast, each individual animal is unique, and each individual will behave slightly different, casting doubt on the reasonableness of the 'average type' assumption. Then what about the fisheries models from Ricker and Beverton and Holt? These model equations represent derivations of the logistic growth equation developed by the Belgian mathematician Verhulst between 1838-1847. As populations cannot increase indefinitely, Verhulst included a 'crowding effect' in the equation that forces population growth to slow down with increasing size towards some equilibrium. In a slightly different formulation this equilibrium population size was later popularized as the 'environmental carrying capacity' of the population, i.e. the maximum number of individuals an environment can support (Hartvigsen & Levin, 2001). A famous early empirical example of populations adhering to this principle includes the experimental growth of yeast in the laboratory by Gause (1932). One might ask whether carrying capacity is in a sense mechanistic if it derives from a crowding effect between individuals. After all there are myriad ecological processes between individuals such as competition for breeding space, competition for reproduction, and mate selection, that will limit population size. Still, the question then remains which of these ecological processes causes the density-dependent effect, and each of these processes, if mechanistically formulated, might lead to a very different equilibrium population size!

Since the 1960's there has been a piecemeal movement towards developing more mechanistic approaches in theoretical population models. At each step, some phenomenological representations were replaced by a more explicit, mechanistic, incorporation of some underlying processes. Although it took a while to truly arrive at the recognition of individual importance. Some landmark studies will be discussed in the next part. These developments have led to important new insights into the possible dynamics of populations, and again marine populations were leading in this development. It also provided an indication of why, despite decades of phenomenological modelling of fish stocks to advise fisheries, these stocks responded very differently than expected and often remained depleted.

Mechanistic developments

Between 1963 and 1972 the American ecologists Robert H. MacArthur, Michael Rosenzweig, and Richard Levins published a series of highly influential papers incorporating more mechanistic processes within traditional Lotka-Volterra equations. First was the mechanistic incorporation of the notion that a predator population could not endlessly keep consuming a prey population with a constant rate. At some point satiation should occur, and predators likely forage less intensely the more satiated they are. Therefore, the 1963 Rosenzweig-MacArthur model incorporated a mechanistic 'functional response'³ of resource consumption by the predator population (Rosenzweig & MacArthur, 1963). This was followed in 1967 and 1972 by studies that incorporated interspecific competition explicitly (MacArthur & Levins, 1967; May & Arthur, 1972). In this case the way in which resource competition between species limits the number of species that can coexist in an environment.

Other publications appeared in the same decade that changed the way population ecologists thought about the dynamics that populations can display. In a flurry of papers produced between 1976 and 1980 the Australian scientist Robert May showed that the dynamical behavior of 'chemistry and physics-inspired' population models can be much more complex than previously thought, depending on the mathematical tools used to examine them. The particular tool May favoured was 'bifurcation analysis'⁴. Whilst ecologists were by now comfortable with model populations of a single species growing towards some stable equilibrium size (e.g. Ricker model), or predator-prey populations cycling endlessly (Lotka-Volterra); May used bifurcation analysis to show the peculiar population dynamics that may lie beyond.

In a 1977 review paper in *Nature* May summarized how simple population dynamics in a system of two species gives rise to 'alternative' stable states (May, 1977). Perhaps even more importantly, in a 1976 contribution to *The American Naturalist*, May showed for

³The notion of functional responses was founded by Maurice Solomon in 1949, and the equations of these functional responses were developed Crawford Stanley Holling (1930-2019) in a series of papers between 1959-1965 (Krebs, 2022).

⁴In bifurcation analysis the behaviour of a set of ordinary differential equations is examined when changing one or multiple parameters 'locally' around an equilibrium. In this way the stability of equilibria can be determined, and the behaviour the system will display between multiple equilibria (Kuznetsov, 2004).

the first time how population dynamics of a single species could exhibit a continuum of stable equilibrium population sizes, stable cycles, and seemingly random ‘chaotic’ dynamics (May & Oster, 1976). The concepts of alternative stable states and chaotic dynamics changed how scientists thought about the impacts of human exploitation on marine populations. Why for example, had most fish stocks continued to decrease and not responded to management interventions as predicted from classic fisheries models? Why did collapsed stocks not necessarily recover, despite the cessation of fishing? However, despite increasing recognition of the extremely complex behaviour of populations these studies caused, the importance of individual life history for population level outcomes remained largely undervalued.

Recognition of the individual

The scientific sentiment on the importance of individual life history for population dynamics only really started to change in the 1980s. In 1984 Earl E. Werner and James F. Gilliam published a widely influential review paper on the role of individual body size in structuring populations and the interactions between populations. Studies mentioned in the paper, including those by the famous Robert MacArthur, had predicted that the ‘average type’ body mass of a species pair with a shared resource should differ by at least an order of 2 if they were to coexist. Yet, Werner and Gilliam asked, how could this ‘general’ theoretical prediction align with the basic observation that in some of the most numerous species groups such as fish, the body weight of an individual can span over 4 orders of magnitude? In other words, that “*the body dimensions experienced ontogenetically often transcend those limits purported to isolate strongly competing species*” (Werner & Gilliam, 1984). Something fishy was going on, but as Werner and Gilliam note “*Paradoxically, ecologists have virtually ignored the implications of these observations for interactions among species that exhibit size-distributed populations*” (Werner & Gilliam, 1984).

Clearly, the effect of individual-level life history processes on population level dynamics was in urgent need of examination. This, however, would require a different type of model formulation. In 1986, the Dutch theoretical biologist Hans Metz and mathematician Odo Diekmann published the first formulation of how to explicitly model individual-level life history development and numerically integrate this to population-level outcomes (Metz & Diekmann, 1986). The approach developed by Metz and Diekmann would come to be known as a ‘physiologically size-structured population model’ or PSPM. In PSPMs individuals are characterized by a certain state, for example individual body-size. How the body size of an individual changes, depends on the condition of the individual (available energy through food intake, current body size), which in turn is dependent on the condition of the environment (resource density, predator, or the density of individuals of the same species competing for similar prey) (de Roos & Persson, 2013a). Much like bookkeeping, one can simply make up a balance of the population level state by summing or integrating over all individuals in the population. The important distinction here with the models discussed before is that what happens to the population is solely the outcome of the (unique) life history events of all the individuals of a population, rather than the multiplication of population size with some average rate. In the following decades this

type of modelling proved particularly useful in understanding fish population dynamics and the impacts of fishing mortality (Persson & De Roos, 2006; Soudijn et al., 2021).

The importance of the individual was also used in newly developed matrix-based approaches. Combining the data-driven power of MPM's with 'fundamental' biological equations that can be integrated across all individuals in a population lead to the development of Integral Projection Models (IPM's) at the turn of the century by the biomathematician Michael R. Easterling, and theoretical ecologists Stephen. P. Ellner, and Philip M. Dixon (Easterling et al., 2000a). Interestingly, although IPMs recognize the importance of the individual, they can be fitted to data through optimization in statistical fashion. The projections made remain extrapolations without a link between the individual condition (energy intake) and the environment (resource density). There is no feedback between the resource and the consumer, meaning that the realized life history of an individual in these models is essentially independent of its environment. Therefore, IPMs remain a hybrid rather than a fully mechanistic, process-based approach.

Concluding, moving in to the 21th century

Moving into the 21th century there is an entire gradient of modelling approaches to understand population dynamics in marine communities. Furthermore, the various approaches developed over the course of a century discussed in this brief history seem to 'stably-coexist' with each other. Studies utilizing Lotka-Volterra equations are still easily found, as are studies relying on the linear correlations that Hjort used. Simultaneously, an endless variation of small extensions to later developed models (Ricker, Beverton-Holt, Rosenzweig-McArthur, MPMs, IPMs) have been published, dealing with particular aspects, such as spatial differences in populations, while maintaining a firm phenomenological character. Which approach is most applicable depends largely on the question being asked. However, it seems that following the famous phrase "all models are wrong, some models are useful" by George Box, ease of applicability often precedes examination of the theoretical underpinning when population models are used to understand population fluctuations. I hope this brief history has shown that for the scientists developing these models, their choices of mathematical formulation were not neutral but based on fundamentally different views on how the natural world operates and how it should be represented. It is therefore always a good idea to a-priori reflect how these perspectives relate to your own before moving on to application. You might find an unexpected modelling approach suits your reasoning best!

1.2 Current themes and challenges

Big data and big changes

The turn of the 21th century⁵ sees science awakening to the concept of humanity as a globally dominant force of change across the (non)living environment (Crutzen, 2002; Crutzen & Stoermer, 2002). In an influential one-page essay fisheries scientist Daniel

⁵Defined here as the period 1995-2005

Pauley coins the term ‘shifting baseline syndrome’ to describe the ‘persistent and collective failure’ of scientists to recognize the magnitude of decreases in populations of marine species from one generation to the next (Pauly, 1995). Other influential studies soon follow illustrating how historic and ongoing overfishing have altered the trophic composition of marine systems across the globe, termed ‘fishing down the food web’ (Pauly et al., 1998a), and how overfishing is the main driver of recent ‘ecological collapse’ of coastal systems (Jackson et al., 2001). Next to the pervasive effects of overfishing, there is increasing evidence of how human-induced climate change is altering marine populations. Ocean warming is first shown to drive shifts in the distribution of marine fish populations (Perry et al., 2005), as well as changing the phenology of plankton (Edwards & Richardson, 2004), fueling concerns for phenological mismatches with higher trophic levels. Additionally, ocean acidification is recognized as a threat to the early life history development of populations of marine invertebrates (Kleypas et al., 1999; Wolf-Gladrow et al., 1999; Turley et al., 2006). The concentration of studies highlighting the alarming, widespread, negative (indirect) effects of anthropogenic activities on marine populations at the turn of the century shifts the focus of marine population ecology towards better understanding, predicting, and, potentially, mitigating these effects⁶. These studies lay the foundation for the current dominant paradigm of marine population ecology in an era of global change.

At the same time, science and society are entering the era of ‘big data’, characterized by a continuous inflow of petabytes of information presenting new opportunities and challenges to understand complex issues across disciplines (Spengler, 2000; Palmer et al., 2005; Feigelson & Babu, 2012; Aronova et al., 2010; Brumfiel et al., 2011; Khoury & Ioannidis, 2014). In a famous study Chinese scientists Min Chen, Shiwen Mao, and Yunhao Liu show how the worldwide data volume doubled nine times between 2006-2011 and continues to increase exponentially (Chen et al., 2014). The amount of genomic data alone is found to double every 18 months (Villars et al., 2011). The field of ecology is no exception to the ‘big data’ boom (Hampton et al., 2013; Farley et al., 2018). In the context of marine population ecology some illustrative examples include: the continuous remote sensing of ocean systems from space to detect zooplankton and phytoplankton blooms (Gower et al., 2005, 2008; Basedow et al., 2019); the development of automated biodiversity monitoring networks through the large scale deployment of arrays of acoustic and camera sensor networks (Heupel et al., 2006; Colbo et al., 2014; Aguzzi et al., 2019; Giddens et al., 2021); the large scale collection and sequencing of environmental-DNA data (Goodwin et al., 2017; Ruppert et al., 2019; Truelove et al., 2022), and the aggregation of multidecadal (fisheries) surveys into large curated and publicly accessible resource databases (ICES, 2023).

Parallel to these developments is the focus on how to best harness big data to guide policymaking. Popular in this respect are the creation and use of global databases of

⁶Later studies add another layer of complexity to understanding how marine populations respond to global change; as studies show populations of species groups such as cephalopods and jellyfish buck the trend of global decline, and instead are increasing in large parts of the world (Brotz et al., 2012; Doubleday et al., 2016a)

‘average type’ demographic traits such as growth, fecundity, and mortality (Then et al., 2015; Beukhof et al., 2019a; Salguero-Gómez et al., 2016a; Froese et al., 2010). The ‘holy-grail’ of such trait-based approaches is to use big data to identify a limited set of ‘key’ traits that yield generalizable predictions on population functioning and responses across taxonomic groups (Funk et al., 2017; Salguero-Gómez et al., 2018; Kissling et al., 2018a). In the context of marine population ecology examples include the identification of a limited set of traits explaining how populations of marine fish will respond to climate-change (Beukhof et al., 2019c,d).

Machine-learning

As ‘big data’ transforms the scale of information scientists work with, the methods used for scientific enquiry change. Machine-learning starts to branch out from the domain of computer science and quickly proves its aptness in pattern recognition and predictive power using big data across scientific disciplines (Hastie et al., 2001; Fradkov, 2020). Popular commentators declare ‘the end of theory’ as machine-learning will make the traditional scientific method obsolete. The argument is that ‘*with enough data, the numbers speak for themselves, correlation replaces causation, and science can advance even without coherent models or unified theories*’ (Anderson, 2008). Population ecologists, too, are quick to adopt machine-learning models for analyzing their data. The complex, non-linear, and highly dimensional datasets full of feedbacks typical of ecology have always been difficult to analyze. The high variation between organisms, populations or systems under study means that rarely, if ever, ecological research produced a convincing ‘general’ theory or law, typical of other natural sciences (Pulliam & Waser, 2010; Fox, 2019). Advocates of machine-learning propose this might all be about to change with the ‘infusion’ of the machine-learning into the traditional scientific method (Peters et al., 2014). This will transform ecology through data-driven paradigm shifts. The superior data fitting and predictive capabilities of machine-learning methods fuel the perspective that although “*most Machine Learning methods tend to behave like black boxes . . . the functional relationships are embodied in the fitted ML models*” (Yu et al., 2021). The promise here is that as long as scientists provide sufficient big data, machine-learning will ultimately provide the underlying process that is ‘hidden’ in the dataset. This line of reasoning gets a further push in popularity as the first algorithms are developed to approximate relationships from fitted machine-learning models (Ribeiro et al., 2016; Lundberg & Lee, 2017a; Lundberg et al., 2020b). From the perspective of the machine-learning advocate it seems like a matter of time before the ‘black-box’ becomes ‘translucent’ and the transition towards true ecological understanding using machine-learning is completed (Lucas, 2020; Yu et al., 2021).

Pushback

There is some pushback against the radical empiricism embodied by the vision of a fully ‘data-driven’ science (Anderson & Abrahams, 2009; Coveney et al., 2016a; Succi & Coveney, 2019). An oft-invoked limitation to machine-learning is that the modelled relationships and predictions, by design, do not extend beyond the data to which they have been exposed. An oft-invoked reply is that we just need to increase the amount and type of data collected. If the world was full of sensors continuously monitoring everything,

ultimately machine-learning would learn the functional relationships between all these inputs. However, there are other drawbacks present in scientific fields such as population ecology that cast doubt on this assumption.

The first drawback is that the data on which machine-learning models are trained are a one-dimensional representation of the outcomes of multi-dimensional processes (Ye & Sugihara, 2016). This can lead to strong correlations between variables in data that are intuitively nonsensical, but also, a lack of correlation between variables that intuitively should be related. For example, Van Leeuwen et al. (2008) and Persson et al. (2014), use fisheries data to show there is no pattern in the data between the growth of a predator, cod, and the densities of their main prey, sprat, or the growth of sprat and the densities of their main prey, zooplankton. Thus, across trophic levels, functional relationships we know must exist (growth of individual predators through energy intake from prey), are not necessarily present in this type of data. Hence, these relationships can also not be ‘learned’ from such data.

A second drawback to the application of machine-learning approaches for fundamental ecological learning is the limited temporal resolution at which population data can be collected. Collecting data on marine populations remains an extremely labor-intensive task. The largest marine population surveys have collected data for decades but can generally only sample annually or quarterly. This means that total dataset size, from a machine-learning perspective, is tiny compared to the complexity of the system it is meant to model. This in stark contrast to, for example, climatic datasets, where temperature fluctuations and precipitation patterns can be monitored near continuously. Limited temporal resolution in survey data also means that the observations, such as quarterly biomass, are the outcome of months of unobserved biological processes. Methods for more automated large-scale surveying might increase the temporal resolution of data, but, in turn, will lack other important data-dimensions. Inferring functional relationships from ecological data therefore seems to remain a puzzle with many scattered pieces.

1.3 What to expect from this thesis

The 21st century has seen rapid changes in the (non)living environment and the methods used for scientific enquiry. An era where global change meets big data, with many scientific fields such as marine population ecology caught in the middle. These developments show the need for a coherent research vision to ensure the future health of marine ecosystems. This thesis therefore revolves around the main question of:

How to best move forward to the goal of understanding how and why marine populations fluctuate over time in an era of big data and global change?

To answer this question, I will explore the different modelling perspectives present in marine population ecology. Specifically, I explore whether big-data combined with data-driven approaches will be sufficient to understand how marine populations respond to

global change. Or that we gain more insight and understanding from formal theoretical work. I argue that this, in fact, is not a new discussion, but mirrors the century old debate of scientific inference through ‘**pattern**’ versus ‘**process**’ (see brief history section). At its core, it is a question of whether phenomenological representations can ultimately replace mechanistic ones in the scientific pursuit of understanding nature. What has changed are the extremes of the gradient of approaches available. A century ago, in the time of Hjort and Volterra, linear regression and ordinary differential equations completed the gradient. Now distribution-free machine-learning approaches occupy one extreme, and theoretical models recognizing individual variation occupy the other.

The individual chapters of this thesis explore and contribute to the development of this gradient of approaches, with the aim of evaluating and improving their use in understanding the responses of marine populations to global change (Fig. 1). The thesis starts on the pattern side of the gradient. Chapter 2 describes the development and application of a deep-learning species distribution model to examine the interspecific interactions and stability of benthic invertebrate communities using big data. Chapter 2 moves towards ‘causality’-based machine-learning approaches applied to multidecadal survey datasets to understand spatio-temporal variation in habitat use by marine fish. Chapter 3 links to Box 1, in which I question how to validate ‘causality’-based machine-learning approaches and examine the performance of one such model on a synthetic dataset with known underlying relationships. This is followed by Box 2, in which a large language model is provided the opportunity to write a brief rebuttal.

The next two chapters move up the gradient by examining more traditional approaches to understand population responses to changing environmental conditions. Chapter 4 uses non-linear statistical approaches to detect and quantify changes in the phenology of coastal habitat use of fish in relation to abiotic variables. Chapter 5 extends matrix population models relying on average type traits with more mechanistic representations to simulate population responses to climate change and the chapter discusses how additional life history complexity affects generality of predictions. Finally, Chapter 6, represents the process end of the spectrum, in which I examine the role of formal theory in understanding population regulation in deep-sea ecosystems.

From pattern to process in modelling the population dynamics of marine communities

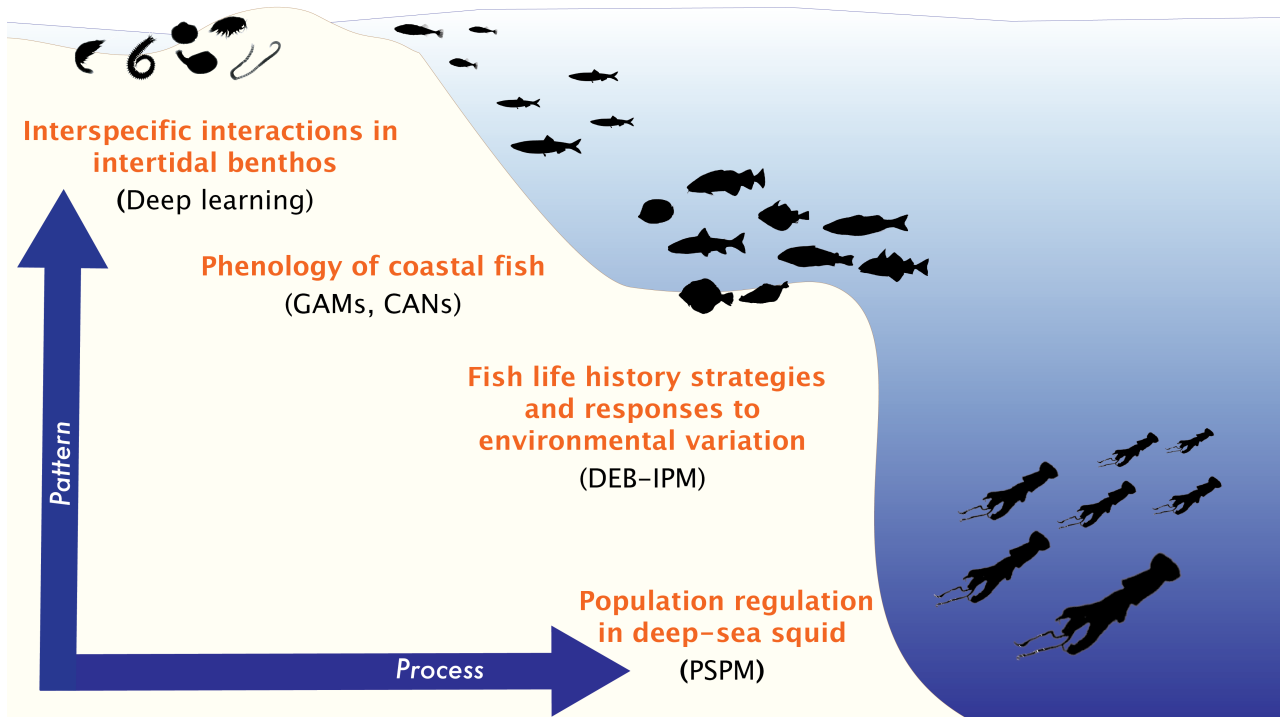


Figure 1.1: Schematic representation of the research conducted within the context of this thesis utilizing different approaches along the pattern to process gradient and different marine communities.

Chapter 2

Benthic invertebrates in the Wadden Sea form a stable community characterized by facilitating relationships

This chapter is based on: Rademaker, M., de la Barra, P., van Leeuwen, A., & Bijleveld, A.I. (in review). Benthic invertebrates in the Wadden Sea form a stable community characterized by facilitating relationships.

Abstract

Entire tidal food webs rely on the presence and productivity of benthic invertebrates. These invertebrates recycle nutrients, decompose organic matter, and function as food for myriad species at higher trophic levels. Nevertheless, little is known about the interspecific interactions between benthic invertebrates and their relation to ecosystem structure, function, and stability. Here, we used a deep-learning species distribution model to characterize the interspecific interactions occurring in an intertidal benthic invertebrate community while accounting for abiotic factors. The data includes > 30.000 samples collected between 2008-2020, over a spatial grid of more than 2400 km². The benthic invertebrates in the Wadden Sea were shown to form a stable community where species engage in relatively few strong interactions in a larger network of weak interactions. This corroborates classical theory on stability-connectivity relations. We provide a steppingstone for species-specific analysis by showing that numbers of interaction link to functional species traits.

2.1 Introduction

Soft-sediment tidal flats are among the most productive ecosystems in the world and deliver important services to coastal communities (Barbier et al., 2011; Douglas et al., 2017). However, these ecosystems are under intense pressure from human exploitation and development (Murray et al., 2019). Benthic invertebrates are central to the biological functioning of soft sediment tidal flats by recycling nutrients, decomposing organic matter, and as a primary food source for a wide range of organisms (Douglas et al., 2017; Jung et al., 2017; van Roomen et al., 2012; Poiesz et al., 2023). Research has only very recently begun to unravel how interactions between different benthic invertebrates affects this functioning (Schenone & Thrush, 2020). Studying these interspecific interactions is important as they are a driving force in the structuring and stability of the species communities in ecosystems (Clements et al., 1926; Allee et al., 1949; Bertness & Callaway, 1994; De Ruiter et al., 1995; Lindeman, 1942). Increasing our knowledge on the interspecific interactions between benthic invertebrates would therefore yield valuable insights into the status and biological functioning of soft-sediment tidal flat ecosystems.

Interspecific interactions are classically divided into positive interactions, such as facilitation and mutualism (Bertness & Callaway, 1994; Stachowicz, 2001; Bascompte & Jordano, 2007), and negative interactions, such as predation and competition (Schoener, 1983; Connell, 1983; Menge & Sutherland, 1987). However, the type of interaction effect observed is scale dependent. For example, although predation represents a negative effect for prey at the individual level, it can have a positive effect at the population level through reduced competition between remaining prey individuals (Yodzis, 1988). These types of indirect positive effects are termed 'emergent facilitation' and enhance community diversity (de Ruiter & Gaedke, 2017). Interspecific interactions have also been found to play a key role in regulating biodiversity and community stability (Pennekamp et al., 2018; Ratzke et al., 2020; Neutel et al., 2002; Allesina & Tang, 2012). Stable communities are typically characterized by a minority of strong interspecific interactions embedded in a majority of weak interspecific interactions (Paine, 1992; Wootton, 1994; McCann et al., 1998). However, interspecific interactions do not exist in isolation of the relationships that species have with other spatial, temporal and abiotic processes occurring in an ecosystem. Research should therefore strive to simultaneously account for abiotic and spatio-temporal processes. In this study, we present such an approach to examine the interspecific interactions of the benthic invertebrate community in the Wadden Sea.

The Wadden Sea ecosystem consists of soft-sediment intertidal flats that stretch along the northern coastlines of the Netherlands and Germany up to the tip of Denmark (Wolff et al., 2010). The ecology of several of its most common and economically valuable benthic invertebrates have been well studied (Reise et al., 1989; Beukema & Dekker, 2020a). Median grain size and inundation time were found to be the most important abiotic factors in shaping benthic invertebrate distributions in this system (Compton et al., 2013). Furthermore, a large spatial-auto-correlation component was observed when explaining the distribution of benthic invertebrates in the Wadden Sea based on abiotic conditions

(Kraan et al., 2010). Both predatory (Beukema et al., 2000), competitive (Flach, 1992), and facilitating (Lackschewitz & Reise, 1998) relationships have been observed between several common benthic invertebrates in the Wadden Sea. However, the simultaneous effect of these different abiotic, spatial and interspecific processes across the species community remains unknown. A system wide study accounting for interspecific, abiotic and spatial processes would therefore yield valuable new insights into the structuring and functioning of the benthic invertebrate community in the Wadden Sea.

Here we present an approach to study the interspecific interactions of benthic invertebrates in the Wadden Sea while accounting for abiotic and spatial processes using deep learning species distribution models (DL-SDM) (Botella et al., 2018; Rademaker et al., 2019; Rew et al., 2021). We used the data and observed patterns in interspecific interactions between benthic invertebrates to address four main research questions; (i) What is the stability of the benthic vertebrate community as a whole? (ii) How many strong interspecific interactions do individual benthic invertebrate species have compared to the total number of possible interspecific interactions, (iii) is the community of benthic invertebrate species characterized by negative or positive interspecific interactions, and (iv) do functional traits affect the number and type of interspecific interactions between species? The first two research questions link back to community stability. Stable communities are characterized by few strong interspecific interactions embedded in a majority of weak interactions and have relatively low variability in species composition, biomass, or abundance. The third research question links back to the internal structuring of the species community by identifying the dominance of competitive or facilitating relationships. Finally, the fourth research question examines the link between the functioning of a species and community structuring. Together, these four questions will provide new insights into the biological functioning of the benthic invertebrate community of the Wadden Sea, and soft-sediment tidal flats in general.

2.2 Material and methods

We perform a community-wide analysis of benthic invertebrates in the Wadden Sea to examine interspecific interactions between benthic invertebrates, the link between interspecific interactions and functional traits, and the stability of the community as a whole. To this end, we used a big dataset derived from over a decade of systematic monitoring of benthic invertebrates across the dutch part of the Wadden Sea.

2.2.1 Data collection

The NIOZ has systematically monitored benthic invertebrate populations across the entire dutch part of the Wadden Sea (2400 km²) from 2008 (Bijleveld et al., 2012; Compton et al., 2013), in a program called the Synoptic Intertidal Benthic Survey (SIBES). The SIBES program annually samples ~ 4800 stations positioned in a 500x500m grid, in combination with a set of varying numbers of additional sampling points (Bijleveld et al., 2012). At each site a core sample of 0.0177m² is taken at a depth of approximately 25 cm, as well as a sample for sediment characteristics using a centrifuge tube at 4 cm depth

(Kraan et al., 2009). Benthic invertebrate extraction, preparation, species identification and abundance and biomass estimation procedures from the core samples are detailed elsewhere (Compton et al., 2013).

2.2.2 Data preparation

We used a subset of sampling points in the SIBES survey dataset from the years 2008-2020 ($N = 34.882$ observations) for our study. The abundances of the 25 most commonly encountered benthic invertebrate species in this subset were used in combination with two spatio-temporal, and six abiotic variables, as predictive features in our model (Table 1). The 25 most commonly encountered species were defined as those with most non-zero abundance entries in the dataset. Mass episodic recruitment events might strongly affect the number of non-zero entries for specific years and bias abiotic relationships found by the model, as larval brood settles over vast areas. We checked for potential biases in the species abundance data due to mass episodic recruitment events by computing the inter-annual variability in occupancy rates for each species (Supplementary table 1). However, we found no evidence of high variation in occupancy rates or large differences between mean and median occupancy indicative of recruitment events skewing the distribution of observed occurrences. Next, we accounted for the spatial autocorrelation in the dataset by computing a Local Moran's I value for each sampling station and year combination (Anselin, 1995). We further included sampling station id as a separate feature representing repeated measures over time. The variables median grain size, and silt were derived from sediment samples taken simultaneously with the benthos samples in the SIBES program, whereas dryval duration, salinity, shear bed stress and wave forcing were derived from previous research (Donker, 2015; Folmer et al., 2017). After omitting any rows in the dataset with absent values, all variables were log-transformed and further scaled by removing the mean and dividing by the standard deviation. Data was split between 70% training dataset, and an equal split of 15% test, and 15% validation data.

2.2.3 Stability metrics

We examined the stability in community composition over the sampled years (research question i) through a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). The analysis was done using function *adonis2* in the R package *vegan* (Oksanen et al., 2010). We used a Bray-Curtis dissimilarity matrix and 4999 unrestricted permutations. Bray-Curtis dissimilarity can take values between zero and one, zero meaning that the compared communities have exactly the same species composition, and one meaning they do not share any species (Quinn & Keough, 2002). For clarity, we express this dissimilarity as a percentage. Due to computing limitations, this analysis was performed on a random sample of 20% of the data. A constrained analysis of proximities, (CAP)(Legendre & Anderson, 1999), was used to display the variation in community composition that can be explained by differences in years. For this, we used the function *capscale* from R package *vegan* (Oksanen et al., 2010), with a Bray Curtis distance matrix calculated on untransformed data. Bray-Curtis community dissimilarities between and within years were also calculated to better understand changes in community composition. Bray-Curtis dissimilarities between the centroids

Table 2.1: Abiotic and biotic variables included as features in the DL-SDM.

Feature	Description
<i>Biotic</i>	
Density	Number of individuals per m ²
<i>Spatio-temporal</i>	
Local Moran's I	Spatial autocorrelation of sample point. Spatial weights were defined using inverse distance weighting (IDW) with a power of 2, and a radius of 10 km. Target species density was used as the attribute.
Sampling station ID	Repeated measures at same sampling stations over multiple years
<i>Abiotic</i>	
Bed shear stress	Mean bottom shear stress due to currents
Dryval duration	Mean fraction of time that the seafloor is exposed to air
Median grain size	Median size of grains in the sediment
Salinity	PSU, equivalent to parts per thousand
Silt	Volume % < 63 μ m
Wave forcing	Median near bed orbital wave velocity

of all years were calculated using the function *multivariate_change* from the R package *codyn* (Hallett et al., 2016), and between samples within each year, using function *vegdist* from R package *vegan*. We also identified species that had a higher contribution to dissimilarity between any pair of years using the function *simper* from R package *vegan*.

2.2.4 Deep learning species distribution model

We modeled the number and type of interspecific interactions between benthic invertebrates (research question ii, iii), while accounting for abiotic and spatiotemporal variables, using a DL-SDM. We used a fixed neural network architecture in our DL-SDM (Supplementary Figure 1) and trained this model to predict the occurrences of each of the 25 target species. The hyperparameters of the model are detailed in Table 2. Because the occurrence data for many species was imbalanced (Bijleveld et al., 2018), with more absences than presences, we included class weights in the loss function (Thai-Nghe et al., 2010). The model was run five times for each species, and precision, recall, and PR-AUC scores were computed during each run for evaluation. The run with the highest PR-AUC score was stored for further analysis. We used PR-AUC instead of the more commonly applied AUC as an evaluation metric, as it is better suited for imbalanced data where the priority lies on correctly identifying the positive minority class, i.e. occurrences (Davis & Goadrich, 2006; Cook & Ramadas, 2020). A PR-AUC score close to 0 would signify the model is unable to identify the minority class, a PR-AUC score of ~ 0.5 would be able to correctly classify the minority class in half the cases, or equal to chance, and A PR-AUC score of 1 means the model achieves perfect classification of the minority class.

Table 2.2: Hyperparameters of the DL-SDM.

Hyperparameter	Type/value
Activation function hidden layers	ReLU
Activation function output layer	Sigmoid
Batch size	32
Dropout	0.2, 0.2, 0.1, 0.0
Epochs	Early stopping (<i>maximum: 1000, restore best weights</i>)
Hidden layers	4
Learning rate	Adaptive (<i>start 0.0001, factor:0.1, patience: 10</i>)
Loss function	Binary Cross Entropy
Neurons per hidden layer	64,32,16,4
Optimiser	Adam
Regularisation	L2 (<i>0.0001</i>)

The DL-SDM showed an approximately linear increase in performance with higher numbers of occurrences in the dataset (Supplementary Figure 2). The model performed poorly for species with fewer than 5.000 occurrences and the PR-AUC values for all species in this group were below 0.50. However, model performance increased for species with 5.000 - 10.000 occurrences in the dataset. Their PR-AUC scores ranged between 0.50 - 0.70, with the exception of one higher outlier species. Finally, the fast majority of species with > 10.000 samples had intermediate to high PR-AUC scores ranging between 0.70 - 0.95. Based on these results, we choose to set a cut-off point between lower and higher performing species at a PR-AUC of 0.70, and only examined the partitioning between abiotic and interspecific interactions of species with PR-AUC values above this score ($N = 12$ species).

2.2.5 Feature extraction and analysis

We extracted relationships modeled between the occurrences of the target species and the biotic, abiotic and spatiotemporal variables, and their importance in terms of feature weights using Shapley Additive Explanations (Lundberg & Lee, 2017b). We applied the Kaiser's criterion and considered all PCA axes with an eigenvalue > 1 for the final structuring of the data (Kaiser, 1960). We then generated a hierarchically clustered heatmap highlighting feature weight and direction (positive/negative relationships) to visualise similarities in species responses to abiotic variables using the R package gplots (Warnes et al., 2016). We structured interspecific relationships found by the model into five categories (strong negative, negative, weak, positive, strong positive), and visualized results across the species community using a heatmap. We determined the boundaries for the five response categories by applying equal width binning of shapley feature importance weights.

2.2.6 Functional traits

We examined the relationship between functional traits and interspecific interactions (research question iv) using a selection of traits of Northwest European marine benthic

invertebrates compiled by Clare et al. (Clare et al., 2022). We first structured these ordinal scaled traits into principal components using a non-linear PCA using the *GIFI* package in R (Mori et al., 2016; Mair et al., 2019). Next we used multivariate linear regression to examine the relationship between the number of interspecific interactions of a species and the principal component scores.

2.3 Results

2.3.1 Community stability

We found a statistically significant, but very small, multivariate difference in the community composition of benthic invertebrates over time (Table 3). Only 5% of the variation in community composition could be explained by differences between years. Visual inspection of the effect size further shows that the dissimilarity between any pair of years is relatively low (10 - 28%; Fig 1.A). This indicates that there is a relatively stable species community of benthic invertebrates in the Dutch Wadden Sea. The years 2010 and 2018 represent the communities that differed most from the rest of the years. In contrast to the low between-year variation in species composition, the within-year dissimilarities in species is much higher, with the median dissimilarity between two samples ranging from 85 to 95% (Fig 1.B). This indicates that there is high heterogeneity in species composition throughout the sampled area. Further analysis showed that only five species were responsible for more than 10% of the dissimilarity between any pair of years: *Scoloplos armiger*, *Pygospio elegans*, *Peringia ulvae*, *Marenzelleria viridis*, *Aphelochaeta marioni* (Fig. 1.C). *P. elegans* was the species contributing more to the dissimilarity between any pair of years, contributing 24% of the dissimilarity between 2013 and 2019.

Table 2.3: Permutational multivariate analysis of variance on the yearly changes in community composition using a Bray Curtis distance matrix. The test examines statistically significant differences in community composition of benthic invertebrates over time, represented by the variable year.

Source	df	SS	R^2	F	p
Year	12	27.59	0.046	6.253	0.001
Residual	1568	576.48	0.954		
total	1580	604.07	1		

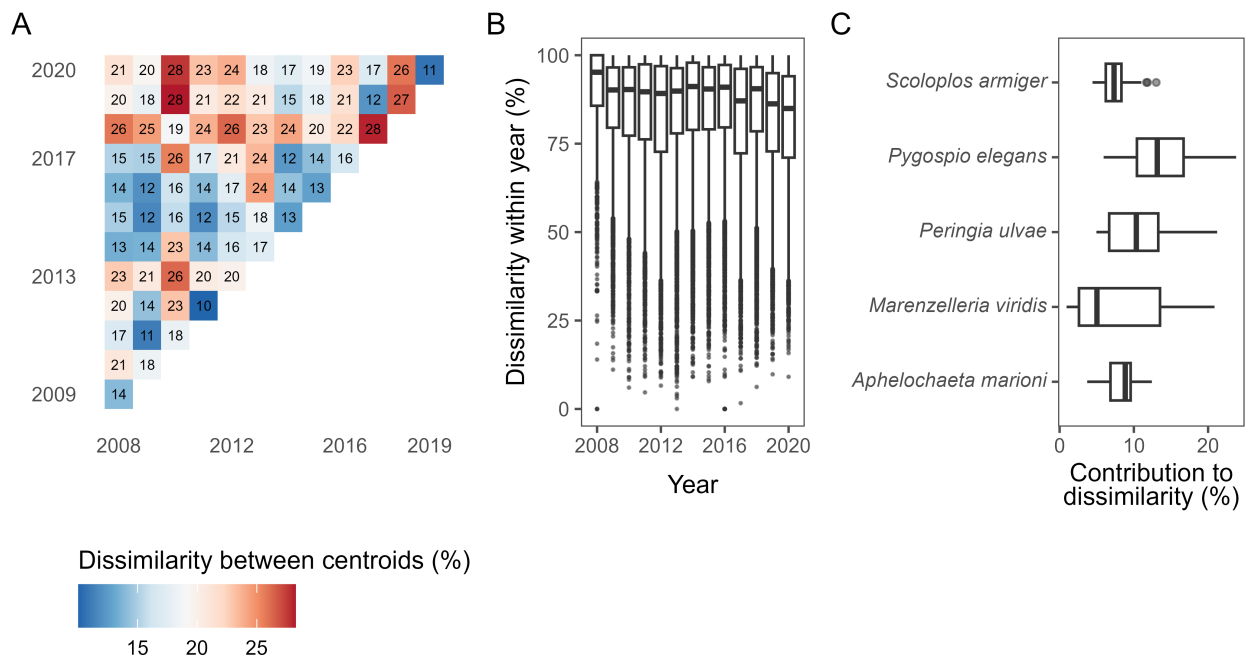


Figure 2.1: Analysis of dissimilarity in species composition of benthic invertebrates between and within years. A. Bray-Curtis dissimilarity between year centroids. B. Bray-Curtis dissimilarity between every pair of samples within each year. C. Contribution of species to dissimilarity between every pair of years. Only species that contributed to at least 10% to the dissimilarity of any pair of year, and their contribution to dissimilarity between years.

2.3.2 Spatial and abiotic interactions

The spatial and abiotic relationships of benthic invertebrates could be grouped into four distinct clusters (Fig. 2). Species in the first cluster generally showed a strong positive relationship with median grain size and salinity. Species in cluster two, also had strong positive relationships with salinity and median grain size, but were distinguished by their strong negative relationship with silt content. Next, species in cluster three were most distinguished by their strong positive relationship with dryval duration. Finally, species in cluster four had a strong positive association with silt content. Across all clusters, species showed intermediate to relatively low levels of spatial autocorrelation, with the exception of *Urothoe poseidonis* in cluster two. Species also shared a relatively weak relationship with bed shear stress and wave forcing across all clusters.

2.3.3 Interspecific interactions

Individual benthic invertebrate species on average engaged in 4.72 ± 1.35 interspecific interactions (Fig. 3); significantly less than the median of 7 co-occurring species observed per sample in the data (Mean $H_0 = 6.67$, $t(11) = 5.037$, $p = 0.0004$; Supplementary Figure 3). The community as a whole was characterized by a minority of strong interactions ($N = 52$) in a majority of weak interactions ($N = 236$, $N_{total} = 288$)(Fig. 4). Most of the non-weak interactions were positive ($N = 46$), while only a few negative

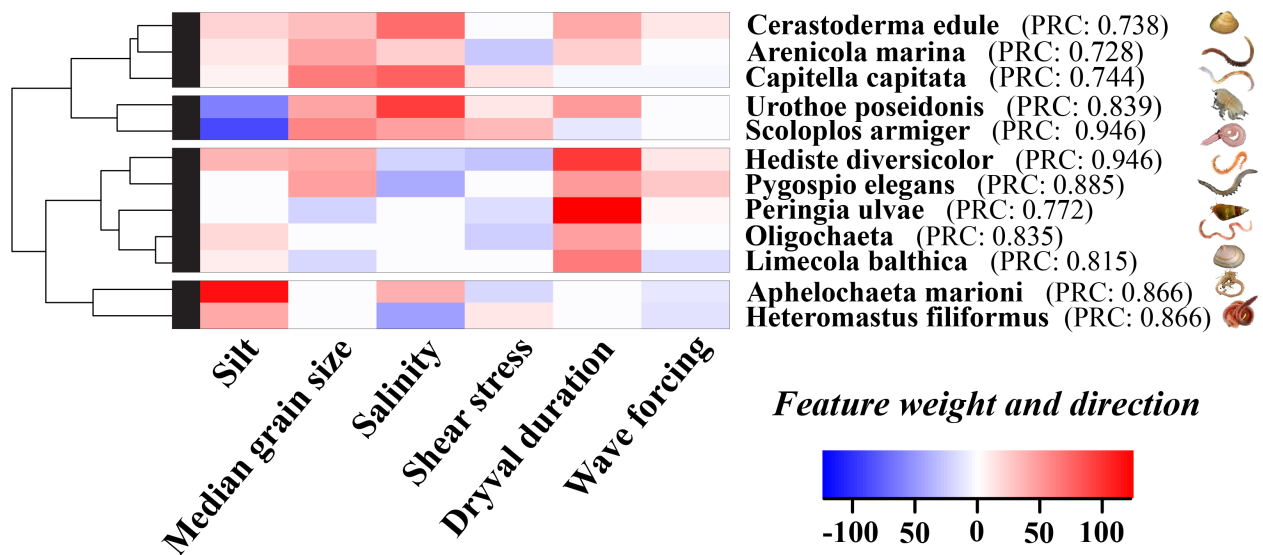


Figure 2.2: Cluster heatmap showing the importance of spatial and abiotic features in predicting the occurrences of 12 benthic invertebrate species in the Wadden Sea. Color type and intensity signify the direction and weight or strength of the relationships (blue = negative relationships, red = positive relationships). Species could be grouped into four distinct clusters whose members were most similar in their abiotic relationships (thick black bars on dendrogram), using hierarchical clustering with Ward’s linkage function.

interactions between species were detected ($N = 6$).

2.3.4 Relation to functional traits

Benthic invertebrate traits could be structured along five principal components that together described 84.12% of the variation in the data (Table 4). PC1 described free-moving scavenger and predatory species that are mixing bioturbators. Mixing bioturbators cause redistribution of sediment and or other particles in both the horizontal and vertical direction. PC2 described short-lived and shallow-living tube dwellers. PC3 described subsurface deposit feeders that are vertical bioturbators. Vertical bioturbators only translocate particles from depth to the surface or vice-versa during feeding and subsequent borrowing. PC4 listed large sized tube-dwelling species, and PC5 surface deposit feeders that are mixing bioturbators.

Multivariate linear regression showed that the amount of interspecific interactions between benthic invertebrates was most strongly related to PC3 (Fig. 4: blue regression line). This indicates that the trait combination loaded on PC3 (subsurface deposit feeding vertical bioturbators) might inform on the number of interspecific interactions. However, the effect size was borderline non-significant, the model explained relatively little variation and had a poor fit ($R^2 = 0.391, t = 2.034, p = 0.056$ Supplementary Fig. S4). We found that the lack of fit was driven to a large extent by a single species (*Aphelochaeta marioni*). *A. marioni* had the highest number of interspecific interactions in the dataset ($N = 7$) but had a different set of traits than those described by PC3. It

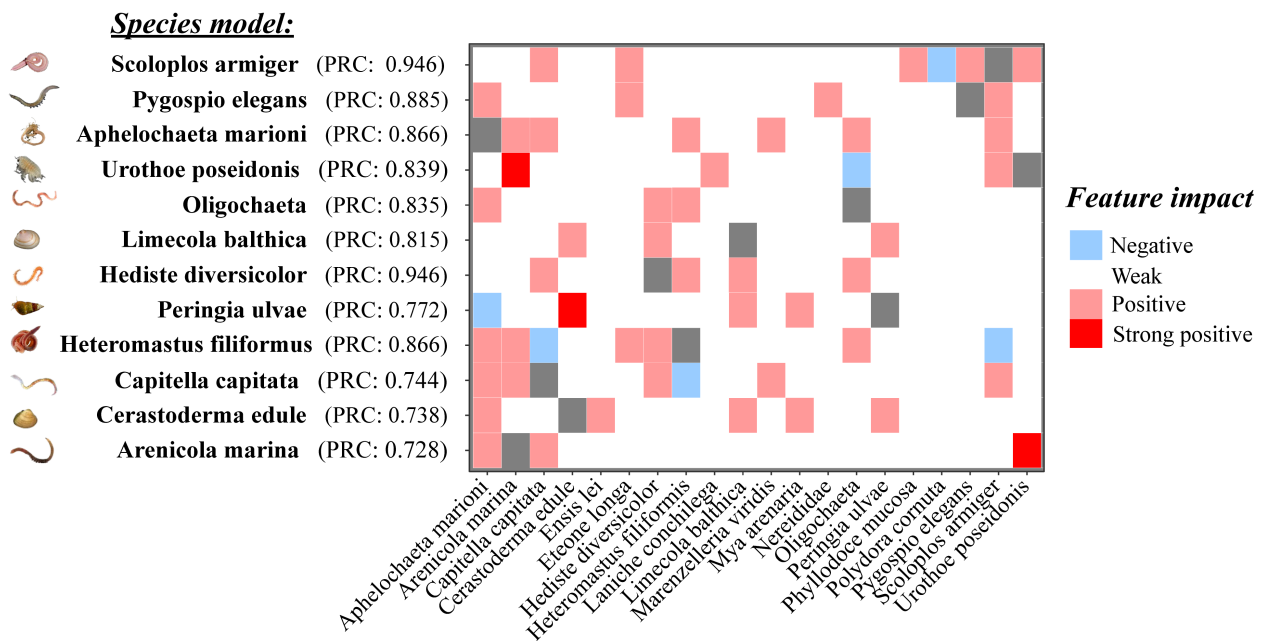


Figure 2.3: Importance of the density of other macrozoobenthos species in predicting the occurrence of 12 benthic invertebrate species in the Wadden Sea. Color type and intensity signify the direction and weight or strength of the relationship. Responses were categorized into bins based on the minimum and maximum feature weights assigned across species. Four species were left out of this figure as they had no relationships, i.e. complete white columns, with all model species occurrences (*Carcinus maenas*, *Corophiidae*, *Nephtys hombergii*, *Spio martinensis*).

Table 2.4: Structuring of the functional traits of benthic marine invertebrates into 5 separate Principal Components. Red values indicate strong positive loadings (> 0.5) and blue values strong negative loadings (< -0.5) of traits on a PCA axis.

TRAITS	PC1	PC2	PC3	PC4	PC5
Maximum size	-0.213	-0.319	-0.161	0.846	-0.116
Maximum age	-0.330	-0.616	-0.418	-0.307	-0.285
Tube dwelling	-0.220	0.503	0.422	0.585	0.121
Burrow dwelling	-0.413	-0.671	-0.069	0.074	0.305
Free living	0.805	-0.213	-0.154	-0.342	0.173
Maximum sediment depth	-0.219	-0.778	0.297	-0.021	0.158
Suspension feeder	-0.594	-0.325	-0.224	0.124	0.457
Surface deposit feeder	-0.306	0.361	0.254	0.086	0.686
Subsurface deposit feeder	0.242	-0.313	0.807	-0.370	0.012
Scavenger	0.788	-0.268	-0.305	0.371	0.199
Predator	0.788	-0.268	-0.305	0.371	0.199
Vertical bioturbator	-0.059	-0.753	0.540	0.158	-0.089
Mixing bioturbator	0.542	0.015	0.105	-0.231	0.575
Surface deposit bioturbator	-0.635	0.071	-0.447	-0.399	0.350
Eigenvalues	3.519	2.884	1.960	1.937	1.476
Var. Explained	25.13	20.59	14.00	13.83	10.54
Cum. Var. Explained	25.13	45.73	59.73	73.57	84.12

therefore had a highly negative PC3 score (PC3 = -0.725). Excluding *A. marioni* from the analysis increased the variation explained by the multivariate linear regression and resulted in a highly significant relationship between species PC3-scores and the number of interspecific interactions ($R^2 = 0.519$, $t = 3.356$, $p = 0.003$), as well as improving model fit (Supplementary Fig. S5). This result indicates that species with a higher number of interspecific interactions were generally subsurface deposit-feeding vertical bioturbators. However, as *A. Marioni* demonstrates this is not the only combination of traits in benthic invertebrates that can lead to high numbers of interspecific interactions.

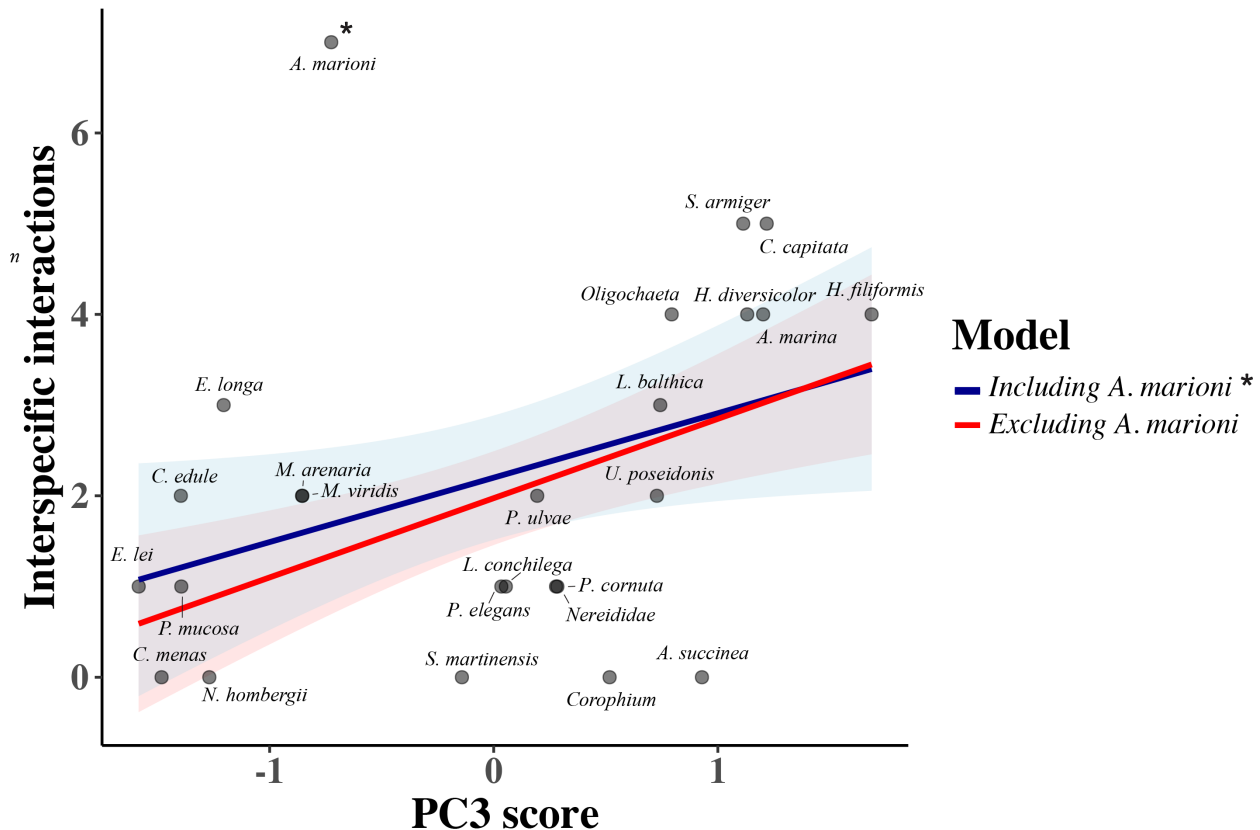


Figure 2.4: Relationship between the number of interspecific interactions and the trait combination expressed by PC3 (subsurface deposit feeding vertical bioturbators) based on multivariate linear regression.

2.4 Discussion

Our results show that the benthic invertebrate community in the Wadden Sea has a temporally stable composition (research question i). This confirms our original hypothesis. The spatial and abiotic relationships of benthic invertebrates in the Wadden Sea could be grouped into four different clusters, while biotic interactions showed species engage in relatively few interspecific interactions (research question ii). These interspecific interactions are predominantly positive (research question iii), and can be linked to functional traits (research question iv), but it remains challenging to interpret these links in a biologically meaningful way.

The observed stability of the benthic invertebrate community (research question i) might be linked to the geological history of the Wadden Sea. Environmental conditions restricted the number of species that could initially establish when the Wadden Sea formed ~ 8000 years ago (Oost, 1995; Reise et al., 2023; Luttikhuisen et al., 2008; Krakau et al., 2012), and the large tidal and sediment dynamics further restrict the number of benthic invertebrates that can persist. As a result, species richness in the Wadden Sea is relatively low, and established species are well adapted to the dynamic nature of the system. Furthermore, naturally established species have shown resilience to perturbations such as the introduction of non-native species in the past (Reise et al., 2023). Therefore, perhaps non-surprisingly, our results also show a temporally stable benthic invertebrate community to be present. The resilience of the benthic invertebrate community to future environmental conditions is less certain, however, as increasingly frequent temperature extremes can be expected to severely impact some of the most dominant species in the system (Beukema & Dekker, 2020b).

We found the abiotic interactions of benthic invertebrates predicted by our model (research question ii) align with previous studies. The strong positive relationships of *S. armiger* and *U. poseidonis* with median grain size have been previously reported for the Wadden Sea (Kraan et al., 2010) and for *C. edule* specifically across multiple European tidal flat systems (Compton et al., 2009). Similar to our findings *L. balthica* has been previously found to prefer smaller medium grain sizes and longer dryval duration (Kraan et al., 2010). Furthermore, both *L. balthica*, *H. diversicolor* and *P. elegans* prefer the shallower depths associated with longer dryval durations (Ysebaert et al., 2002). Salinity preferences are more difficult to interpret as they can appear to differ within the same site depending on the analysis. For example, the occurrence of *H. filiformis* in the Oosterschelde estuary has been found to be positively related to salinity (Ysebaert et al., 2002), whereas the abundance of this species in the same site was reported to be negatively related to salinity (Ysebaert & Herman, 2002). The difference in the combination of abiotic variables taken into account between varying studies and dependent variable (occurrence versus abundance) can make comparing outcomes between studies and systems difficult. This is further complicated by potential changes in the distribution of species across abiotic gradients over time. For example, local long-term monitoring around the Wadden Sea isle of Norderney suggests *H. filiformis*, expanded from an initial preference of muddy to more sandy mudflats, becoming a dominant species in both areas (Dörjes et al., 1987). This example indicates that explicitly modeling temporal dependence in abiotic preferences might therefore be a useful addition to future studies.

Our finding that benthic invertebrate species engage in relatively few interspecific interactions (research question iii) aligns with a body of research showing that more stable species communities are characterized by a minority of strong interspecific interactions embedded in a larger network of weaker interactions (Paine, 1992; Wootton, 1994; McCann et al., 1998). That the vast majority of the interactions were found to be positive, fits the development in community ecology over the past 30 years that facilitative interactions play an important, if not dominant, role in structuring species communities (Bertness & Callaway, 1994; Bruno et al., 2003; Kéfi et al., 2012, 2016). However, the underlying

mechanisms are less well understood because most studies, including our own, generate correlative measures on species interactions based on population-level measures (de Roos, 2021). This makes it inherently impossible to detect the mechanisms occurring at the individual level, where the interactions play out. However, based on existing findings, we can clearly describe interactions for particular, well-studied species. For example for the strong interaction observed in our study between *U. poseidonis* and *A. marina*. Previous studies have shown that *U. poseidonis* inhabits the burrows created by *A. marina* (Lackschewitz & Reise, 1998). The strong positive interaction between the two species thus represents a clear case of facilitation. We also found several new interactions previously unreported in the literature. For example, we find a strong positive effect of *C. edule* density on the occurrence of *P. ulvae*. Both species are known bioturbators (Orvain et al., 2012; Rakotomalala et al., 2015), and *C. edule* has a positive feedback on primary consumers by resuspending microphytobenthos resources back to the planktonic foodweb (Rakotomalala et al., 2015). *P. ulvae* spends parts of the daily tidal cycle as a suspended planktonic feeder in the upper water film (NEWELL, 1962), and might therefore well benefit from *C. edule* presence. Targeted experimental work should be able to test the hypothesis that individual *P. ulvae* significantly benefit from the improved planktonic feeding conditions generated by *C. edule*. Another notable pattern we find are the negative interactions between several polychaete species. For example, there is a negative effect of *S. armiger* and *C. capitata* on *H. filiformis*. Additionally, *S. armiger* itself is negatively affected by *P. cornuta*, and *C. capitata* is negatively affected by *H. filiformis*. Polychaetes are important bioturbators that can affect successional dynamics and carbon cycling in soft-sediment systems (Valdemarsen et al., 2018). Exclusion experiments in the Wadden Sea suggest that the sediment reworking by certain polychaetes, such as *A. marina*, negatively affect the densities of other juvenile polychaete species by creating unfavourable settlement environments (Volkenborn & Reise, 2007). Alternatively, negative interactions between polychaete species might arise from predation; as suggested for the negative relationship observed between the predator *N. hombergii* densities and the densities of their prey *S. armiger* and *H. filiformis* in the Wadden Sea (Beukema et al., 2000). Future experimental work should therefore aim to disentangle whether the negative interactions between polychaetes observed in the present study are due to sediment reworking, or direct predation on early life stages.

The mismatch between the level of observation and the level of interaction makes it difficult to interpret the relationship between species traits and the number of interspecific interactions (research question iv). We found that subsurface deposit feeders that are vertical bioturbators tend to have more interspecific interactions, but why this is the case cannot easily be explained. Other types of bioturbators that might have similar impacts on the environment, such as oxygenating the sediment, did not display higher numbers of interspecific interactions. Furthermore, the fact that five PCA axes were required to structure the traits of 25 species indicates a relatively low overall structuring of traits in the data. We hypothesize that structuring benthic invertebrate traits is difficult because many species are highly plastic in their trait expression. For example, *L. balthica*, *H. diversicolor*, and *C. volutator*, can transition between filter and deposit feeding depending on the density of their populations (Riisgård & Kamermans, 2001; Møller & Riisgård,

2006). These species can thus effectively change their ecological role, which, in turn, changes the potential relationships they have with other species.

Our approach has shown to be a powerful tool to identify and structure interspecific interactions between benthic invertebrates in the Wadden Sea at the population level while simultaneously accounting for abiotic processes. The advantage of this approach is the ability to identify new and previously unknown interactions from large and complex community-level datasets. The disadvantage is the large amount of data required and the fact that interactions remain purely correlative population-level measures. We found several new interactions, some of which could be interpreted using literature, and thereby providing interesting new hypotheses to test in dedicated experimental work. Rather than a catch-all solution for analyzing large ecological datasets, our approach therefore acts as a baseline mapping tool and starting point for future experiments. We hope that such a complementary approach might help pave the way towards a better understanding of the functioning of the benthic invertebrate community in the Wadden Sea.

2.5 Acknowledgements

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Chapter 3

Causal links between North Sea fish biomass trends and seabed structure

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Abstract

Distinct areas of seabed are known to shape benthic habitats and communities, yet little is known about the extent to which they affect the dynamics of marine fish populations. In this study we explore the relationship between distinct areas of seabed, called seascapes, and trends in the biomass density of several North Sea fish species. We divided the North Sea up into ten seascapes using standardized methods. Time series of fish biomass density were derived from the North Sea International Bottom-Trawl Survey (NS-IBTS), and aggregated to the seascape level. We analysed the interdependencies between these time series using a causal association network. We found independent biomass density trends between adjacent seascapes at the time interval of zero in all species assessed. Long term causal dependencies in biomass density occurred at time lags of 1-2 years across different gradients of exchange: (1) both directions from North-South, (2) unidirectional from North-South, (3) unidirectional from South-North, (4) unidirectional from East-West, and (5) no clear direction. Our findings indicate that the separation in (a)biotic conditions between North Sea seascapes can represent relevant barriers to the processes determining the observed fish biomass density. We found that non-fusiform morphology and demersal habitat preferences best explained short term causal dependencies. This combination is particular to the flatfish and ray species included in the present study. Contrarily, the movement of large, long-lived, benthopelagic species best explained long term causal dependencies. Our work highlights how causal association networks can be used to study the temporal dependencies between spatial time series in ecology.

3.1 Introduction

The dynamics of marine fish populations are typically categorized as regulated primarily by top-down processes (i.e. predation), or bottom-up processes (i.e. resource production) (Heath et al., 2014; Vinuela et al., 2014; Wollrab et al., 2012). For example, fish population dynamics in the North Sea were long thought to be driven by bottom-up processes (Lynam et al., 2017). In bottom-up regulated systems, the lowest level driver is formed by abiotic factors (e.g. temperature, salinity, etc.) and their influence on plankton biomass. The available plankton biomass in turn leads to cascades upwards through the food web (Gregory et al., 2009; Kirby & Beaugrand, 2009; Olsen et al., 2011). Top-down interactions, represented by predation pressure from predators and fisheries exploitation, have also been shown to have a large impact on the dynamics of several North Sea fish populations (Fauchald et al., 2011; Engelhard et al., 2014). Furthermore, the interaction between top-down and bottom-up processes in the North Sea ecosystem can give rise to highly complex and non-linear dynamics in fish populations (Lynam et al., 2017). To attain a better understanding of the complexity emerging from such interactions, it is important to have a complete overview of the bottom-up and top-down processes acting upon fish populations in the North Sea.

One potentially important bottom-up process that is often overlooked in regulating fish populations is seabed morphology. Physically distinct areas of seabed, also called seascapes, can act as a bottom-up controlling mechanism by shaping abiotic conditions, leading to the formation of different types of benthic habitat and associated species assemblages (Harris & Baker, 2012). Due to the strong link between seabed morphology and community structure of benthic invertebrates (Beaman et al., 2005; Kaskela et al., 2017), seascapes are often used as a proxy for mapping marine benthic habitats (Kostylev et al., 2001; Brown & Collier, 2008). Yet, we know little about the extent at which seascapes affect the dynamics of fish populations, despite the fact that the few case studies available show it could help explain the spatial distribution of fish resources (Getsiv-Clemons et al., 2012; Pittman & Brown, 2011). Recent research showed that the central and lower part of the North Sea comprises eight distinct seascapes excluding the coastal zone (van der Reijden et al., 2018), and that these were selectively targeted by commercial fishing vessels. Although this preferential selection provides some indirect link to the availability and distribution of fish resources, a more complete study exploring the relationship between seascapes and the population trends of North Sea fish is missing. If seascapes are important, this changes the commonly held perspective on the types of bottom-up processes affecting North Sea fish populations.

To understand the relationship between seascapes and the population trends of North sea fish, we here investigate the temporal interdependencies in fish biomass density between seascapes. We hypothesize that if seascapes are not related to trends in fish populations in the North Sea, biomass density in separate seascapes will be directly dependent on each other. Ecologically, this result could be interpreted as the 'borders' between separate seascapes being diffuse, i.e. not relevant, to the processes determining the amount of

fish biomass observed. In contrast, if seascapes define distinct abiotic environments that are important for the distribution of fish populations, we expect that biomass density in different seascapes is unrelated to each other, although they can still be related across longer time lags. Ecologically, this result could be interpreted as the separation in conditions between seascapes representing relevant barriers to the processes determining the amount of fish biomass observed.

To examine the temporal interdependencies in fish biomass density between seascapes, we use a recently developed causal association network approach (Runge et al., 2019b). The advantage of this data-driven method is that it learns causal associations at various time lags directly from aggregated sets of time series, rather than establishing causality through computer simulation experiments on correlative relationships found in observational data (Runge et al., 2019a). As such, our study also tests a new approach to examine intraspecific dependencies in the biomass trends of North Sea fish.

3.2 Material and methods

3.2.1 Study area

The North Sea is a semi-enclosed shelf extending from 4°W and 62°N (Fig.1a) (Daan et al., 2005). In this study, we focus on the region that includes ICES statistical rectangles 4a,b, and c. We exclude the Norwegian trench, Skagerrak and the waters south of the English channel, as their distinctiveness is well recognized (ICES, 2018a; Bergstad, 1990). Extending the method of van der Reijden et al. (2018), we derive ten separate seascapes (Fig.1b). These seascapes were identified based on the weighted sum of five Bathymetry Positioning Indices (BPI), which express the depth of a pixel relative to the depth of its surroundings. The specific weighted-sum BPI used (Equation 1), highlights large scale patterns in seabed morphology and is strongly linked to benthic communities (Reiss et al., 2009). A full description of the weighted BPI can be found in van der Reijden et al. (2018).

$$BPI_{75km} + 0.9 * BPI_{50km} + 0.8 * BPI_{30km} + 0.7 * BPI_{10km} + 0.6 * BPI_{5km} \quad (3.1)$$

3.2.2 Data preparation

We extracted data on the catch per unit effort (cpue) of nine species of fish collected in the North Sea International Bottom Trawl Survey (NS-IBTS) from 1978-2019 (ICES, 2019) (Table 1). We chose 1978 as the starting year of the time series as all seascapes were systematically sampled within the NS-IBTS from this year onward. The nine selected species covered a variety of different life history strategies and had sufficient positive catch data available in all seascapes across selected years. To minimize bias from potential variability in sampling gear and timing, we only included observations that had been sampled in the same quarter of the year and using the GOV trawl. Next, we

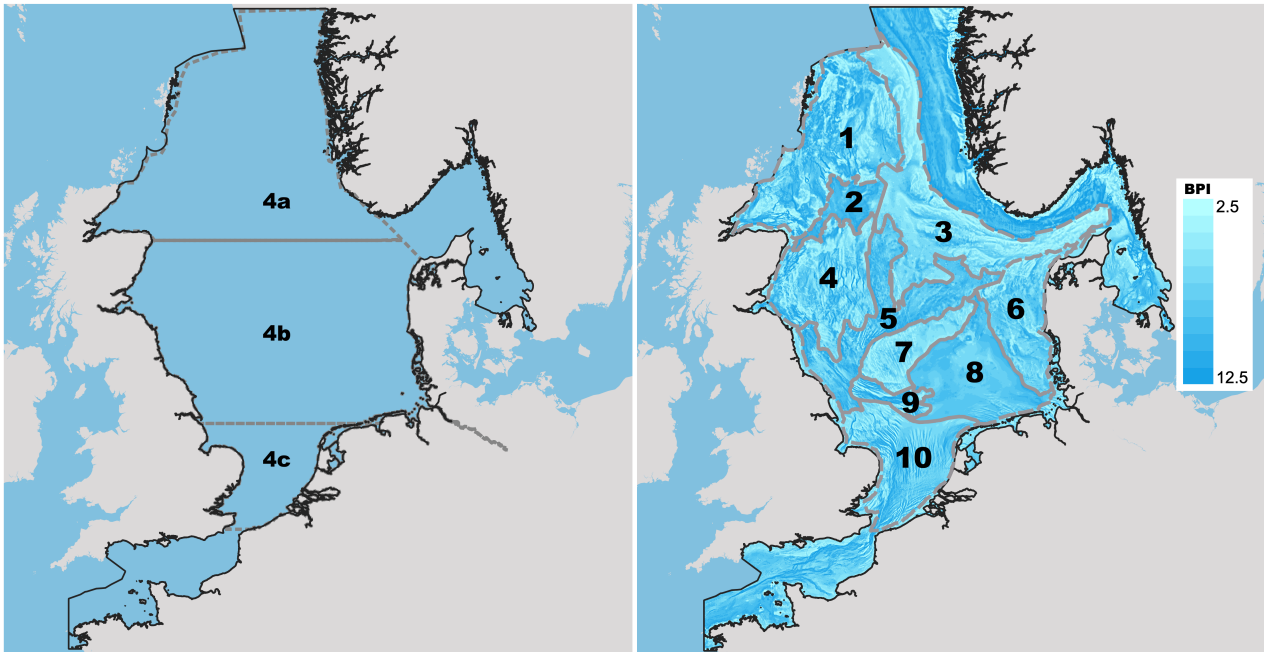


Figure 3.1: The Greater North Sea Ecoregion (solid black line) divided into ICES statistical rectangles 4a, b, c (left), and its division into ten seascapes based on seabed morphology, following the method of van der Reijden et al. (2018) (right).

determined in which seascape each haul was performed based on the shoot longitude and latitude. We estimated the biomass in kg for a given species for each haul by multiplying the number of individuals of a given length class by their length-weight relationship, as derived from FishBase (Froese & Pauly, 2019), and summing over all length classes present in the haul. We then aggregated the data to a single time series per seascape and species, representing the average biomass in kg per haul per year. We refer to this metric as biomass density.

3.2.3 Data Analysis

Causal association network

We define temporal interdependencies in population trends as the existence of time lagged causal dependencies in fish biomass density between seascapes. If seascapes are not related to fish populations in the North Sea, we expect that the time series in fish biomass density between separate seascapes are causally related to each other at the time interval of zero. Contrarily, if seascapes are related to fish populations in the North Sea, we expect that the time series in fish biomass density in separate seascapes are independent of each other at the time interval of zero, although they can be causally dependent across longer time scales.

We applied a causal association network approach recently developed by Runge et al. (2019b), to evaluate the underlying causal dependency structure between the fish biomass density time series from different seascapes (Fig. 2). The linear and non-linear time lagged dependencies between sets of time series can cause inflated or spurious associations to be

Table 3.1: Fish species, records and length to weight conversion used in the study. All length-weight relationships were taken directly from Fishbase (Froese & Pauly, 2019). Slight differences in the number of filtered (unique) hauls between species originate from small differences in the raw NS-IBTS cpue-length-per-hour datasets pulled from the ICES/DATRAS online database for each species (mean 13.667,2 filtered hauls \pm std.dev 104,9 filtered hauls, range 13.430 - 13760 filtered hauls).

Species	Scientific name	n Filtered hauls	n Non-zero hauls	Lt-Wt relationship
common dab	<i>Limanda limanda</i>	13.430	11.847	$0.0068(L)^{3.14}$ $n = 19$
whiting	<i>Merlangius merlangus</i>	13.760	13.364	$0.0063(L)^{3.06}$ $n = 33$
Atlantic herring	<i>Clupea harengus</i>	13.746	12.058	$0.0060(L)^{3.08}$ $n = 114$
Atlantic cod	<i>Gadus morhua</i>	13.743	11.197	$0.0071(L)^{3.08}$ $n = 42$
European sprat	<i>Sprattus sprattus</i>	13.747	8135	$0.0056(L)^{3.09}$ $n = 36$
dragonet	<i>Callionymus lyra</i>	13.682	3825	$0.0214(L)^{2.59}$ $n = 12$
European plaice	<i>Pleuronectes platessa</i>	13.615	9216	$0.0089(L)^{3.04}$ $n = 14$
grey gurnard	<i>Eutrigla gurnardus</i>	13.624	8607	$0.0079(L)^{3.02}$ $n = 15$
starry ray	<i>Amblyraja radiata</i>	13.658	4308	$0.0105(L)^{2.94}$ $n = 6$

included when analyzing their interdependence (Pearl, 2009). These need to be accounted for in order to arrive at an approximation of the 'true' underlying dependency structure. The causal association network utilizes the PCMCI algorithm, as implemented in the package TIGRAMITE in Python (Runge, 2019), that arrives at a solution of the underlying dependency structure through iterative conditional independence testing. Internally, the PCMCI algorithm takes two processing steps. First, given a set of time series, the PC_1 algorithm constructs a graphical model in which all time series and their time lagged components form separate nodes. Then for each of these nodes or time series variables, the PC_1 algorithm identifies all relevant conditions or "preliminary parents" $\hat{\mathcal{P}}(X_t^j)$ in the set $X_t^j \in \{X_t^1, \dots, X_t^N\}$, through iterative conditional independence testing. This conditional dependence can be interpreted as the relation between time series variables 1 and 2, after accounting for the relations existing between all the time series variables within the set. The time series variables with significant relations to the focal time series after accounting for all relationships in the set form the preliminary parents of that focal time series. This first step reduces dimensionality, i.e. it identifies all relevant connections in the graph for a given time series variable and a first estimation of their strength, and will thereby increase the detection power for underlying causal relations. Next, in the second step, the MCI algorithm addresses the false positives, i.e. spurious or inflated links found between the time series variables. It does so by repeating the iterative conditional independence tests, but now conditioning on both the preliminary parents of X_t^j and the time shifted parents of $X_{t-\tau}^i$ (Runge et al., 2019a). Thus the graphical model contains the focal time series variable, it's preliminary parents, and their preliminary parents. This second step is therefore well suited to identifying spurious or inflated relationships originating from common drivers. Those time series variables with significant relations to the focal time series variable after this second iterative testing phase are included in the final causal association network. The final causal association network thus represents the algorithms approximation of the underlying causal dependency structure existing between the set of time series.

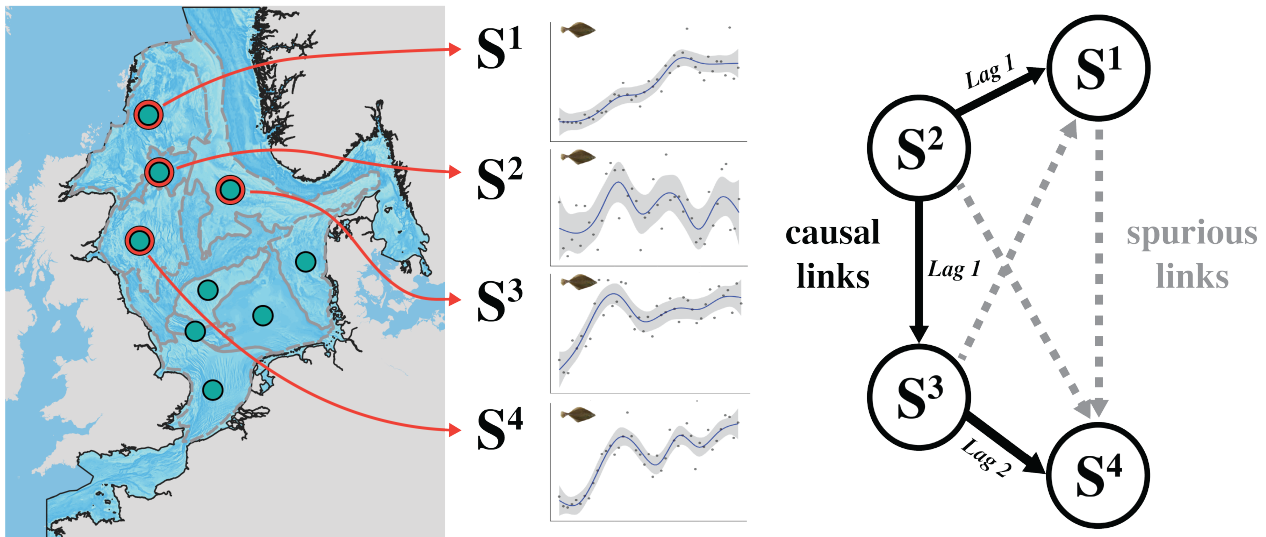


Figure 3.2: Each of the ten seascapes (left) has an associated time series of fish biomass density, e.g. S^{1-4} (centre), of which we estimate the underlying causal dependency structure in a causal association network (right). Common drivers and indirect effects can yield spurious associations, that are accounted for in our approach. Figure adapted from Runge et al. (2019b)

Our time series covered 42 years, which is extensive in ecology, but relatively limited in data science. We therefore used the linear partial correlation test, a maximum time lag of two years, and let the PC_1 algorithm choose the optimal α level for condition selection. As the linear partial correlation test is sensitive to outliers, we applied a 95% winsorization to the data prior to analysis (Reifman & Keyton, 2010). Confidence intervals were generated using bootstrapping, and inferences on the conditional dependence between time series were made using a shuffle test with 3000 trials. We further corrected the results for the total number of pairwise tests performed by applying the False Discovery Rate procedure of Benjamini and Hochberg (Benjamini et al., 1995). The final causal association network included those links between time series significant at the α level of 0.05. If links occurred between two time series at multiple lags, the strongest link was included in the network. Rather than printing the full causal association network found for each species, which would result in a cluttered and unclear overview, we report the results as follows: (1) For each species, we report the number of seascapes with biomass density trends independent of their adjacent seascapes at time lag zero. This provides a link back to our initial hypothesis that the contrasting conditions in seascapes are reflected in contrasting biomass density trends. (2) We produce a species-specific map where relationships at time lag zero are indicated by the borders between adjacent seascapes, and relationships over longer time lags between all seascapes are indicated by arrows.

Post-hoc test to link life histories to causal relationships

We conducted a post-hoc test to better understand the variables driving the observed dependencies in biomass density between seascapes at different time lags. More specifically, we used a Random Forest Classifier (RFC) model to predict the presence of causal rela-

tionships between seascapes based on a set of 17 variables pertaining to life history, the biomass density of different life stages, and environmental conditions (S1.Table1).

Variable collection

We extracted nine features related to life-history strategies from the marine fish trait database of Beukhof et al. (2019b). Next, for every year and seascape combination, we calculated the absolute difference in biomass density of small and large size-classes in the juvenile and adult life-stages. To do this, we first determined the length at maturation to split the IBTS data between adult and juvenile biomass density. Next, for each of these groups, we made an equal split between the 50% largest and 50% smallest individuals in terms of length. We then aggregated the data into a single data frame listing the biomass density of the four groups (small juveniles, large juveniles, small adults, large adults) in each haul. Next, we computed the mean biomass density of each group per haul per year. Finally, we calculated the difference in mean biomass density per haul per year between different seascapes for each group. This dataframe was combined with the life-history trait dataframe to produce the final feature dataset for training. As there was a class imbalance in the label data between the number of samples with and without causal lag, we used a cost-sensitive learning approach and weighted the classes accordingly their representation in the dataset (Weiss et al., 2007).

Model training and performance

We further optimised hyperparameters of the RFC through a grid search on the maximum depth, minimum samples per split, minimum samples per leaf and the number of trees. The final RFC model with causal lag zero as label included 300 trees, with a maximum depth of 40 splits, a minimum 10 samples per leaf and split. The final RFC model with causal lag one-two as label consisted of 500 trees, with a maximum depth of 40 splits, a minimum of 10 samples per leaf and 15 per split. Before training, we split 50% of the data into a validation set, and, during training, we used stratified K fold cross validation with 5 splits (Refaeilzadeh et al., 2009). We used Area Under the Receiver Operating Characteristic curve (AUC) values and a confusion matrix, from which we could calculate recall and precision, to evaluate model performance. The model was run twice, once with causal lag zero as the label feature, and once with causal lag one-two as the label feature. The model performed well on the validation set in both runs, with an AUC of 98.0% and 98.2%, a recall of 95.2% and 97.1%, and precision of 93.0% and 91.6% respectively. This is further illustrated in the confusion matrixes in the supplementary material (S1.Figure1).

Variable importance

We calculated the importance of each of the 17 variables in predicting the presence of a causal dependency between seascapes at various time lags using the TreeExplainer function from the SHAP package (Lundberg et al., 2020a). TreeExplainer is based on game theory and approximates Shapley values to compute the contribution of a target variable to the predicted output of tree based machine learning models (Lundberg & Lee, 2017b; Shapley, 1953). It does so by rerunning model predictions on the test dataset

using all different combinations between variables excluding the target variable, and then repeats this process, now including the target variable. The algorithm then computes the contribution of the target variable based on the average difference in predicted outcomes (Molnar, 2020).

3.3 Results

Causal associations

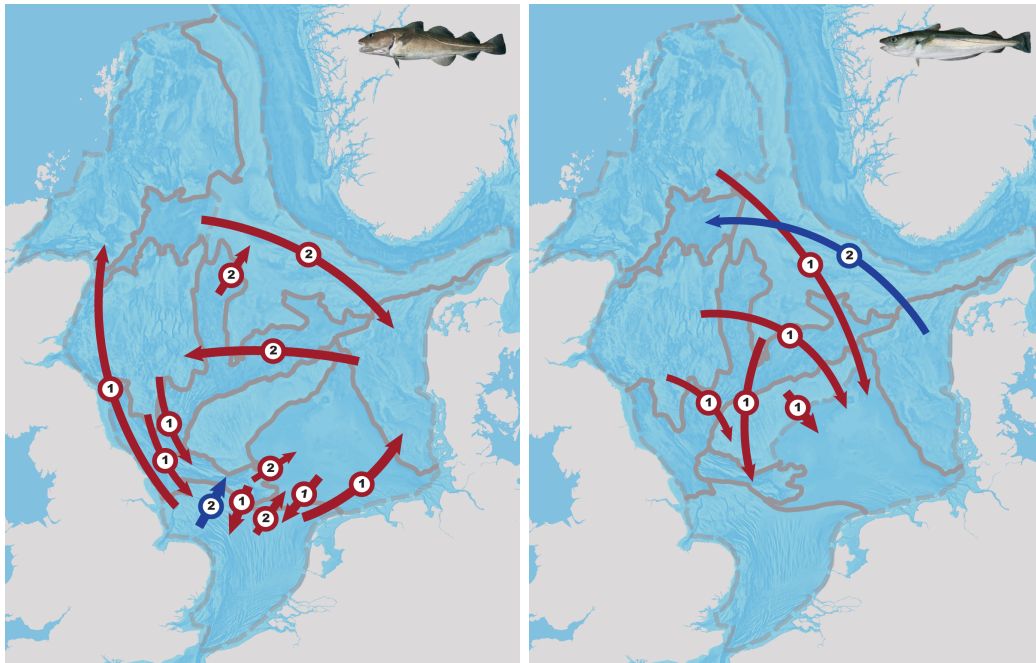
The final causal association networks of all nine species indicated the existence of independent trends in fish biomass between adjacent seascapes at a time lag of zero years. The mean number of seascapes with biomass density trends that were independent of adjacent seascapes at a time lag of zero was 4.7 ± 2.4 SD. This level of independence in biomass density trends at a time lag of zero was highest for Atlantic cod (*Gadus morhua*) (8 out of 10 seascapes), European plaice (*Pleuronectes platessa*) (7 out of 10 seascapes) and Atlantic herring (*Clupea harengus*) (7 out of 10 seascapes). It was lowest for starry ray (*Amblyraja radiata*) (1 out of 10 seascapes) and dragonet (*Callionymus lyra*) (2 out of 10 seascapes). This was interpreted as the separation between seascapes representing relevant barriers to the processes determining the observed biomass density of Atlantic cod, European plaice and Atlantic herring, but not to those of the starry ray and dragonet. In the remaining four species, independence in fish biomass density trends between adjacent sites at a time lag of zero ranged between 3-6 out of ten seascapes. In these cases, only certain seascapes represented relevant borders to the processes determining the observed biomass density, whereas the biomass density trends were directly dependent on each other in the remaining adjacent seascapes. An additional type of relationship observed were temporal dependencies at a time lag of zero between non-adjacent seascapes (Table 2).

Species could be further subdivided based on the level of causal dependencies in biomass density trends between seascapes at longer time lags of 1-2 years, and the directional gradient in these dynamics. Atlantic cod (*Gadus morhua*), European plaice (*Pleuronectes platessa*), whiting (*Merlangius merlangus*), and starry ray (*Amblyraja radiata*), were characterized by time lagged causal dependencies between distant seascapes in both directions along the North-South gradient (Fig. 3). In grey gurnard (*Eutrigla gurnardus*) and Atlantic herring (*Clupea harengus*), exchanges occurred predominantly unidirectional from South-North (Fig. 4a,b). In dragonet (*Callionymus lyra*), exchanges occur from East-West and North-South (Fig. 4c). Finally, there was only a single time lagged exchange in European sprat (*Sprattus sprattus*) (Fig. 5a), and no time lagged exchanges in common dab (*Limanda limanda*) (Fig. 5b).

Table 3.2: Time-lag zero links between non-adjacent seascapes indicative of spatial population synchronization.

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
S1				<i>P, E</i>	<i>A</i>	<i>L, C_l</i>	<i>P</i>	<i>L, M</i>	<i>C_l</i>	<i>G, A, L</i>
S2					<i>E</i>			<i>G, L</i>	<i>S</i>	<i>P</i>
S3				<i>A, C_l</i>					<i>E</i>	<i>S, C_l</i>
S4							<i>E</i>	<i>P, S</i>	<i>L</i>	<i>G</i>
S5										
S6							<i>L</i>		<i>L, A, C_l</i>	<i>E, A, C_l</i>
S7										<i>M, C_l</i>
S8										
S9										
S10										

L= *Limanda limanda*, *A*= *Amblyraja radiata*, *C_l*= *Callionymus lyra*, *C_h*= *Clupea harengus*, *E*= *Eutrigla gurnardu*,
G= *Gadus morhua*, *M*= *Merlangius merlangus*, *P*= *Pleuronectes platessa*, *S*= *Sprattus sprattus*



(a) *Gadus morhua*

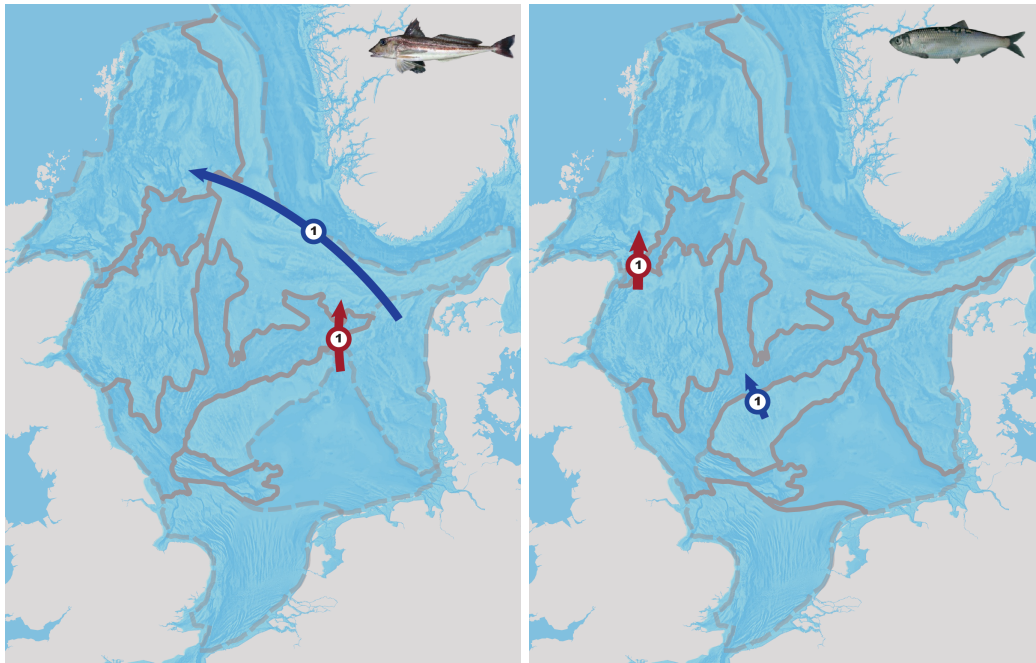
(b) *Merlangius merlangus*



(c) *Amblyraja radiata*

(d) *Pleuronectes platessa*

Figure 3.3: Causal relationships in mean fish biomass density ($\text{kg}\cdot\text{haul}^{-1}\cdot\text{year}^{-1}$) between different seascape. In all four species, time-lagged exchanges occur predominantly in both directions between more Northern and Southern seascape. Arrow color and width represent the type and strength of the relationship (red = positive, blue = negative, thin = weak, thick = strong) between different areas. The associated time-lag is listed on the arrow and if a contemporaneous relationship was present, the border between the areas was removed.



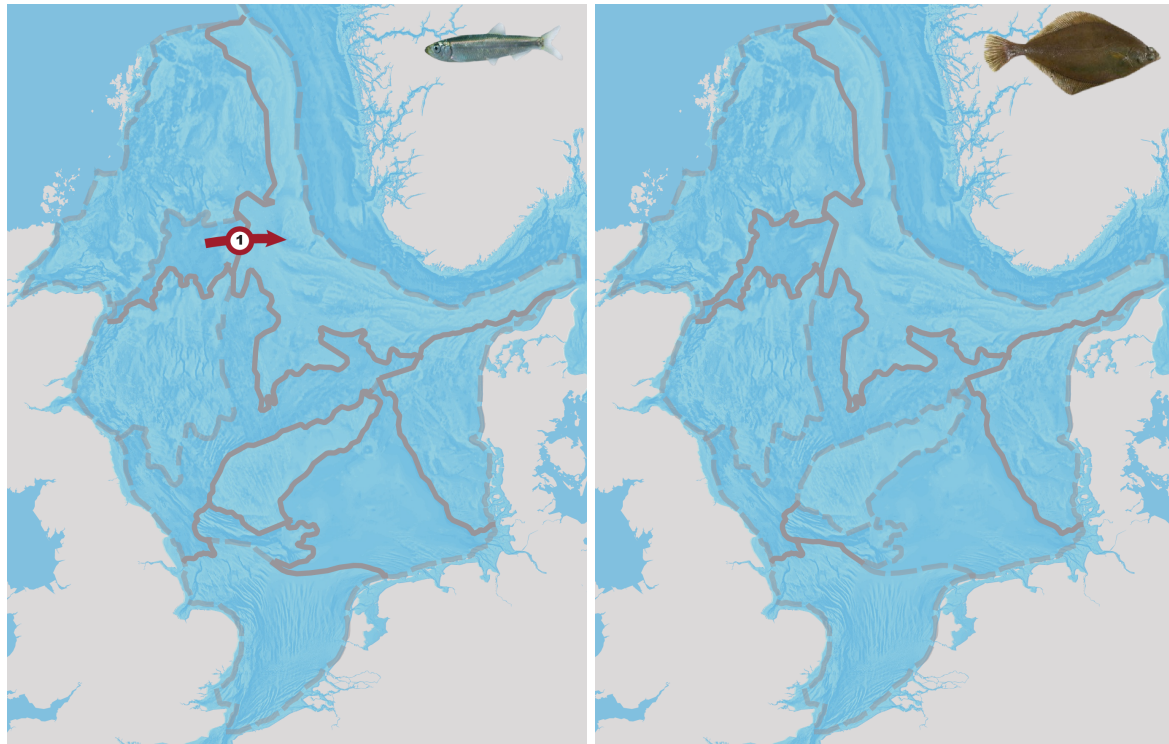
(a) *Eutrigla gurnardus*

(b) *Clupea harengus*



(c) *Callionymus lyra*

Figure 3.4: Causal relationships in mean fish biomass density ($\text{kg}\cdot\text{haul}^{-1}\cdot\text{year}^{-1}$) between different seascapes. In species (a) and (b), a few time-lagged exchanges occur from Southern to Northern seascapes. In species (c), exchanges went from Northern to southern and Eastern to Western seascapes. Arrow color and width represent the type and strength of the relationship (red = positive, blue = negative, thin = weak, thick = strong) between different areas. The associated time-lag is listed on the arrow and if a contemporaneous relationship was present, the border between the areas was removed.



(a) *Sprattus sprattus*

(b) *Limanda limanda*

Figure 3.5: Causal relationships in mean fish biomass density ($\text{kg}\cdot\text{haul}^{-1}\cdot\text{year}^{-1}$) between different seascapes. In species (a) there is a single time-lagged exchange and in species (b) no time-lagged exchange, both species therefore lack a clear gradient of exchange. Arrow color and width represent the type and strength of the relationship (red = positive, blue = negative, thin = weak, thick = strong) between different areas. The associated time-lag is listed on the arrow and if a contemporaneous relationship was present, the border between the areas was removed.

Post-hoc test

The Random Forest Classifier found that species with a non-fusiform body type, that are strictly demersal, with low to intermediate fecundity and maximum age, were most important in predicting the presence of a causal relationship between seascapes at a time lag of zero years (Fig.6a). This is opposite to those variables best explaining longer term causal dependencies at time lags of one to two years (Fig. 6b). In that case, long-lived, benthopelagic species of large maximum size best predict the presence of causal relationships between seascapes. Furthermore, the probability of long term causal dependencies between seascapes was positively impacted by small differences in juvenile biomass density and negatively impacted by large differences.

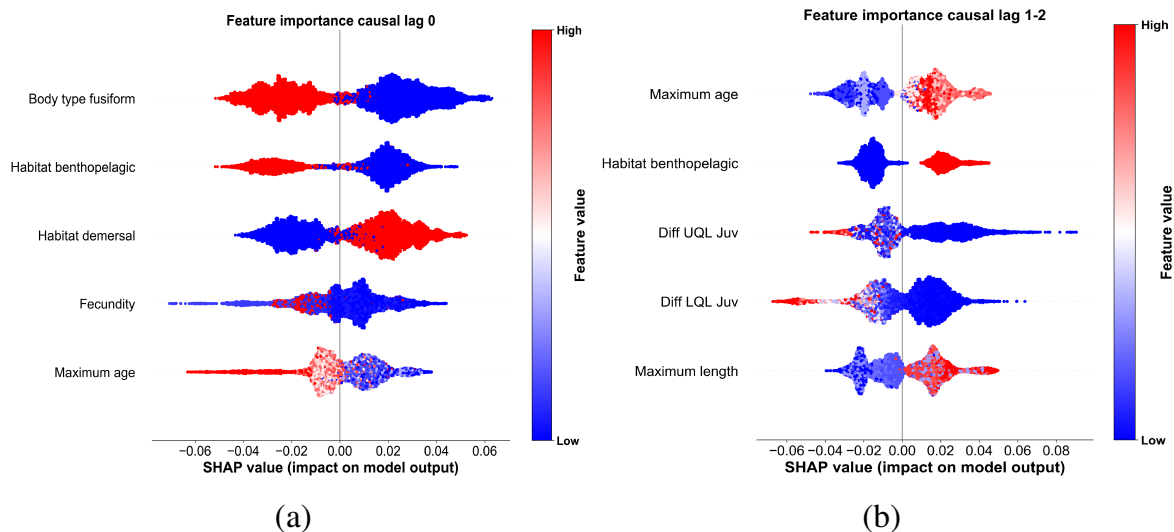


Figure 3.6: Ordered variable importance plots for RFC models predicting the presence of a causal relationship between seascapes at a time-lag of zero (a) or one-two years (b). Each dot represents an individual sample from the validation dataset. Dot color indicates the value of the variable. The position on the x-axis indicates the impact on the predicted probability of a causal lag existing between seascapes.

3.4 Discussion

We found evidence for relationships between the spatial organisation of the seabed structure, i.e. seascapes, and population trends of several fish species in the North Sea. The relationship was expressed as the absence of a causal dependency between fish biomass density trends in adjacent seascapes at a time lag of zero. This finding provides the insight that seascapes can function as a bottom-up driver of North Sea fish population dynamics. However, a considerable level of caution is warranted in interpreting the results, as the relative standard error in estimated biomass density over time frequently exceeded 30% for species and seascape combinations (S2. Table2).

We further found both positive and negative causal dependencies between seascapes at time lags of one to two years in most species. Species such as Atlantic cod, European plaice, whiting and starry ray displayed clear directional gradients in these longer term dependencies along a North-South gradient. Positive long term dependencies can potentially be explained by both movement of adult biomass to, and recruitment of juvenile biomass in the dependent seascapes. Negative long term dependencies cannot be explained by the process of recruitment. However, they can still be explained by movement of biomass away from a dependent seascape to surrounding areas following accumulation of biomass in the driving seascape. The dependent seascape could in this case be considered suboptimal, and the driving seascape more optimal. This would be the inverse process of that described by the basin model theory (McCall, 1990), in which there is adult movement away from optimal basins, or seascapes in this case, to suboptimal surrounding basins following the build up of biomass in the former (Hintzen et al., 2014; Bertrand et al.,

2008).

Our post-hoc test provided a deeper understanding of the ecological meaning of the observed dependencies at different time lags. We found that non-fusiform morphology and demersal habitat preferences best explained short term causal dependencies. This combination is particular to the flatfish and ray included in the present study. This might be due to multiple factors. Flatfish such as European plaice exhibit more restricted movement patterns and stronger selection of small scale variations in sediment type compared to benthopelagic species such as Atlantic cod (Griffiths et al., 2018; Gibson & Robb, 2000; Hinz et al., 2006). Therefore, smaller scale processes than those delineated by the seascapes might be more important in these species at the zero year time lag. Long term causal dependencies in biomass density between seascapes were best explained by the adults of large, long-lived, benthopelagic species. In these species, the recruitment of juveniles is unlikely to drive the observed dynamics because differences in juvenile biomass negatively affected the probability of long term causal dependencies.

In this study, we also addressed a missing link between seascape-specific fisheries activities in the North Sea (van der Reijden et al., 2018), and the biomass of harvested stocks. van der Reijden et al. (2018, Fig. 3) showed beam-plaice fishing intensity to be highest in seascape 10, 7 and the northern part of seascape 6, while otter-mix fishing was highest in the centre of seascape 9 and along the north and southern border of seascape 8. If these fishing activities affect the distribution of fish biomass, we might have expected to see some effect of this in the post-hoc test. An example would be that short term exchanges in (adult) biomass between intensively and less intensively fished adjacent seascapes are important in explaining the observed causal dependencies. However, no specific combination of seascape pairs was found to be important in explaining the observed dependencies. Although it might be tentative to place an explicit link between seascape specific fisheries activities and exchanges in fish biomass, separate quantitative analysis, including North Sea wide fishing intensity, would be required to provide more conclusive evidence. The study of van der Reijden et al. (2018) was based on Dutch fishing fleet data. Consequently, seascapes that are assumed to be free from high fishing pressure based on Dutch data, might turn out to be intensively utilised by the fleets of other nations.

The methodological novelty of our study lies in the application of a causal association network for hypothesis testing using ecological time series. These kind of data are typical of long-term monitoring programs, and causal association networks therefore have a potentially wide applicability in ecology. The advantage of this specific causality based approach is that it explicitly accounts for inflated or spurious correlation between time series (Pearl, 2009). Using a method that accounts for this confounding effect differentiates our work from other, recent research examining dependencies between time series of fish populations and the environment. For example, Milligan et al. (2020) examined time lagged dependencies between resource productivity and abundances in deep sea fish using additive models in combination with cross-correlation analysis. Additive models

are a popular tool in ecology because they can include the effects of categorical and continuous covariates in fitting statistical trends to population time series (Zuur et al., 2017; Pedersen et al., 2019). Cross-correlating such fitted statistical trends to extract time lagged dependencies increases the risk of finding spurious relationships inherent to time series analysis (Olden & Neff, 2001; Runge et al., 2014; Yule, 1926). Although causal association networks explicitly account for this confounding effect, they are not able to include both categorical and continuous covariates a priori. Additional insights can be gained indirectly through post-hoc testing as in the present study. This approach however, does not provide the explanatory power on the effects of environmental covariates that additive modelling provides. Therefore, a decision on which combination of methods to apply in future ecological studies will depend on both (1) the types of environmental effects a researcher wants to include in examining trends, and (2) the need to explicitly model time lagged dependencies.

In conclusion, our study provides an indication that seascapes can function as a bottom-up driver of North Sea fish population dynamics. The presence of causal dependencies between seascapes were best explained by different types of life history traits at different time lags. In a qualitative comparison with previous research, we did not find a clear link between seascape-specific fishery activities and biomass trends. Finally, the suitability of using causal association networks to model spatial time series in ecology will depend both on the types of effects a researcher wants to include and the need to model time lagged dependencies.

3.5 Acknowledgements

We would like to thank Karin van der Reijden for explaining seascape delineation, and Misha Zhemchuzhnikov for his advice on data visualization.

Box 1

Application of a data-driven causality approach on synthetic ecosystem data highlights challenges in model validation

Draaijer R, & Rademaker M.

The myriad of nonlinear interactions and feedbacks occurring between individual organisms of different species makes ecosystem data particularly challenging to analyze. Data-driven machine-learning approaches have proven to be particularly adept at identifying correlative interdependencies in highly dimensional complex datasets; often outperforming traditional statistical methods in terms of predictive capacity (Ij, 2018). For example, Knudby et al. 2010 show how machine-learning approaches outperform traditional statistical models when predicting fish-habitat relations. Machine-learning models have further been shown to be able to predict the occurrence and level of catastrophism in ecosystems shifts (Deb et al., 2022). Although high predictive power is useful in specific contexts, it does not equal to increased understanding of the processes giving rise to observed patterns. Recent approaches in ML therefore increasingly utilize causality-based frameworks to address this issue (Peters et al., 2017; Nauta et al., 2019). In contrast to maximizing predictive performance, these machine-learning approaches aim to discover and quantify the causal interdependencies of the underlying system (Runge et al., 2019a). In chapter 2, I applied one such approach to model the causal interdependencies between time-series of fish biomass in the North Sea. However, the question remains how to validate the relationships identified by such causal-inference models from observational ecological data. One way is to examine the relationships identified by data-driven causal inference frameworks on synthetic ecological data with known underlying relationships. Here, we tested whether a causal inference framework based on attention-based convolutional networks (Nauta et al., 2019) could identify the occurrence and directionality of relationships from a synthetic time-series dataset of a marine ecosystem. The synthetic time-series data was generated using a stage-structured population model of a well-studied tri-trophic marine ecosystem ((Van Leeuwen et al., 2008); Fig. 1). The system models the life-stage specific population biomass of a consumer species (sprat), and a predator species (cod). Whereas

all consumer life stages share the same resource (zooplankton), different life stages of the predator have access to different alternative resources. The predator in turn, is subjected to life-stage specific anthropogenic fishing pressure. We assessed the performance of the causal-inference network across 144 different experimental scenarios representing different combinations of temporal resolution (high, mid, low), signal to noise ratio (1:0, 1:0.1, 1:1, 1:10), feature scaling (power transformation, min-max transformation), and ecosystem phase (complete dynamics, transient phase, equilibrium phase). We found the performance of the causal inference network was poor across all simulated scenarios (Mean $F1'$: 0.23 ± 0.16); meaning the network was unable to identify the underlying causal dependencies between time-series in the dataset. This made model performance on our synthetic ecosystem dataset considerably lower compared to what might be expected given the performance of the same model on 41 medical and financial reference datasets ($F1'$: $0.62 - 0.78$; Nauta et al. (2019)). The outcomes of our study highlight the difficulty of validating the relationships identified by data-driven causality frameworks in highly dimensional ecological datasets.

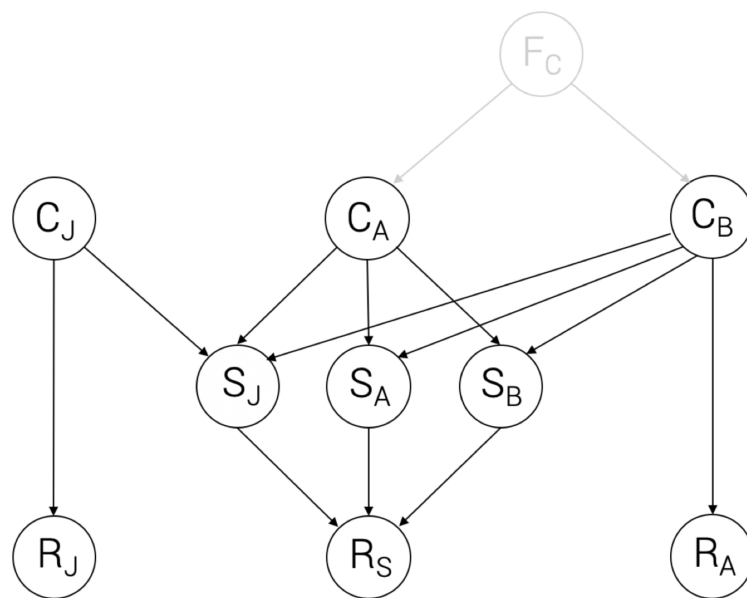


Figure 3.7: Description of the size-structured model used to generate a synthetic ecosystem dataset. The first trophic level is represented by juvenile, small-and large adult cod (C_j , C_a , C_b), followed by juvenile, small-and large adult sprat (S_j , S_a , S_b), and available (zooplankton) resources (R_j , R_s , R_a). In addition, fishing mortality is imposed on adult cod stages (F_c). The model representation is reprinted and adapted from Van Leeuwen et al. 2008.

Chapter 4

Local reflects global: Life-stage dependent changes in the phenology of coastal habitat use by North Sea herring

This chapter is based on:

Rademaker, M., Peck, M.A., & van Leeuwen, A. (Accepted/Forthcoming). Local reflects global: Life-stage dependent changes in the phenology of coastal habitat use by North Sea herring. *Global Change Biology*

Abstract

Climate warming is affecting the suitability and utilisation of coastal habitats by marine fishes around the world. Phenological changes are an important indicator of population responses to climate-induced changes but remain difficult to detect in marine fish populations. The design of large-scale monitoring surveys does not allow fine-grained temporal inference of population responses, while the responses of ecologically and economically important species groups such as small pelagic fish are particularly sensitive to temporal resolution. Here, we use the longest, highest-resolution time series of species composition and abundance of marine fishes in northern Europe to detect possible phenological shifts in the small pelagic North Sea herring. We detect a clear forward temporal shift in the phenology of nearshore habitat use by small juvenile North Sea herring. This forward shift can best be explained by changes in water temperatures in the North Sea. We find that reducing the temporal resolution of our data to reflect the resolution typical of larger surveys makes it difficult to detect phenological shifts and drastically reduces the effect sizes of environmental covariates such as seawater temperature. Our study therefore shows how local, long-term, high-resolution time series of fish catches are essential to understand the general phenological responses of marine fishes to climate warming and to define ecological indicators of system-level changes.

4.1 Introduction

Climate warming has caused well-documented shifts in the distribution of species in terrestrial and aquatic ecosystems (Pecl et al., 2017) including changes in the dynamics of fish populations across the globe (Sydeman et al., 2015; Rijnsdorp et al., 2009; Perry et al., 2005). In several coastal zones, phenological shifts in the occurrence of adult and larval fish have also been observed (Langan et al., 2021; Asch, 2015). In parallel, industrial fishing has altered the abundance, structure, and reproductive characteristics of marine fish populations (Pauly et al., 2002, 1998b; Jackson et al., 2001; Grift et al., 2003). As opposed to large-scale effects on populations that may be readily detectable, understanding the role of external environmental processes on local or regional population dynamics is more challenging (Heath et al., 2012). Small pelagic fish species pose an especially complex case, as their populations can exhibit both ‘volatile’ short-term dynamics in response to local or regional conditions, and long-term ‘stable’ cyclicity due to larger scale climate events (Tourre et al., 2007; Schwartzlose & Alheit, 1999). Furthermore, many species exhibit ontogenetic shifts in habitats, spending part of their life cycle in coastal or estuarine zones, which may constrain the ability of species to cope with warming (Petitgas et al., 2013). The importance of external environmental processes can, therefore, be life stage-specific (Dahlke et al., 2020; Peck et al., 2013). The local dynamics of small pelagic fish are an essential component to better understand potential changes in areas historically important to the life cycle dynamics of species, and to examine whether the phenology in the use of important habitats may have shifted over time.

The Atlantic herring (*Clupea harengus*) is a common, ecologically and commercially important small pelagic fish species in areas of the North Atlantic such as the North Sea (Whitehead et al., 1984; Dahle & Eriksen, 1990) where the population is composed of separate autumn- and winter-spawning stocks with life stage-specific distributions (Dickey-Collas et al., 2010). In the southern North Sea, Atlantic herring is also commonly observed in the Wadden Sea, which with its shallow coastal waters serves as a spawning, nursery, and feeding ground for many North Sea fish species (Tulp et al., 2017). However, much is unknown about the habitat utilization of the Wadden Sea by Atlantic herring. This is primarily because herring and other small pelagic fishes cannot be properly sampled in the demersal trawl surveys used to annually monitor fish populations in these near-shore waters (Maathuis et al., 2023). Furthermore, the coarse temporal resolution of these large-scale surveys does not allow inferences on seasonally important factors. Limited temporal resolution also prevents the detection of potential phenological shifts that might have occurred during the past few decades. This limits our understanding of the external processes governing the local dynamics of herring and other fish moving between shallow coastal nursery and feeding grounds of the Wadden Sea and offshore waters of the North Sea. Local survey efforts conducted at high temporal resolution are needed to help fill such important gaps in knowledge on potential climate-driven changes in phenology and habitat utilization.

Survey efforts with sufficiently high temporal resolution to examine climate-driven

changes in phenology are rare in the marine environment, particularly those with historical coverage allowing comparisons over multiple decades. Although long-term high temporal resolution time-series exist for lower trophic levels such as plankton (Hosie et al., 2003), they are particularly rare for higher trophic levels such as fish. However, the Royal Netherlands Institute for Sea Research (NIOZ) has consistently used a kom-fyke to collect standardized catch data of marine fishes moving between the North Sea and Western Wadden Sea through the Marsdiep tidal race since the 1960's (van der Veer et al., 2015) (Fig. 1). This survey is unique in northern Europe due to its daily temporal resolution. Previous analyses of these data have identified phenological shifts such as changes in the day of first occurrence, peak occurrence, and last occurrence of members of the Wadden Sea fish community over the past five decades (Van Walraven et al., 2017). Given its daily resolution, this time series allows a finer-scale exploration of changes in the phenology of species such as Atlantic herring. From a methodological standpoint, the preselection of specific days (first occurrence, peak occurrence, last occurrence) as a phenological yardstick for peak migration may obscure shifts in species such as herring that, due to their schooling and flexible foraging behaviour, exhibit marked daily variation in habitat use or occupancy. Furthermore, it remains unknown if and how potential shifts in phenology differ among young juvenile and adult herring. More detailed phenological analysis would reveal if local dynamics in coastal habitat use by North Sea herring align with the larger regional and global population responses to climate-driven warming observed in marine fish.

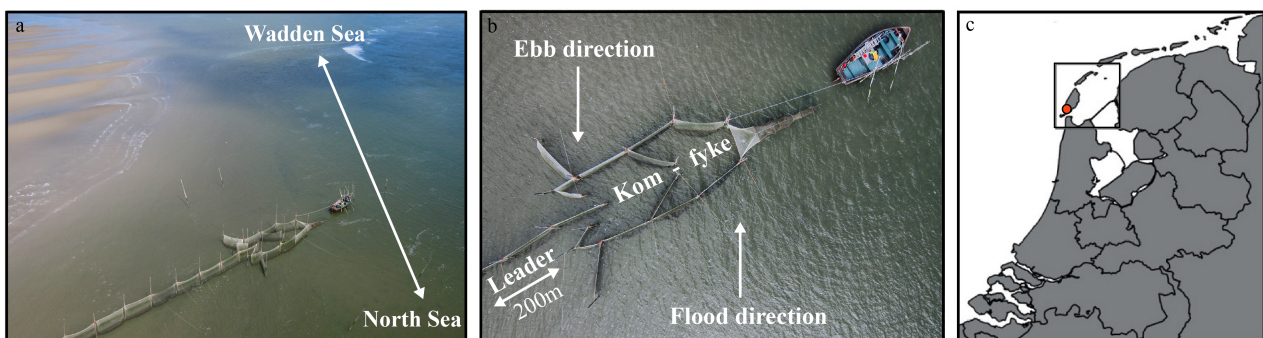


Figure 4.1: Set-up of the NIOZ kom-fyke (a,b) and its geographic position on the border between the North Sea and Wadden Sea (c). Images a and b used with permission from van Walraven (personal communication).

Here, we examined potential life-stage specific changes in the population dynamics of Atlantic herring moving between the North Sea and Wadden Sea using long-term time series of weekly standardized herring catches (1981-2021) collected by the NIOZ kom-fyke. We used a generalized additive modelling (GAM) approach to decompose the overall trend in weekly standardized herring catches into distinct annual, seasonal, and environmental signals. These results allowed us to identify temporal trends in herring abundance, body size, and reproductive status in the Western Dutch Wadden Sea. We also examined potential changes in the seasonal trends in herring abundance over the past four decades, i.e. phenological shifts. Finally, we checked the sensitivity of our outcomes with respect to changes in the sampling design of the Kom-fyke by re-running

our analysis with different sampling frequencies. Our analyses on the longest, most high-resolution time series for marine fish in Northern Europe will advance understanding of the factors determining the movement and phenological shifts of herring and potentially other temperate small pelagic fishes from offshore to nearshore waters. Our work underscores the importance of maintaining highly temporally resolved, long-term ecological time series for examining the dynamics of climate-driven phenological shifts.

4.2 Material and methods

To examine phenological changes in North Sea herring and the factors contributing to potential changes in these dynamics, we analysed the number of herring in daily spring and autumn catches from 1982 - 2021. We also included information on fish life-stage, based on dissections of herring captured in the same program. Below we describe the source of the data and steps in data preparation and analysis in detail.

4.2.1 Data sampling

Fish catches

We used catches in the long-term time-series data from the NIOZ kom-fyke program. The leader net of the kom-fyke extends 200 meters from the shoreline into the subtidal zone where two chambers with a mesh-size of 10 x10 mm collect fishes (van der Veer et al., 2015). Additional details on the kom-fyke netting and other gear and program specifications are provided by Van Der Veer et al. 1992. The kom-fyke is emptied daily during two annual sampling periods that run approximately from the end of March through the end of June, and from the start of September through the beginning of November. The timing of this monitoring coincides with the well-known seasonal ingress of fish from the North Sea into the Wadden Sea in spring, and the emigration of young-of-the-year fish from the Wadden Sea to the North Sea in autumn. Kom-fyke sampling is discontinued in high summer due to net fouling by macro-algae blooms. Sampling does not occur in winter due to increased risks to equipment and personnel posed by storms and ice floes. Catches were sorted according to species and the total length (TL, ± 0.5 cm) of each individual was measured. If herring catches were too large to count all specimens individually, a well-mixed, volume-based subsample was taken, to ensure all different size classes remained proportionally represented. For the historical developments of the fyke program and sample counting see van der Veer et al. 2015.

Abiotic factors

We collected data on local Wadden Sea surface water temperature, regional North Sea surface water temperatures, lunar illumination, and local tidal range as abiotic explanatory variables. Local Wadden Sea surface water temperatures have been measured continuously by the NIOZ Jetty monitoring setup (NIOZ, 2023), located approximately 500 meters from the fyke (Fig. 1). Regional North Sea surface water temperatures and tidal ranges near the fyke (Den Helder) were collected from publicly accessible weather buoy and acoustic sensor data (Rijkswaterstaat, 2023). We calculated the maximum possible lunar illumination received for each sampling date using the Lunar package in R (Lazaridis,

2022).

4.2.2 Data preparation.

Phenology data

We defined a time window when daily sampling data were available from both the fyke sampling and abiotic factors for a 39-year period (1982-2021). We performed additional filter operations on the dataset to minimize any bias due to data measurement or entry errors, as well as potential overestimation of catches due to weather events preventing the daily emptying of the fyke. We only included samples with >12 and <48 hours of fishing effort, and samples with reported body sizes falling within the species limits known from literature. The catch data were standardized by taking the weekly summed catch per unit effort (CPUE), and the weekly mean of the abiotic factors. We chose weekly over daily CPUE to correct for a lack of fishing on some days. The final time-series consisted of 934 sampled weeks of log-transformed herring catches and abiotic factors spread over 39 years. Resolution in the time series varied slightly during two periods. First, there were no catch data from early 2020 when the covid pandemic prohibited fieldwork. Second, the temporal resolution in regional North Sea water temperatures was lower for certain weeks in the 1980's compared to 1990-2021. Therefore, we ran our model multiple times, excluding and including these parts of the time series, to examine qualitative, and quantitative changes in model outcomes. We found that only the effect of tidal range changed depending on the inclusion of these time periods, but the effect of all other covariates remained the same. We therefore chose to include these periods in the time-series and excluded the tidal range effect from detailed interpretation.

Dissection data

We used dissection data performed on a subset of weekly catches from 2005-2021 to assess trends in the reproductive status of herring in the kom-fyke (N=480). The reproductive status of individuals was determined based on a six-point scale of gonadal ripening (Supplementary Table 1). We used this information to determine the length at which 50% of individuals had reached maturity using logistic regression (L_m50) (Supplementary Figure 1). The abundance data were then divided into juvenile (TL < cm) and adult (TL > cm) categories to examine how the relative contribution of these two life stages to catches might have shifted over time.

4.2.3 Data analysis

We used generalized additive models (GAMs, (Wood, 2006)) to examine temporal changes in the local population dynamics of herring moving between the Wadden Sea and North Sea in relation to abiotic factors. We fitted our additive models using the function `gam` from the package `mgcv` (Wood, 2015). Our base-model included North Sea and Wadden Sea water temperatures, lunar illumination, tidal range, week, year, and the interaction between week and year as covariates, next to a temporal autocorrelation component ρ (eqn. 1).

$$E(y_i) = \alpha + f_1(\text{Year}_i) + f_2(\text{NS temp}_i) + f_3(\text{WS temp}_i) + f_4(\text{Lunar}_i) + f_5(\text{Tidal range}_i) + f_6(\text{Week}_i) + f_7(\text{Week}_i, \text{Year}_i) + \rho \quad (4.1)$$

Where smooths $f_1 - f_6$ represent the main effects of year, North Sea and Wadden Sea water temperatures, lunar illumination, tidal ranges, and week respectively. The smooth f_7 is a tensor interaction product that models how the seasonal effect of week on herring catches varies over the years. A tensor interaction allows assessment of the separate singular effects of two variables versus their interaction effect, which is why we chose this type of interaction term. We used the automated variable selection procedure developed by Marra and Wood to identify significant model terms (Marra & Wood, 2011). Next to this, we checked for model fit by examining model convergence and residual diagnostic tables and plots (Quantile-Quantile, density distribution, response vs. fitted values, and autocorrelation) using the `gam.check()` and `resid.check()` functionalities in the R package `mgcv` and `itsadug` respectively (Wood, 2015; van Rij, 2020). The base model converged, explained 43.5% of variation, 45% of null deviance, and had good residual fit diagnostics (Table 1, Supplementary Figure 2,3). We checked for potential extrapolation artifacts in seasonal trends due to the temporal gap between fishing seasons within a year by running the same model on subsets of spring data only ($R^2 = 29.2\%$; Deviance = 31.2%) and fall data only ($R^2 = 33.1\%$; Deviance = 34.8%). The predicted week trend and the interaction between week and year remained qualitatively similar between these models and the full-data model (Supplementary Figure 4, 5).

Table 4.1: Smoother fit diagnostics. Low p-values (k-index <1) can indicate the number of knots used in constructing the smoother is too low. Except for S(Year), all smoothing terms in the model had good fit. We varied the number of knots in S(Year), but found no difference in smoother shape or fit, and therefore kept the automatically selected smooth with 9 knots in the model.

Smooth	Spline	Knots	Edf.	K-index	p-value
S(Year)	Thin plate	9	2.326	0.60	<0.001
S(NS temp)	Thin plate	9	0.747	0.96	0.13
S(WS temp)	Thin plate	9	1.286	1.01	0.56
S(Tidal range)	Thin plate	9	0.403	1.05	0.89
S(Lunar)	Thin plate	9	2.038	1.02	0.69
S(Week)	Cyclic cubic	8	6.102	1.06	0.93
S(Week, Year)	Cyclic cubic, Thin plate	12	2.12	1.04	<0.001

Next, we attempted to expand our base model to examine the role of body size in driving the phenological trends by including herring size-class in cm's as an additional covariate. The expanded model with continuous body size converged, and explained 47% of variation, implying that body sizes carry additional relevant information. However, the model also suffered from considerably worse fit, especially heteroskedasticity. Residual plots indicated that the model could not adequately predict small catch numbers close to zero, systematically overestimating them. This is due to zero-inflation when accounting for continuous size classes, i.e. for most size classes catches are zero. To address this

issue, we first tried fitting a zero-inflated negative binomial, and a zero-inflated poisson distribution to untransformed catch data. However, due to the large range and variation in catches (0-5000), choosing a zero-inflated poisson or negative binomial distributions on untransformed catches did not improve fit. Fit could be improved when only ‘average’ catches were included. However, the high ‘outlier’ catches are of particular interest in this study as they represent peak migration points. We therefore chose to examine how the role of body size and life stage have shifted over time by visually inspecting ridgeline plots, rather than including size class as a covariate in the model.

Finally, we examined how the modelled effects change with respect to monitoring design by rerunning the model with lower sampling frequencies (single fishing day per week, single fishing day per two weeks, single fishing day per month). We used these frequencies to have an approximate qualitative comparison to the outcomes expected in large fisheries surveys with limited temporal resolution. For the single sample per week case, we used the first fishing day of every week, for the biweekly case we used the first fishing day of every odd week, and for the monthly sample we used the first fishing day of the month. We examined model fit and summary statistics and extracted the predicted partial effects for each covariate to examine how both the significance and the effect size changed under each sampling regime.

4.3 Results

The abundance of herring fluctuated strongly during the 1982 -2021 period (Fig. 2a; Mean weekly standardized catch: $3\,198 \pm 10\,501$ individuals, Median weekly standardized catch: 356 individuals). Our additive model reflected these fluctuations, predicting a large seasonal component that matched the peak-to-peak periodicity, but not the amplitude, of observed herring abundance. The model, therefore, underestimated the absolute values of the minima and maxima in herring catches. The fitted trend could be decomposed into significant partial smoother effects of year, week, lunar illumination, tidal range, and regional North Sea water temperatures (Table 2).

Table 4.2: Approximate significance of covariate smoother terms in the additive model ($R^2 = 43.5\%$, Deviance = 45%). Significance of a covariate smoother indicates that the null-hypothesis is rejected, which means that the partial additive effect of a covariate upon weekly standardized catches cannot be modelled using a flat line. The ecological significance of the effect must be interpreted based on the effect size.

Smooth	Edf.	Knots	F	p-value	p-value
s(Year)	5.755	9	5.072	<0.001*	<0.001
S(NS temp)	4.864	9	0.719	<0.001*	0.13
S(WS temp)	4.887	9	0.000	0.511	0.56
S(Tidal range)	1.546	9	0.859	0.004*	0.89
S(Lunar)	2.223	9	1.592	<0.001*	0.69
S(Week)	5.931	8	11.918	<0.001*	0.93
S(Week, Year)	5.662	12	3.929	<0.001*	<0.001

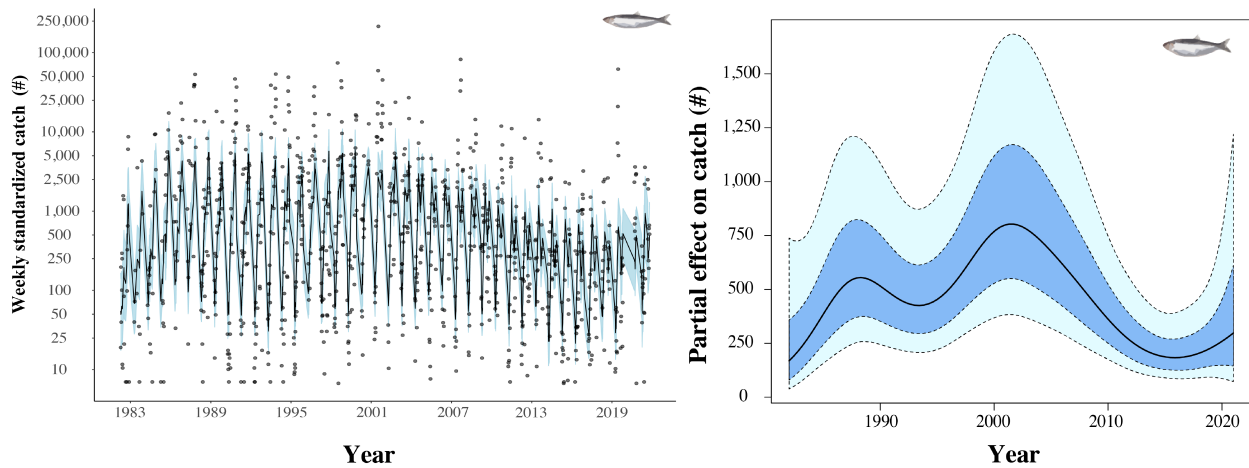


Figure 4.2: (a) Fitted additive model predictions of weekly standardized herring catches $\pm 95\%$ CI in the NIOZ kom-fyke from 1982 - 2021. Grey dots represent the observed values. The gap in early 2020 is due to covid restrictions prohibiting fieldwork. Rerunning the model excluding the gap did not alter the shape or significance of individual smooth terms in the generalized additive model (b) Partial effect of year on weekly standardized herring catches. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the point-wise 95% CI.

4.3.1 Partial effects

The partial effect of year identified strong periods of increase and decrease in predicted herring catches during the past four decades (Fig. 2b). Weekly standardized catches were predicted to be lowest at the start of the time series in 1982 with 169 individuals (95% CI (38, 738)). Subsequently, there was a period of gradual increase in catches, up to 803 individuals, 95% CI (383, 1 684) in 2001. However, this period was followed by a strong decrease back to low levels of 183 individuals, 95% CI (86, 391) in 2015, and 298 individuals, 95% CI (73, 1 219) in 2021. The narrowing and decrease in upper and lower confidence bounds during the period of decline in the last two decades indicate a general decrease in peak weekly standardized catches in individual years during this time period.

We find a strong seasonal signal in herring catches depending on the week sampled within the year (Fig. 3a). Predicted catches differed by up to two orders of magnitude between weeks 10-20 (~ 25 individuals, 95% CI (6, 110)) and weeks 30-40 ($\sim 1 186$ individuals, 95% CI (261, 5 379)). We also observed a forward temporal shift in the seasonal trend over time (Fig. 3b), with a relative increase in predicted catches in spring and summer (\sim weeks 16-30), and a relative decrease in predicted catches in late fall (\sim weeks 40-50).

Regional water temperatures in the North Sea were found to be more important for changes in the abundance of herring than local water temperatures in the Wadden Sea. Relatively cold North Sea water temperature ($5-10^{\circ}\text{C}$) lead to approximately five-fold increases in predicted catches ($\sim 1 554$ individuals, 95% CI (267, 9 023)) compared to those expected

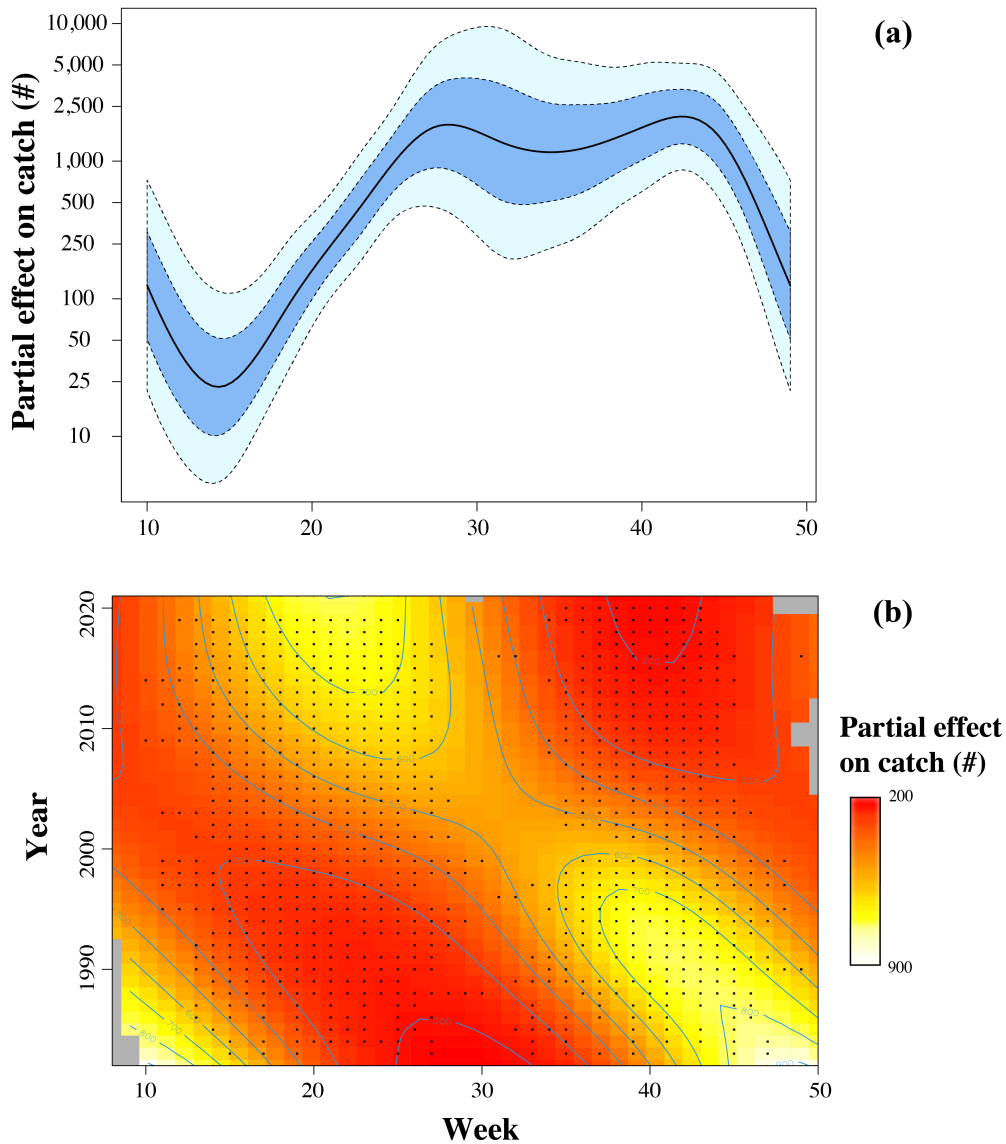


Figure 4.3: a) Partial effect of week number on weekly standardized herring catches. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the pointwise 95% CI. (b) Partial interaction effect of week and year on standardized herring catches. Over time there has been a relative increase in catches early in the year (weeks 15 – 22) and a relative decrease in catches late in the year (weeks 35 – 45). The color bar shows the magnitude of the effect. The sampling effort is divided into two catch seasons per year (spring and fall) represented with black dots. Consistency of the effect with respect to sampling season is shown in Supplementary Figure 4 & 5.

under the long-term mean annual water temperature of 12.8 °C (348, 95% CI (171, 709)) (Supplementary Figure 6). Lunar illumination had a much smaller effect on changes in herring abundance. Periods of full moon and the change to new moon increased weekly standardized catches by ~ 200 individuals compared to catches outside these periods (~ 517 vs. 329 individuals; Supplementary Figure 7). The effect of tidal range varied between periods of high and low tidal ranges, but we found this effect to be inconsistent with respect to time-series resolution, whereas all other partial effects were consistent. We, therefore, exclude tidal range from detailed interpretation.

4.3.2 Sampling frequency

We find that moving from weekly standardized catches based on daily sampling to standardized catches based on a single fishing day every week, biweekly, or per month, significantly changed effect sizes and caused poor model fits due to heteroskedasticity (Table 3; Supplemental Figures 8-10). The effect of North Sea water temperature was no longer found when sampling frequency was decreased. The lunar effect disappears when samples were taken biweekly or monthly. In contrast, the significant effect of year, season, and changes in the seasonal effect over years remained present for all sampling frequencies. However, the effect sizes were reduced by almost a hundred-fold with decreased sampling frequency. Visual inspection indicated that the resulting smoother plots were qualitatively similar in the year and seasonal trend between sampling frequency designs (Supplementary Figure 11, 12), but there were large differences in the plots of changing seasonal trends over time, complicating the interpretation of phenological shifts at reduced sampling frequencies (Supplementary Figure 13). Only in the monthly sampling case is a phenological shift visible but the effect size of the change in standardized catches over time was negligible.

Table 4.3: Comparison of model performance and approximate covariate effect sizes under different sampling frequencies. Approximate effect sizes were calculated by extracting the predicted partial effect sizes for each individual covariate from the model and taking the mean and the standard deviation. A mean with a high standard deviation indicates a non-constant and likely significant effect size of the covariate, while a mean with a low standard deviation indicates the fitted effect can be represented by a flat line and the covariate is therefore likely insignificant

Fishing effort	Daily sampling	Once per week	Biweekly	Monthly
<i>Model summary</i>				
R^2	43.5%	28.5%	32.4%	24.6%
Deviance	45%	29.8%	34.1%	27.9%
<i>Partial effect size (Mean \pm sd)</i>				
s(Year)	443 \pm 823***	3.43 \pm 0.77***	3.5 \pm 0.95***	1.93 \pm 0.62**
S(NS temp)	1095 \pm 1705***	3.38 \pm 0.20	3.32 \pm 1.49 \cdot 10 ⁻⁶	3.32 \pm 2.8 \cdot 10 ⁻⁷
S(WS temp)	403 \pm 0.002	3.20 \pm 0.29	3.32 \pm 1.49 \cdot 10 ⁻⁶	2.93 \pm 0.64
S(Lunar)	383 \pm 59***	3.13 \pm 0.40***	3.32 \pm 3.2 \cdot 10 ⁻⁷	3.16 \pm 0.34
S(Week)	757 \pm 669***	4.17 \pm 2.00***	4.3 \pm 2.02***	3.99 \pm 1.79***
S(Week, Year)	446 \pm 206***	3.5 \pm 1.37***	3.5 \pm 1.33***	3.36 \pm 0.48*
***($0 < p < 0.001$), **($0.001 < p < 0.01$), *($0.01 < p < 0.05$)				

4.3.3 Changes in body size

The relative contribution of size classes remained similar over time but differed markedly between seasons (Fig. 4). In both the spring and autumn seasons, catches were dominated by juveniles between 5 - 15 cm in TL. Although larger adult herring (20 - 30 cm TL) were also abundant in samples collected in spring and summer, they were very rare in autumn and winter samples. Furthermore, compared to the 1980s, smaller fish have become more abundant with smaller minimum size classes observed in the most recent decade. The size class distributions provided evidence that small juvenile herring drive the observed changes in the kom-fyke time series as opposed to changes in catches of adult individuals

(Fig. 4).

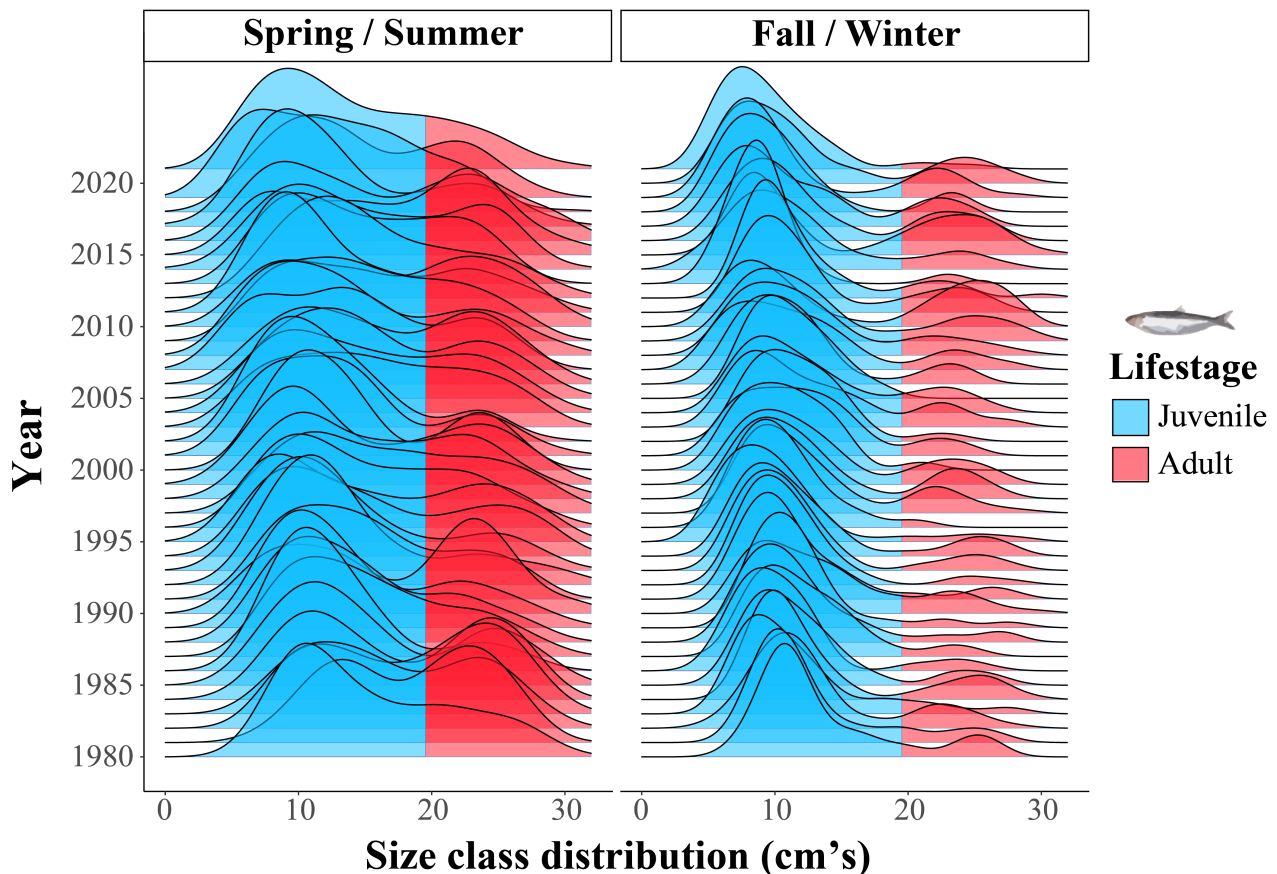


Figure 4.4: Annual and seasonal distributions of size classes in standardized herring catches from the kom-fyke. Colors are illustrative for the Lm50 maturation size of dissected individuals (19.5 cm, Supplementary Figure 1), although there will be small year-to-year differences in maturation size.

4.4 Discussion

Our analyses of the longest, highest-resolution time-series of marine fish species composition and abundance in Northern Europe detects phenological shifts in North Sea herring. Phenological shifts are challenging to detect in ecosystems but can indicate important climate-driven changes in the suitability and use of different habitats (Cohen et al., 2018; Socolar et al., 2017). Changes in the spatial coverage and timing of survey efforts between years and geographic heterogeneity between survey locations can all confound the detection and interpretation of phenological changes (Staudinger et al., 2019; Jordaan et al., 2013; de Keyzer et al., 2017). In marine fish populations, the detection of phenological shifts is further complicated by tradeoffs in the spatial versus temporal sampling resolution of survey designs and the specificity of sampling gear (Staudinger et al., 2019). The longest and spatially largest marine fish surveys, such as bottom trawl surveys in the northeast and northwest that target benthic species, are performed either annually or quarterly and follow a random stratified sampling design (Despres-Patanjo et al., 1988). These surveys, designed to monitor the abundance and biomass of commercially important marine fish, have proven to be powerful in detecting broad horizontal (longitudinal or latitudinal) or depth shifts of fish in response to climate-driven warming

(Dulvy et al., 2008; Nye et al., 2009). However, these survey designs possess several factors that confound phenological analyses, namely their low temporal resolution, interannual variation in sampling locations, changing spatial coverage, and bias in species catchability.

As opposed to long-term quarterly or annual broad-scale surveys, long-term ‘local’ monitoring surveys with high temporal resolution have been very important in detecting climate-driven changes in the phenology and coastal habitat use of fish communities, e.g. in Narragansett Bay, RI (USA) (Langan et al., 2021). It remains challenging, however, to document phenological changes in marine fish at the species level (Sims, 2004). Using the power of large numbers, community-wide advances in the phenology of fish larvae have been predicted based on quarterly surveys conducted over multiple decades (Asch, 2015), but no species-level predictions could be made. In this type of approach, quarterly sampling data have to be aggregated across many species and statistically interpolated to monthly averages before subjecting these interpolated values to a (linear) regression to arrive at an (extrapolated) prediction of phenological change of the community at a daily resolution. This complicated procedure highlights a mismatch between the level of observation and the desired level of inference. In species with highly variable abundances, such as herring, statistically interpolated data used to ‘fill’ missing temporal resolution will likely deviate considerably from catch values obtained with higher temporal sampling frequency. Our species-specific outcomes show how the interpretation of phenological shifts is complicated when moving from high-resolution daily sampling to weekly, biweekly, or monthly sampling frequencies. In our analysis, predicted catches declined a hundredfold with decreasing sampling frequency as the chance of sampling peak migration days was greatly reduced. Furthermore, visual inspection of smoother plots no longer revealed a clear phenological shift, or did not have ecologically relevant effect sizes with decreasing sampling frequency. Our results, therefore, stress the importance of long-term local monitoring surveys that can maintain high temporal resolution in improving our broader understanding of how different marine fish species respond to climate-driven changes by shifting their phenology of habitat use.

Changes in sea water temperature are known to be a major determinant of the distribution of small pelagic fish species such as clupeids (Peck et al., 2021; Schickele et al., 2021). We found a clear signal of regional North Sea water temperatures on herring catches in the coastal Wadden Sea system. The North Sea is among the fastest warming large marine systems on the globe (Belkin, 2009). Furthermore, the Marsdiep tidal basin, in which the kom-fyke is situated, has experienced an approximate 1.5 °C increase in temperature over the past 25 years (Philippart et al., 2017). The large positive effect of relatively cold North Sea water temperatures on weekly catches in herring aligns with our finding of a relative increase in herring catches earlier in the year with time. Warming and increased water temperature, therefore, provide the most credible explanation for the forward phenological shift observed in herring in the present study. From this perspective, changes in these local dynamics reflect larger-scale response patterns in fish populations observed in other regions of the world (Langan et al., 2021; Asch, 2015). Additionally, lunar illumination played a weak role in describing changes in the abundance of herring in our passive

sampling gear. Lunar illumination can be important in the timing of migration movement as well as for prey availability and foraging success (Grau et al., 1981; Hernández-León, 2008).

Life-stage specific habitat utilization, such as juveniles using shallow coastal waters as nursery areas, is important for the life cycle closure and maintenance of large population sizes for many groups of marine species (Beck et al., 2001; Roughgarden et al., 1988; Gillanders et al., 2003), including commercially important fish such as flatfish and clupeids (Le Pape & Cogné, 2016; Ray, 2005)). Here, we found life-stage specific changes in the coastal habitat use by North Sea herring. Changing suitability and use of such habitats due to climate-driven seawater warming can have potential broader, ecosystem-level consequences (Pörtner & Peck, 2010). Warming sea waters greatly reduced the nursery function of the Wadden Sea for flatfish such as plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), and flounder (*Platichthys flesus*), whereas conditions have improved for the more warm-tolerant sole (*Solea solea*) (Tulp et al., 2017; van der Veer et al., 2011, 2022). For pelagic species such as Atlantic herring, the long-term nursery function of the Wadden Sea was understudied. Our result that catches were dominated by small (5 to 10-cm) juvenile herring indicates that the Wadden Sea serves as a nursery for this species. This corroborates the recent results of Maathuis et al. 2023 who reported large numbers of clupeids passing through the Marsdiep tidal inlet based on echosounder measurements. However, the long-term trend of decreasing herring abundance that we report here confirms a decline in this nursery function of this habitat (Tulp et al., 2017). Furthermore, in contrast to flatfish species (van der Veer et al., 2022), herring spawning stock biomass in the North Sea has also decreased in recent decades (Arneberg et al., 2023), suggesting that the decreasing nursery function of the Wadden Sea for herring is not directly compensated for by increased use of other nursery areas.

An important question that remains is how changes in phenology observed in the present study might impact the growth, development, and physiological status of sensitive life stages in marine fish. This is important because the rate of growth and development of juvenile fish is tightly linked to both ecological (competition, food availability), and physiological (thermal tolerance) processes that can have major impacts on population and community dynamics (Pinsky et al., 2019; Gårdmark et al., 2015). For example, increasing temperatures in the Wadden Sea coincided with decreases in the in-situ abundance and, at the same temperatures, decreased individual growth in the laboratory in eelpout (*Zoarces viviparus*) (Pörtner & Knust, 2007). Moreover, populations in temperate areas have been reported to be more sensitive to extirpation if juveniles are unable to build up enough reserves during times of abundant resources to get through resource-limited winters (Van de Wolfshaar et al., 2008). The timing of resource availability might shift under climate-driven warming and this has been suspected to lead to potential mismatches between the phenology of marine fish and the phenology of their prey resources (Cushing, 1990) (but see (Kharouba et al., 2023; Samplonius et al., 2020)). This widely studied but difficult to (dis)prove phenomenon is known as ‘phenological mismatch’ (Renner & Zohner, 2018; Kharouba et al., 2023), and the consequences of phenological mismatches have been studied most extensively in (migratory) birds (Zhemchuzhnikov et al., 2021).

The general consensus is that organisms at lower trophic levels are more likely to advance their phenology than organisms at higher trophic levels (Thackeray et al., 2016, 2010), and that advancing phenology in resource availability negatively affects the growth and survival of individual offspring at higher trophic levels (Lameris et al., 2022). However, despite the negative impact on offspring at the individual level, no negative effect has been found on demographic measures at the population level (Reed et al., 2013). The lack of a population-level effect is thought to be due to density-dependent compensatory mechanisms, but this hypothesis remains untested. These studies from different systems show how understanding the general impacts of phenological shifts on fish populations requires wider research focus; where population-level measures are linked to both fine-scale data on individual development as well as to resource availability. Making these types of links for marine fish will require improved integration of existing surveys and modelling methodologies in future studies. Combining local surveys with high temporal resolution of different trophic levels will play a key role in this process by placing changes in marine fish phenology within a wider ecosystem context. This would enable studies to, for example, make fine-scale inferences on whether changing phenology of small juvenile fish follows changes in phytoplankton productivity; or whether changing phenology and body condition of small juvenile fish affect the prey selection and reproductive success of predators that are less likely to change their phenology, such as seabirds and marine mammals. In this way, local long-term high-resolution time series of fish catches can be valuable in defining general thresholds of climate-driven warming and aid in defining ecological indicators of system-level change (Moyano et al., 2020).

4.5 Acknowledgements

We would like to thank all the NIOZ staff, students, and volunteers involved in various ways in organizing and collecting the kom-fyke monitoring program over the past decades. We would like to thank Anita Koolhaas for her work on the fyke database and her help in the preparation of the dataset used in this study. Next, we would like to thank Luc de Monte, Dennis Mosk, Hidde Kresin, and Robert Twijnstra as the present fyke crew combining the role of boat drivers, managing the day-to-day operations, and emptying of the fyke. From the past fyke crew we would like to thank Sieme Gieles, Marco Kortenhoeven, Bas Wensveen, Suzanne Poiesz, and Henk van der Veer. We would also like to thank our dissection team, many of whom were part of the aforementioned fyke crews, for processing all the fish.

Chapter 5

Why we cannot always expect life history strategies to directly inform on sensitivity to environmental change

This chapter is based on:

Rademaker, M., van Leeuwen, A., & Smallegange, I.M. (2024). Why we cannot always expect life history strategies to directly inform on sensitivity to environmental change. *Journal of Animal Ecology*, (93): 348–366.

Abstract

Variation in life history traits in animals and plants can often be structured along major axes of life history strategies. The position of a species along these axes can inform on their sensitivity to environmental change. For example, species with slow life histories are found to be less sensitive in their long-term population responses to environmental change than species with fast life histories. This provides a tantalizing link between sets of traits and population responses to change, contained in a highly generalizable theoretical framework. Life history strategies are assumed to reflect the outcome of life history tradeoffs that, by their very nature, act at the individual level. Examples include the tradeoff between current and future reproductive success, and allocating energy into growth versus reproduction. But the importance of such tradeoffs in structuring population-level responses to environmental change remains understudied. We aim to increase our understanding of the link between individual-level life history tradeoffs and the structuring of life history strategies across species, as well as the underlying links to population responses to environmental change. We find that the classical association between life history strategies and population responses to environmental change breaks down when accounting for individual-level tradeoffs and energy allocation. Therefore, projecting population responses to environmental change should not be inferred based only on a limited set of species traits. We summarize our perspective and a way forward in a conceptual framework.

5.1 Introduction

The wide diversity in life history traits observed across plant and animal species can be summarized by two main axes reflecting different strategies in speed of life and reproduction (Capdevila et al., 2020; Gaillard et al., 1989; Salguero-Gómez et al., 2016b). This is typically reflected by the ranking of fast-growing, short-lived species with high fecundity at one extreme of the speed of life axis (also referred to as the fast-slow continuum), and slow-growing, long-lived species with low fecundity at the other (in the next paragraph, we discuss in more detail the processes that shape these life history strategies). Similarly, highly semelparous species with a single reproductive event in their lifespan and high mortality are ranked at one extreme of the reproductive strategy axis, and iteroparous species with high spread in reproduction and low mortality on the other (Healy et al., 2019). When looking at only a particular group of living beings, the nature of the second axis might be variable depending on the traits considered, e.g. in mammals the second axis can relate to development rather than reproduction (Stearns, 1983). Early demographic modelling studies predicted that the long-term population responses of plant and animal species with slow life histories are buffered against increasing environmental variation (Morris et al., 2008), because the long-lasting adult stage typical of slower life histories allows these populations to better tolerate changes in the year-to-year variation expected under increasing environmental variation than faster ones. The degree of environmental variation is a useful proxy in demographic models to assess the potential impacts of climate change on populations (Stireman et al., 2005); where certain regions are expected to experience higher variability in climatic conditions, and others less (Lewis & King, 2017; van der Wiel & Bintanja, 2021). However, predictions from more recent demographic analyses regarding the sensitivity of faster versus slower populations to increasing environmental variation are inconclusive. When the vital rates of growth and reproduction are described more mechanistically using the tradeoff between growth and reproduction, populations of species with fast life-histories are less sensitive in their long-term population responses (Smallegange & Berg, 2019; Smallegange et al., 2020), and when vital rates are described phenomenologically, based on random variation of statistical averages, populations of species with slow life-histories are less sensitive in their long-term population responses to environmental variation (Paniw et al., 2018). Furthermore, the timescale considered matters. Populations of species with slow life histories have been found to be more sensitive in their short-term responses to disturbances than populations of species with fast life histories (Gamelon et al., 2014), and to be generally more sensitive to increases in mortality (Lebreton, 2006, 2011). These contrasting findings highlight the need to improve our mechanistic understanding of how the structuring of life history variation and population responses to environmental variation link together.

The historical foundation of the speed of life axis, also referred to as the fast-slow continuum, is based on the concept of life history tradeoffs (Gaillard et al., 2016). Empirical studies using traits measured at the population or species level find that there are general tradeoffs underlying the structuring life history variation. A range of vertebrate-specific studies showed that underlying the speed of life axis is a trade-off in the value of traits related to reproduction and survival (reviewed in table 1 in (Gaillard et al., 2016). Here,

species range from high adult survival and low fecundity on one extreme of the speed of life axis, and low adult survival and high fecundity on the other. The existence of a speed of life axis was also found to depend on the selection of traits included and confounding factors accounted for (Jeschke & Kokko, 2009); with body size and phylogenetic relatedness considered the most important confounding factors. More recent studies structured life history variation across vertebrates, invertebrates, and plant species, in both terrestrial and aquatic systems. These studies still find speed of life as the primary axis of life history variation (Paniw et al., 2018; Healy et al., 2019; Capdevila et al., 2020). However, both fecundity and survival, important components of the speed of life axis in previous vertebrate-specific studies, are no longer consistently loaded on the main axis of life history variation. This means that the life history tradeoffs inferred from the structuring of traits can also be slightly different. However, structuring population or species-level traits does not represent the only way to account for life history tradeoffs.

Life history tradeoffs reflected by species or population traits are shaped by limitations in energy allocation that fundamentally operate at the level of the individual organism (Cody, 1966; Stearns, 1989). Organisms have a limited amount of time or energy available and therefore allocating more energy to one biological function, such as growth, will leave less energy available to allocate to other functions (Gaillard et al., 2016). Primary examples are the life history tradeoff in energy allocation between growth and reproduction (Gadgil & Bossert, 1970; Reznick, 1983), and between allocating energy to current versus future reproduction (Williams, 1966a,b). Accounting for energy allocation processes at the individual organismal level is important as it allows for emergent differences in dynamics between populations or species even if they have similar traits. Such emergent differences, for example, might help explain the different life history strategies that may be observed between populations of the same species (Gamelon et al., 2021; Nilsen et al., 2009). It also ensures that the law of energy conservation is not violated, and therefore prevents the creation of ‘free’ biomass in model projections. This is important as it limits any extrapolation biases that might otherwise occur when projecting population responses based on life history strategies. Extending previous studies of life history variation by explicitly accounting for energy allocation at the individual organismal level might therefore lead to new insights on the links between life history tradeoffs, traits, strategies, and population responses to environmental variation.

In this study, we aim to assess if life history tradeoffs in energy allocation link to the structuring of life history strategies, and how they inform on population responses to environmental change. To this end, we parameterized Dynamic Energy Budget Integral Projections Models (DEB-IPMs) (Smallegange et al., 2017) for 34 species of ray-finned fish *Actinopterygii*. We choose ray-finned fish as our biological model system as they represent the most numerous group of vertebrates (Near et al., 2012), and display a particularly wide range of life history strategies also found in other species groups (Beukhof et al., 2019b), that can also be found in other animal groups. In DEB-IPMs, the demographic rates of growth and reproduction are based on an individual-level tradeoff between energy allocation into growth versus reproduction (Kooijman & Metz, 1984). Additionally, we extended these DEB-IPMs by incorporating skip and obligate breed-

ing decisions at the individual level across semelparous and iteroparous species. These decisions represented the individual-level tradeoff between allocating energy in current versus future reproduction. We used the parameterized DEB-IPMs to answer (i) how life history traits structure into life history strategies when applying a demographic modeling approach explicitly accounting for energy allocation tradeoffs at the individual level, and (ii) if individual-level life history tradeoffs align with the patterning of traits along the life history strategy axes when using this approach. These two questions help elucidate the links between life history tradeoffs in energy allocation operating at the individual organismal level, population-level traits, and life history strategies across populations of different species. We then tested if (iii) population sensitivity to environmental variation covaries with either of the primary life history strategy axes, and also if (iv) population sensitivity to environmental variation covaries with individual life history traits. Finally, we used a perturbation analysis to assess (v) if trait importance might shift over the gradient of environmental variation. Together, these results help improve our understanding of how life history tradeoffs, traits, and strategies, link together to shape population responses to environmental variation.

5.2 Material and methods

5.2.1 Brief summary of the DEB-IPM

A DEB-IPM is a population model that tracks the survival, growth, and reproduction of cohorts of individuals in a population (Smallegange et al., 2017). The individuals in the population are exposed to environmental variation, affecting their feeding level, and, consequently, the energy available for individual growth and reproduction. Individuals within a certain cohort are exposed to the same sequence of environmental conditions over time, but do not necessarily experience the exact same feeding level at each time step; with some individuals being slightly more successful in gathering resources than others given a certain environment. This means that the life history trajectory of each individual in the model is unique. The individual-level life history functions used to model growth, reproduction and survival in the DEB-IPM are parametrized using a set of life history traits derived from demographic studies at the population level. The individual-level life history functions are then integrated over discrete time and a continuous size distribution, to yield population-level outcomes, such as projections of population size and population growth rates. The population-level outcomes of the DEB-IPM are therefore an emergent property of individual-level processes and tradeoffs. We use a selection of 34 ray-finned fish species as model organisms in the DEB-IPM. These species were selected because their life histories have been studied in particular detail and together they represent the full range of life history strategies observed in this species group (McBride et al., 2015). As many important life history processes such as growth, maturation, reproduction, and survival in ray-finned fish are dependent on body size, rather than age (Peters, 1986; Kozłowski, 1996; Stige et al., 2019), we express the individual level life history functions in our DEB-IPM as a function of individual body size.

5.2.2 Brief summary of environmental variation

We model environmental variation over time by exposing individuals in the population to a temporal sequence of good and bad environments. This translates into individuals experiencing high $E(Y)_{high}$ or low $E(Y)_{low}$ feeding levels, with individual variation in feeding level $\sigma(Y)$. Feeding level is a relative measure that captures the level of satiation of an organism from empty (feeding level = 0) to completely satiated (feeding level = 1). The ordering of the temporal sequence of environments experienced by individuals is determined by the level of environmental autocorrelation (ρ). We use environmental autocorrelation to express environmental variability because real-world environmental variation often shows temporal autocorrelation (Inchausti & Halley, 2002; Ruokolainen et al., 2009; García-Carreras & Reuman, 2011). Specifically, ρ expresses the level of correlation between the environments experienced at subsequent time steps. Positive values ($0 > \rho > 1$) mean environmental conditions at the next time step are likely to be similar to those experienced at the current time step. Negative values ($-1 < \rho < 0$) mean that environmental conditions at the next time step are more likely to be different from those experienced at the current time step. We examine population responses over the entire gradient of $-1 < \rho < 1$, thus exposing populations to a gradient from highly variable to highly invariable environments.

5.2.3 Individual level life history functions

Individual life history trajectories are captured in the DEB-IPM by four fundamental functions: (1) The growth function $G(L(t))$ describes the probability that an individual grows from length L at time t to L' at $t + 1$, conditional on survival. (2) The survival function $S(L(t))$ denotes the probability that an individual survives from time t to $t + 1$ given that it is of length L . (3) The reproduction function $R(L(t))$ describes the number of offspring produced from time t to $t + 1$ by a female of length L at time t . (4) The parent-offspring function $D(L', L(t))$ denotes the probability that a female of length L at time t produces offspring of length L' at $t + 1$, conditional on reproduction. We adjusted the reproduction and survival functions to approximate the individual-level tradeoff of allocating energy into current vs. future reproduction for the different types of breeders that occur in our dataset: Iteroparous obligate breeders, which have multiple reproductive events over their life cycle and reproduce every season irrespective of environmental conditions. Iteroparous skip breeders that also have multiple reproductive events over their life cycle, but pass up on the opportunity to breed in bad environments. Finally, semelparous skip breeders that have a single reproductive event in their life cycle followed by death, and pass up on the opportunity to breed in bad environments.

(1) Growth function

Body growth of fish is typically indeterminate and food supply driven (Sebens, 1987), following a von Bertalanffy growth curve:

$$G(L', L(t)) = \frac{1}{\sqrt{2\pi\sigma_L^2(L(t+1))}} e^{-\frac{(L' - E(L(t+1)))^2}{2\sigma_L^2(L(t+1))}} \quad (5.1)$$

where $E(L(t+1))$ is the expected growth of individuals of length L :

$$E(L(t+1)) = \begin{cases} L(t)e^{-r_B} + (1 - e^{-r_B})L_m E(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise} \end{cases} \quad (5.2)$$

with r_B as the von Bertalanffy growth coefficient (dimensionless), L_m as the maximum length, $E(Y)$ as the expected feeding level, scaled between zero and one, and σ_L^2 the individual variance in length at $t+1$.

$$\sigma^2(L(t+1)) = \begin{cases} (1 - e^{-r_B})L_m\sigma^2(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise} \end{cases} \quad (5.3)$$

where $\sigma(Y)$ is the standard deviation of the expected feeding level between individuals.

(2) Survival function

The survival of individual fish is generally size-dependent, especially in the early life stages, with a decrease in predation mortality for increasing body sizes (Stige et al., 2019). Size-dependent survival is modelled using an exponential function. In iteroparous obligate and iteroparous skip breeders it takes the form:

$$S(L(t)) = \begin{cases} e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L \leq \frac{L_m E(Y)}{k} \\ 0, & \text{otherwise} \end{cases} \quad (5.4)$$

where μ_p is the adult background mortality rate due to predation, and k denotes the fraction of assimilated energy allocated to metabolic maintenance and growth, following the Kooijman-Metz model (Kooijman & Metz, 1984). Semelparous skip breeders have two additional conditional statements on this survival function, that ensures they die after having reproduced.

$$S(L(t)) = \begin{cases} e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L \leq L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa}, \\ e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L > L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa} \text{ \& } E(Y)_{t-1} = E(Y)_{low}, \\ 0, & \text{if } L > L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa} \text{ \& } E(Y)_{t-1} = E(Y)_{high}, \\ 0, & \text{otherwise} \end{cases} \quad (5.5)$$

with $E(Y)_{low}$ as the low expected feeding level, $E(Y)_{high}$ as the high expected feeding level, and L_p is the size at maturation.

(3) Reproduction function

Following the Kooijman-Metz model (Kooijman & Metz, 1984), we assume a quadratic scaling of reproductive output with female body size. In iteroparous obligate breeders, the reproduction function takes the form:

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \phi \left(E(Y) R_m \frac{L(t)^2}{L_m^2} \right), & \text{if } L_p < L < L_m E(Y) \\ \phi \left(\frac{R_m}{1-k} \left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m} \right] \right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \quad (5.6)$$

where ϕ is the survival during the egg and larval phase, R_m is the maximum reproduction in number of eggs of an individual of maximum size L_m , and L_b is the size at birth. Iteroparous and semelparous skip breeders pass up on the opportunity to breed in bad environments. This imposes an additional restriction on the fundamental reproductive function as compared to iteroparous obligate breeders:

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ 0, & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{low}, \\ \phi \left(E(Y) R_m \frac{L(t)^2}{L_m^2} \right), & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{high}, \\ \phi \left(\frac{R_m}{1-k} \left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m} \right] \right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \quad (5.7)$$

(4) Parent-offspring association function

The parent-offspring association function describes the probability that the offspring of an individual of length L is of length L' at $t + 1$.

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \frac{1}{\sqrt{2\pi\sigma_{L_b}^2(L(t))}} e^{-\frac{(L' - E_{L_b}(L(t)))^2}{2\sigma_{L_b}^2(L(t))}}, & \text{otherwise} \end{cases} \quad (5.8)$$

where $E_{(L_b)}$ is the expected length at birth of the offspring, and $\sigma_{(L_b)}^2$ is the expected variation in offspring size, as measured at the next population census in the model at $t + 1$.

5.2.4 Parametrization of individual-level life history functions

A set of eight traits are used to parameterize the individual level life history functions in the DEB-IPM: Larval transformation length (L_b), variation in transformation length (σ_{L_b}), von Bertalanffy growth coefficient (r_B), maturation length (L_p), maximum adult length (L_m), maximum number of eggs produced by adult of maximum length (R_m), egg and larval stage survival rate (ϕ), and natural mortality rate (μ_p). We collected the values of these traits from scientific literature (values and references in Table 1). Where multiple studies were available, for example from studies of different populations, an average was taken. The trait values in Table 1, therefore, represent a generalized life history of a species based on combining information from multiple populations where available. We were able to collect species-specific values for six of these DEB-IPM parameter traits directly from scientific literature. We calculated two of the traits, survival during the egg and larval phase, ϕ , and variation in offspring size, $\sigma_{L_b}^2$, manually:

$$\phi = 1 - e^{(-M \cdot n)} \quad (5.9)$$

where M is the instantaneous mortality coefficient of the species during the egg and larval phase, and n is the duration of the egg and larval phase, both in unit days. M and n values were collected from scientific literature (values and references in Table 1).

$$\sigma_{L_b}^2 = (c_i \cdot \left| \left| \frac{\min_{L_b} - \mu_{L_b}}{3} \right| \right|)^2 \quad (5.10)$$

in which \min_{L_b} represents the minimal larval or hatching size, collected from scientific literature, μ_{L_b} is the mean of the distribution of larval size, assumed to follow a normal distribution, and c_i is a multiplier constant set to 0.1, 0.5 or 1.0 for species with low, medium and high spread in spawning, respectively. The rationale being that species releasing all eggs in a single event will have a lower variation in offspring size measured at the next population census compared to species that release eggs daily over an extended period of time. The equation itself is an adaptation of the z-score formula to calculate the standard deviation of a normal distribution (Abdi, 2007).

Table 5.1: Species life history trait table including references for the parametrization of the DEB-IPM models. Parameter values were obtained from published studies and the references are listed in parentheses behind the trait values. Units are listed in the top row. L_b = Larval transformation length, $\sigma(L_b)$ = variation in transformation length, R_m = maximum number of eggs produced by adult of maximum length L_m , ϕ = fraction egg and larval survival, r_B = von Bertalanffy growth coefficient (dimensionless), L_p = maturation length, L_m = maximum length, μ_p = Natural mortality rate.

Species	$L_b(mm)$	$\sigma(L_b)(mm)$	$R_m(no.eggs)$	$\phi(t^{-1})$	$r_B(-)$	$L_p(cm)$	$L_m(cm)$	$\mu_p(t^{-1})$
1. <i>Acanthochromis polyacanthus</i>	25.0 (2000)	0.327 id	225 (1985)	0.195 (1996)	1.392 (2019)	9.07 (2000)	15.3 (1996)	0.477 (2019)
2. <i>Anmodytes marinus</i>	50.0 (2003)	0.767 id	13133 (2002)	0.005 (1997)	0.490 (2002)	14.0 (2001)	21.0 (2002)	0.600 (2004; 1998)
3. <i>Anchoa mitchilli</i>	20.0 (1983; 1967)	3.033 id	21006 (2002)	0.001 (1993)	0.480 (2002)	3.69 (1991)	11.0 (1963)	2.360 (1995)
4. <i>Anguilla anguilla</i>	80.0 (2005; 2018; 2007)	1.228 id	2500000 (2002)	0.002 (2009)	0.140 (2002)	54.00 (1977)	145.0 (2002)	0.230 (1999)
5. <i>Chaetodon multicinctus</i>	19.5 (2017; 1989)	3.050 id	14509 (1986)	0.001 (1986; 2009)	1.330 (1986)	7.10 (1986)	9.5 (1986)	0.518 (2016)
6. <i>Clupea harengus</i>	41.0 (2005)	0.600 id	141075 (2002)	0.001 (1993)	0.320 (2002)	16.70 (2002)	51.0 (2002)	0.168 (1963; 1959)
7. <i>Danio rerio</i>	14.0 (2014)	1.667 id	500 (1973)	0.033 (2012; 1994)	1.200 (2002)	2.50 (2002)	3.8 (2002)	1.515 (1999)
8. <i>Dicentrarchus labrax</i>	17.0 (2005)	0.225 id	520228 (2002)	0.001 (1993)	0.120 (2002)	42.00 (2013)	103.0 (2002)	0.240 (2018b)
9. <i>Engraulis engrasicolus</i>	14.5 (2010)	1.867 id	226500 (2002)	0.001 (1993)	0.470 (2002)	11.50 (2016)	21.0 (2002)	0.900 (1993; 1974; 1967)
10. <i>Engraulis japonicus</i>	40.0 (2007; 2004)	6.167 id	160000 (2008)	0.001 (1993)	1.700 (2002)	8.18 (2004)	18.0 (2002)	0.630 (1993)
11. <i>Engraulis mordax</i>	35.0 (1977; 1981)	0.536 id	21006 (2002)	0.002 (1993)	0.380 (2002)	13.50 (1980)	24.0 (2002)	0.970 (1981)
13. <i>Gadus morhua</i>	20.0 (2007)	1.392 id	5900000 (2002; 2014)	0.001 (1993)	0.160 (2002)	68.30 (2002)	123.0 (2002)	0.216 (1963; 1975; 2001; 1966)
14. <i>Gasterosteus aculeatus</i>	15.0 (2007)	2.000 id	470 (2002)	0.139 (1997; 1958)	2.237 (2002)	5.50 (2002)	10.0 (2002)	1.060 (1950)
15. <i>Gillichthys mirabilis</i>	15.0 (1996)	1.000 id	27000 (1996; 2005)	0.013 (1975)	0.790 (2009)	10.00 (1963)	21.0 (1999)	4.761 (1973; 2005)
16. <i>Lepomis gibbosus</i>	15.0 (1982)	2.100 id	5000 (1973; 1939)	0.008 (1993)	0.395 (2004)	7.00 (2014)	20.0 (1998)	0.540 (1981)
17. <i>Melanogrammus aeglefinus</i>	20.0 (2007)	1.392 id	969000 (2002)	0.001 (1993)	0.220 (2002)	34.90 (2002)	110.0 (2002)	0.430 (1990)
18. <i>Menidia beryllina</i>	24.0 (2007)	3.417 id	223 (2002)	0.113 (1996)	1.140 (2002)	4.50 (1996)	15.0 (1991)	0.993 (1982)
19. <i>Micropterus salmoides</i>	40.0 (2007)	6.167 id	82000 (1962)	0.016 (1993)	0.245 (2008)	25.00 (1976)	70.0 (1980)	0.450 (2005)
20. <i>Oryzias latipes</i>	15.5 (2004)	1.950 id	141 (2011)	0.033 (1994; 2014)	3.650 (2011)	2.20 (2004)	4.5 (2011)	1.515 (1999)
21. <i>Perca fluviatilis</i>	20.0 (1982)	0.255 id	157594 (1975)	0.041 (1993)	0.332 (2008)	19.20 (2002)	40.0 (1991)	1.170 (1981)
22. <i>Pleuronectes platessa</i>	14.0 (1993)	0.667 id	552000 (2017)	0.007 (1993)	0.130 (2002)	30.80 (2002)	100.0 (1986)	0.140 (1964; 1989)
23. <i>Pomoxis annularis</i>	16.0 (1982)	1.233 id	325677 (1954)	0.002 (1993)	0.246 (2005)	20.50 (1982)	51.0 (1997)	0.84 (1998)
24. <i>Pseudopleuronectes americanus</i>	13.0 (2007)	0.177 id	648836 (2002)	0.001 (1993)	0.310 (2002)	27.40 (2002)	64.0 (1986)	0.300 (1955)
25. <i>Rutilus rutilus</i>	14.9 (1990)	0.132 id	190000 (2008)	0.033 (1994)	0.107 (2013)	10.27 (2008)	50.2 (2011)	0.400 (2007)
26. <i>Salmo salar</i>	26.7 (1981; 2007)	0.145 id	10794 (2002)	0.013 (1993)	0.270 (2002)	73.10 (2002)	150.0 (2002)	0.740 (2012)
27. <i>Salmo trutta</i>	28.0 (2016)	0.200 id	8616 (2002)	0.013 (1993)	0.240 (2002)	20.20 (1976)	94.0 (2002)	0.670 (2006)
28. <i>Salvelinus alpinus</i>	24.8 (2008)	0.165 id	5400 (1996)	0.013 (1993)	0.075 (2010)	38.98 (2010)	107.0 (2002)	0.170 (1975)
29. <i>Sander vitreus</i>	20.0 (1982)	0.237 id	600000 (1969)	0.017 (1993)	0.266 (2003)	42.90 (2002)	107.0 (1973)	0.440 (2001)
30. <i>Sardina pilchardus</i>	15.5 (2010)	1.667 id	169000 (2002)	0.001 (1993)	0.360 (2002)	14.30 (2013)	27.0 (2002)	0.667 (2009; 2010)
31. <i>Scophthalmus maximus</i>	38.4 (1976; 1984)	3.022 id	5000000 (2017)	0.001 (1993)	0.250 (2002)	34.70 (2002)	100.0 (1986)	0.246 (1973; 2009; 2006)
32. <i>Solea solea</i>	12.0 (2005)	0.750 id	300000 (2002)	0.001 (1993)	0.320 (2002)	24.60 (2007)	70.0 (2002)	0.100 (2005)
33. <i>Sprattus sprattus</i>	25.0 (2005)	3.583 id	14630 (2002)	0.001 (1993)	0.600 (2002)	10.00 (2011; 2012)	16.0 (1988)	0.377 (2019)
34. <i>Trisopterus luscus</i>	18.0 (1976; 2018)	2.500 id	521738 (2002)	0.001 (1993)	0.430 (2002)	19.20 (2008)	46.0 (2002)	1.330 (1950; 1984)

5.2.5 Population level integration and outcome variables

The individual-level growth, survival, reproduction, and parent-offspring association functions in the DEB-IPM are integrated over the length domain Ω to describe the dynamics of the total number of female individuals in a population N , from time t to $t + 1$ (Easterling et al., 2000b).

$$N(L', L(t + 1)) = \int_{\Omega} [D(L', L(t))R(L(t)) + G(L', L(t))S(L(t))]N(L, t)dL \quad (5.11)$$

Given a simulation of τ steps, the log of the stochastic growth rate of the population, $\log(\lambda_s)$ can then be calculated.

$$\log(\lambda_s) = \frac{1}{\tau} \sum_{\tau=0}^{\tau-1} \log \frac{\mathbf{p}(t+1)}{\mathbf{p}(t)} \quad (5.12)$$

We define the sensitivity of the population to variation in the environment as the difference between maximum and minimum $\log(\lambda_s)$ across simulated environments.

$$\Delta \log(\lambda_s) = \log(\lambda_{s_{Max}}) - \log(\lambda_{s_{Min}}) \quad (5.13)$$

The population-level outcome variables of growth rates and sensitivity to environmental variation are therefore an emergent property of individual-level processes and tradeoffs included in the DEB-IPM.

5.2.6 DEB-IPM implementation and simulations

Stochastic demographic model simulations

We implemented the parametrized DEB-IPMs into a stochastic demographic model using *Matlab* (version R2021a) to calculate stochastic population growth rates ($\log(\lambda_s)$) and sensitivity to environmental variation ($\Delta \log(\lambda_s)$). We ran simulations for each of the 34 model species, across an environmental autocorrelation range of $\rho = -1 : 1$, with a step size of 0.001. Each simulation consisted of 50,000 time steps, with an initial transient of 400 time steps, a starting population of one individual in each size bin, and a randomly chosen initial environmental state (see also Tuljapurkar et al. 2003; Smallegange et al. 2014).

Stochastic demographic model details

The stochastic demographic model was defined as $\mathbf{p}(t+1) = \mathbf{A}(t) \cdot \mathbf{p}(t)$. The vector $\mathbf{p}(t)$ is the population vector at time t , and $\mathbf{A}(t)$ is a DEB-IPM at time t , defined by a two-state Markov chain habitat transition matrix \mathbf{H} (Caswell, 2001b):

$$H = \begin{bmatrix} 1-p & q \\ p & 1-q \end{bmatrix} \quad (12)$$

In the habitat transition matrix, p equals the probability of switching from a good to a bad environment, and q equals the probability of switching from a bad to a good environment. The autocorrelation level in the model equals $\rho = 1 - p - q$ (Caswell, 2001b). We used a fixed frequency of good environments of $f = 0.5$ for all levels of environmental autocorrelation examined. The feeding levels of individuals in good and bad environments are associated with positive ($\log(\lambda_s) > 1$), and negative ($\log(\lambda_s) < 1$), population growth rates, respectively. We set the feeding levels associated with good and bad environmental states at $E(Y)_{high} = 1.0$, and $E(Y)_{low} = 0.7$, for all species, and the variation in experienced feeding levels between individuals $\sigma(Y)$ at an intermediate level of $\sigma(Y) = 0.3$ (Smallegange et al., 2017). Summarizing, at each time step in the stochastic demographic model, the DEB-IPM at time t , $\mathbf{A}(t)$ is calculated based on the experienced

feeding level $E(Y)$ at time t , determined by the habitat transition matrix, and subsequently stored.

5.2.7 PCA analysis

We used a varimax rotated, phylogenetically informed PCA (pPCA; (Revell, 2009)) to structure species life history traits into life history strategies, following the procedure outlined in (Paniw et al., 2018; Capdevila et al., 2020; Salguero-Gómez et al., 2016b), implemented using *R* (version 4.2.1). The life history traits included in this analysis were the eight DEB-IPM parameters and sensitivity to environmental variation $\Delta \log(\lambda_s)$. Trait values were log-transformed and scaled with a mean of one and a standard deviation of zero to meet pPCA assumptions. We constructed a species-level phylogenetic tree prior to performing the pPCA using data from the Open Tree of Life (<https://tree.opentreeoflife.org>, (Hinchliff et al., 2015)), and the *R* package *ROTL* (Michonneau et al., 2016). We used branch lengths as the measure of phylogenetic relatedness between species. Branch lengths were computed using the *compute.brLen* function, and polytomies resolved using the *multi2di* function, from the *R* package *ape* (Paradis et al., 2004). We then checked that the constructed tree was rooted and there were no branches with zero length before implementing the pPCA. We implemented the pPCA using the *phyl.pca* function from the *R* package *phytools* (Revell, 2012). The pPCA linked the phylogeny to the life history traits using a modified covariance matrix, and simultaneously estimated Pagel's λ with maximum likelihood methods (Revell, 2009; Capdevila et al., 2020). Pagel's λ expresses the phylogenetic signal strength in trait evolution under a Brownian motion model (Blomberg & Garland Jr, 2002). A Pagel's λ value of zero indicates that the correlation in traits observed between species are independent of their shared evolutionary history, whereas a value of one indicates the correlation in traits is fully determined by it (Meireles et al., 2020; Revell, 2010). We applied the Kaiser's criterion to select the number of PCA-axes to keep, retaining only those axes with an eigenvalue > 1 (Kaiser, 1960). One species with outlier values for sensitivity and mortality, as determined based on z -scores (*G. mirabilis*; $\Delta \log(\lambda_s) = 1.77$, $z_{\Delta \log(\lambda_s)} = 4.18$; $\mu_p = 4.76$, $z_{\mu_p} = 4.65$) was excluded from the pPCA-analysis. Finally, we checked for the influence of phylogeny and body size on the final structuring of life history strategies (see Jeschke & Kokko for a detailed discussion; (Jeschke & Kokko, 2009)), by running pPCA analyses with and without phylogeny, and with and without a correction for body size. Body size was corrected for by using the residuals of linear regressions of \log_{10} -transformed values of traits versus \log_{10} -transformed adult body mass (Gaillard et al., 1989; Bielby et al., 2007). The resulting pPCA analyses allowed us to examine if the observed life history strategies differ when explicitly accounting for individual-level life history tradeoffs (research question i), whether life history tradeoffs align with the patterning of traits into life history strategies (research question ii), and if sensitivity to environmental variation covaries with either of the primary life history strategy axes (research question iii), or individual life history traits (research question iv).

5.2.8 Perturbation analysis

We used a perturbation analysis to examine which of the eight life history traits listed in table 1 most strongly affected $\log(\lambda_s)$, and how trait importance might shift over the

gradient of environmental autocorrelation (research question v). Each trait parameter i was perturbed by 1% and the elasticity of $\log(\lambda_s)$ calculated.

$$e_i^{(\log(\lambda_s))} = \frac{\log(\lambda_{\gamma_i}) - \log(\lambda_s)}{\gamma_i} \quad (5.14)$$

Where the elasticity of $\log(\lambda_s)$ to perturbation of trait i by fraction γ_i , equals the difference in population growth rate with and without perturbation, divided by the fraction perturbed. This approach adds detailed insights into the sensitivity to environmental variation at the individual species level.

5.3 Results

5.3.1 Life history strategies sensitivity to environmental variation

We find that species life history traits in ray-finned fish structure along three separate pPCA axes that cumulatively explain 78% of the total variation in life histories (Table 2: Full Model (FM), pPC1: 48.6%, pPC2: 17.2%, pPC3: 11.7%). Phylogenetic relatedness has little effect on species trait values in this analysis (Pagel's $\lambda = 6.7 \cdot 10^{-5} \pm 3.5 \cdot 10^{-7}$). Trait loadings indicate pPC1 and pPC2 are analogous to the fast-slow and reproductive strategy axes observed in previous studies (Fig. 1). Specifically, pPC1 shows the coupling of traits relating to growth and survival, with the highest positive loadings for maximum length (L_m), maturation size (L_p), and negative loadings for mortality rate (μ_p), variation in offspring size ($\sigma(L_b)$), and growth rate (r_B). This reflects a trade-off between growth and survival, i.e. larger, slow-growing species with high survival, versus smaller, fast-growing species with lower survival. Trait patterning on pPC2 shows a negative coupling between egg-and larval survival rate (ϕ), and the maximum number of offspring produced (R_m). This reflects a tradeoff between allocating energy in many offspring with lowered survival versus fewer offspring with increased survival.

Sensitivity to environmental variation, ($\Delta \log(\lambda_s)$), was only very weakly correlated with pPC1 and pPC2, and instead most strongly loaded onto pPC3 (Table 1: FM). Checking for the effect of phylogeny and body size does not alter this result (Table 1: FM - Phylogeny; FM - body size residuals). When phylogeny is excluded, the loading of $\Delta(\log(\lambda_s))$ is further reduced on pPC1, while remaining similarly weak on pPC2, and strongly loaded on pPC3. Correcting for body size changes the ordering of the principal components, but $\Delta(\log(\lambda_s))$ remains strongly loaded on a separate axis with offspring size, and weakly loaded on the fast-slow and reproductive axes. Therefore, across our three pPCA models, we find no evidence of $\Delta(\log(\lambda_s))$, i.e. sensitivity covarying with either the fast-slow axis or the reproductive strategy axis.

Next, we examined a potential interaction effect between the fast-slow and reproductive

Table 5.2: Phylogenetically informed PCA loadings of life history traits and sensitivity to shifts in environmental variation on the first three principal components for three different models: Full Model with all traits and phylogeny, Full Model without phylogeny, and Model with phylogeny and body size corrected traits. Bold values indicate the principal component with which each trait is most strongly associated. Definitions of the descriptions of the PCA axes on the bottom bar: *fast-slow* fast slow continuum, *reprod.:* reproductive strategy axes, *sens.:* sensitivity to shifts in environmental variation.

pPCA	Full model (FM)			FM – Phylogeny			FM – Body size residuals		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
<i>Eigenvalue > 1</i>	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
<i>Cum. variance explained</i>	0.486	0.658	0.775	0.486	0.658	0.775	0.285	0.480	0.615
$\Delta \log(\lambda_s)$	0.289	-0.025	-0.690	-0.090	-0.042	-0.604	0.065	0.699	-0.135
r_B	-0.868	0.178	-0.183	-0.426	0.006	-0.149	-0.093	0.529	-0.624
ϕ	-0.182	0.918	-0.052	-0.005	0.729	-0.123	-0.922	0.033	0.023
R_m	0.591	-0.736	-0.066	0.250	-0.504	-0.013	0.901	0.106	0.081
μ_p	-0.709	0.176	0.055	0.364	0.022	0.058	-0.145	0.001	-0.299
L_p	0.905	-0.279	-0.057	0.458	-0.073	-0.058	0.442	-0.011	-0.769
$\sigma(L_b)$	-0.653	-0.413	-0.422	-0.344	-0.435	-0.316	0.446	0.678	0.296
L_b	0.294	0.047	-0.766	0.232	0.121	-0.699	-0.072	0.626	-0.050
L_m	0.941	-0.213	-0.016	-0.480	-0.014	-0.028	-	-	-
	fast-slow	reprod.	sens.	fast-slow	reprod.	sens.	reprod.	sens.	fast-slow

strategy axes on sensitivity, by excluding $\Delta(\log(\lambda_s))$ from the pPCA and modeling it as a function of pPCA scores using multiple linear regression (Table 3). pPC1, pPC2, pPC3, and pPC1 x pPC2 scores only explained 7.5% of the variation observed in sensitivity across species. The model's F-statistic and associated p-value indicate there is no relationship between any of the predictors and sensitivity, and that it does not perform better than an intercept-only model. Finally, the residual standard error almost equals the intercept effect size, and is much larger than the other estimated effects, further indicating the poor predictive power of the PCA scores in terms of predicting $\Delta(\log(\lambda_s))$. Visually examining sensitivity values across the pPC1-pPC2 gradient also does not indicate a clear PC1-PC2 interaction pattern to be present (Supplementary figure 1). Therefore, we find no evidence of $\Delta(\log(\lambda_s))$ covarying with the interaction between the fast-slow and reproductive strategy axis in our study. Examples of species with similar life history strategies and contrasting responses to environmental variation are provided in Figure 2.

5.3.2 Life history traits and sensitivity to environmental variation

In the pPCA analysis, $\Delta \log(\lambda_s)$ consistently negatively loaded on a separate axis together with offspring size L_b ; indicating that species with smaller offspring sizes also tended to have lower sensitivity to environmental variation. However, when examined individually, the relationship between L_b and $\Delta \log(\lambda_s)$ was found to be highly non-significant (Supplementary Table 1). This indicates that rather than being strongly associated to each other, L_b and $\Delta \log(\lambda_s)$ have in common that they are strongly dissociated from the patterns in trait loadings on pPC1 and pPC2. Additional testing confirmed no statistically significant relationship between $\Delta \log(\lambda_s)$ and any of the eight life history traits included in the study (Supplementary Table 1). Although we did not find a clear relationship between sensitivity and traits across species, our perturbation analysis did show differences in trait

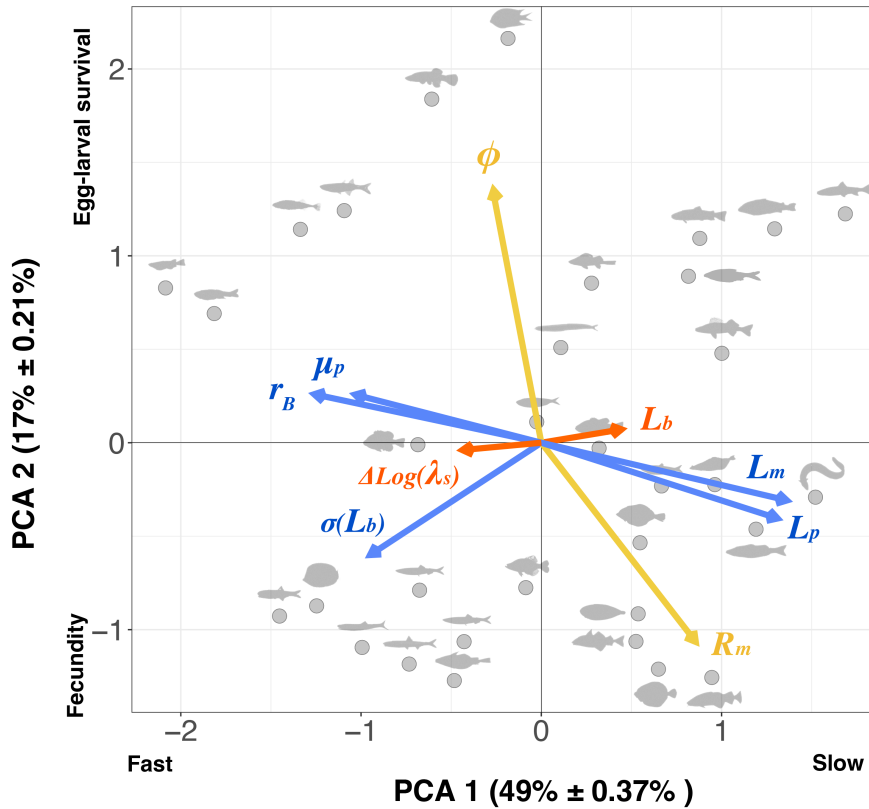


Figure 5.1: Biplot of phylogenetically corrected principal component analysis (pPCA), with the percentage of variance explained in brackets (\pm SE) for the 8 life history traits included as parameters in the DEB-IPMs, and the DEB-IPM derived trait of sensitivity ($\Delta \log(\lambda_s)$). Arrow lengths indicate mean loading of each trait, and arrow colour indicates to which pPCA axis it is most strongly associated (blue: pPC1, yellow: pPC2, and orange: pPC3). pPC1 is most strongly associated with growth and mortality traits, pPC2 most strongly with reproductive traits, and pPC3 with sensitivity and size at birth. Points represent the pPCA scores of the sample species on this two-dimensional space, which can be further identified by their silhouettes.

importance in driving the population growth rates of individual species (Fig. 3). Furthermore, there was a clear influence of reproductive decisions on these results. In 70% of iteroparous obligate breeders, maturation length L_p is the most important trait driving population growth rate, and there is generally no shift in trait importance depending on the degree of environmental autocorrelation. In iteroparous skip breeders, however, maximum length L_m (72%), and von Bertalanffy growth rates r_B (55%), are more important than L_p in driving population growth rates. Finally, in semelparous species, egg-larval survival rate ϕ is the most important trait driving population growth rates (60%), followed by r_B and L_p (both found in 40% of species). The variation in trait importance across the gradient of autocorrelation is generally inconsistent, i.e. specific traits can be important drivers of population growth rates both when environments are highly variable, or highly invariable. Notably, there is a pattern in the importance of egg-larval survival, which was only observed in species with relatively small adult body sizes (*G. aculeatus*, *A. mitchilli*, *E. engrasicolus*, *E. japonicus*, *F. heteroclitus*, *D. rerio*, *M. berylina*, *O. latipes*).

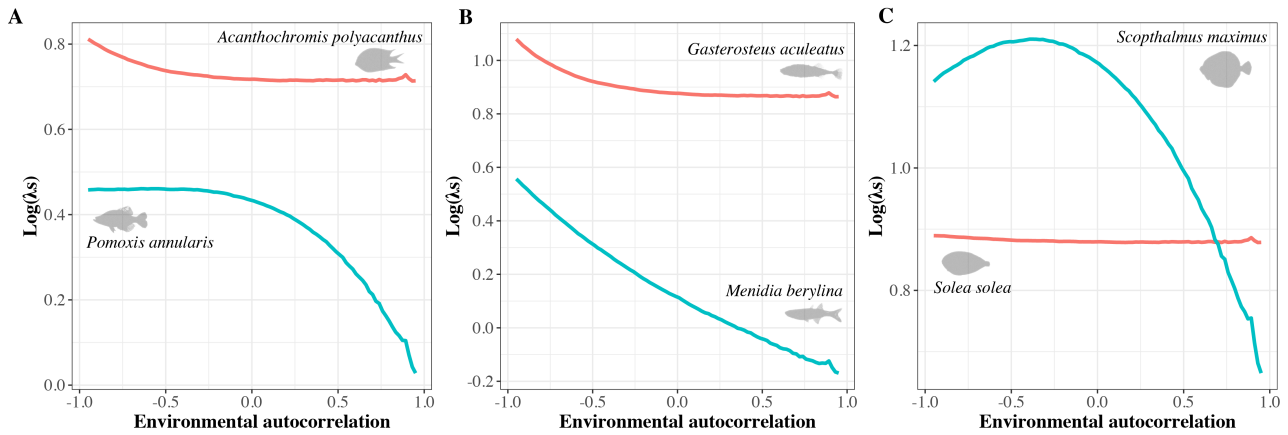


Figure 5.2: Examples of species with similar life history strategies and contrasting population growth rates ($\text{Log}(\lambda_s)$) in response to environmental autocorrelation. (A) Species with similar position on PC-1 only and dissimilar responses, (B) Species with similar low PC1 and high PC2 scores (top-left Fig.1) and dissimilar responses, (C) Species with similar high PC1 and low PC2 scores (bottom-left) and dissimilar responses.

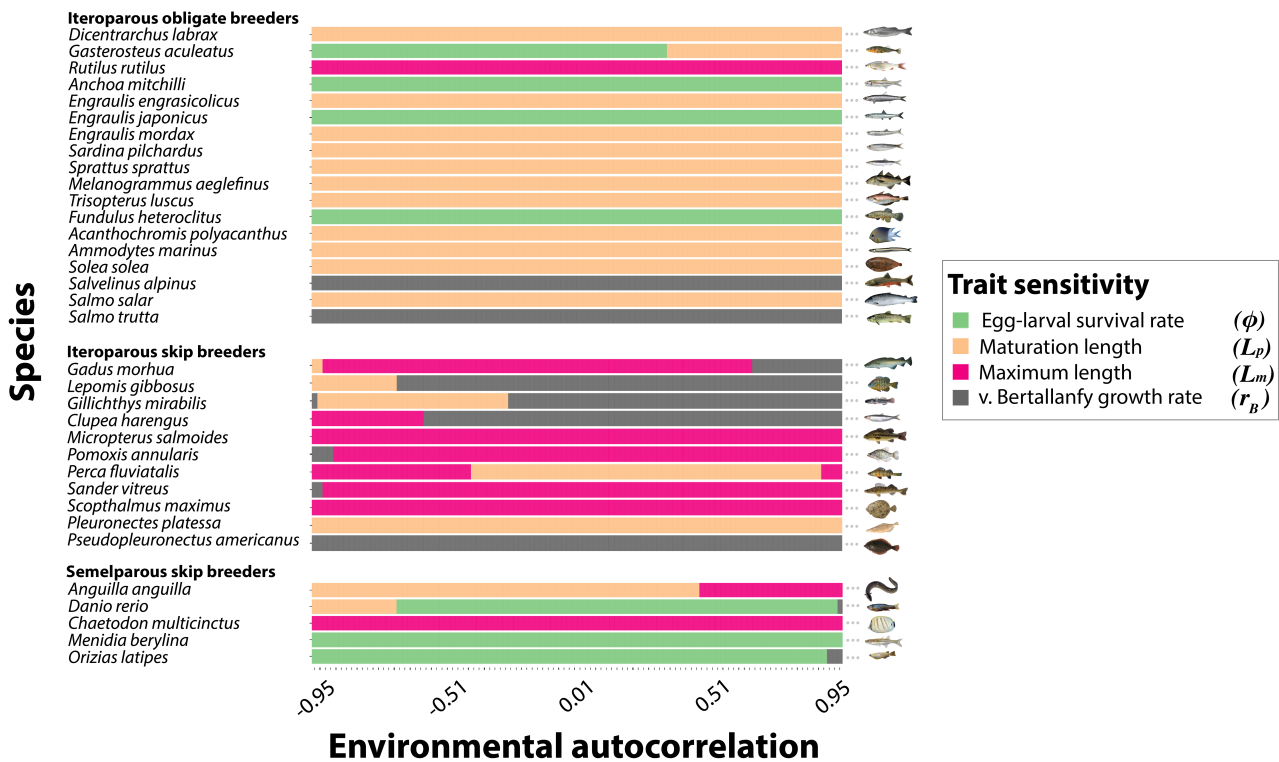


Figure 5.3: Species level perturbation plot highlighting the life history traits most strongly affecting population growth rate $\text{log}(\lambda_s)$ across the gradient of environmental autocorrelation. In the underlying perturbation analysis each trait was perturbed by 1% and the elasticity of $\text{log}(\lambda_s)$ calculated. Model species are grouped depending on the reproductive decisions included in the DEB-IPM: (top) Iteroparous obligate breeders (centre), Iteroparous skip breeders, and (bottom) Semelparous skip breeders, respectively.

5.4 Discussion

5.4.1 Life history tradeoffs, traits, and strategies

We find three primary life history strategy axes when explicitly accounting for energy allocation tradeoffs at the individual level (research question i). This includes the classical fast-slow axis and the often-reported secondary reproductive strategy axis (Stearns, 1992; Healy et al., 2019; Paniw et al., 2018; Morris et al., 2008; Capdevila et al., 2020), and a third axis for population sensitivity to environmental variation. Our results show differences between the life history tradeoffs in energy allocation that we incorporated at the individual level (growth versus reproduction, future versus current reproduction) and the life history tradeoffs reflected by the patterning of species traits along our fast-slow and reproductive strategy axes (research question ii). This indicates that individual-level life history tradeoffs do not necessarily apply to the population and species level. The assumption that the structure of individual differences in life history traits resembles in important ways the structure of variation across species underpins the pace of life syndrome (POLS), in which behavioural and physiological differences between individuals are postulated to covary with the slow-fast life-history continuum (Réale et al., 2010). Our results provide one explanation for why we lack robust empirical support for the predictions of the POLS framework (Laskowski et al., 2021). We argue we do not find an alignment because the general tradeoffs in energy allocation faced by all individual organisms do not necessarily reflect the potential selective pressures and opportunities posed by the environment in which populations occur. For example, in marine systems, species can realize relatively high fecundity through a combination of oviparity and external fertilization (Gross & Shine, 1981; Benun Sutton & Wilson, 2019). This strategy is not available to terrestrial species and comes at a cost of increased mortality when depositing undeveloped eggs in the external environment. This can for example explain why many marine species groups such as large ray-finned fish can combine the slow growth, longevity and low adult mortality rates typical of slow life histories with the high fecundity and high offspring mortality rates typical of fast life histories (Beukhof et al., 2019b). Differences in selective pressures and opportunities between environments might also explain why populations of the same species can exhibit very different life history strategies in different areas (Gamelon et al., 2021). It is still important to account for the individual-level tradeoffs in energy allocation when examining life history variation even if they don't reflect the tradeoffs in traits at the population or species level. This is because they impose critical energetic constraints on individual development and reproduction that translate through in population dynamics (Karjalainen et al., 2016). Without such energetic constraints, the law of conservation of energy would be violated and biomass freely created in demographic model studies, affecting projected population production, structure and responses to the environment. Although demographic vital rates in our study are dependent on the energy

5.4.2 Responses to environmental variation

We failed to find a significant link between life history traits and strategies in ray-finned fish, and their sensitivity to environmental variation (research questions iii,iv). The implications of these results extend beyond the immediate species modeled. The large

range of environmental conditions that were simulated (~ 50,000 scenarios per species), in combination with the range in trait combinations across species, and the reproductive decisions incorporated in our models, provide broad insights into the idiosyncrasy of population responses to environmental variation. Part of the wide range of environmental variation that was simulated, e.g. extremely negative autocorrelation, might not generally be expected to occur in nature. However, recent studies show, for example, how terrestrial arctic species are already facing increasingly high interannual variability in environmental conditions (Schmidt et al., 2023), leading to very unpredictable feeding environments between years. The absence of a general link between population responses and species life history strategies also aligns with other demographic studies in terrestrial systems that have shown different populations of the same species can display highly different life history strategies and therefore different population responses (Gamelon et al., 2021; Nevoux et al., 2010; Nilsen et al., 2009). This intraspecific variation in life history strategies also highlights a potential limitation concerning the comprehensiveness of our current study. For example, different populations of *Salmo salar* can display different life history strategies, where some populations migrate to sea and others remain fully resident (Fleming, 1996; MacCrimmon & Gots, 1979). Both types even exist sympatrically in some populations (Verspoor & Cole, 1989). Because our study used life history trait values averaged across multiple populations, we therefore overlook this potentially important source of intraspecific variation in life histories between populations. However, we believe that this does not negate, but rather strengthens and adds to the general message of our results: a need to study and account for individual-level life history complexity in order to examine complex population responses. If included, population responses might have been reasonably expected to be more idiosyncratic rather than more general. This strongly aligns with other recent findings. For example, Van de Walle et al. (2023a) show that although across species a slow-fast continuum could be identified as the main axis of life history variation, there is no alignment to this pattern when examining the populations of a species individually. The authors therefore conclude that individual life-history variation is likely idiosyncratic across species. The importance of accounting for individual-level life history complexity to understand population level outcomes is also not an altogether new perspective. For example, a long line of ecological research shows that populations accounting for size-structure and individual growth have very different dynamics than those in which individuals are all assumed to be identical (de Roos & Persson, 2013b). However, added complexity comes at a cost. Studies accounting for successively more individual-level complexity typically can examine fewer species, lowering sample size (34 in our study), and the outcomes are more system specific. This contrasts with the statistical power of broad cross-taxonomical approaches to use big functional-trait datasets to derive general inferences across large groups of species and systems (Kissling et al., 2018b; Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016a), that in turn come at the cost of reduced mechanistic insight.

5.4.3 Perspective

Our results show that the classical association between life history strategies and responses to environmental variation breaks down when explicitly accounting for individual-level life history tradeoffs. Contributing factors are that (i) tradeoffs can differ between levels

of organisation, and (ii) we must account for individual-level tradeoffs in order to have a link between individual processes and population-level responses that is based on first principles, such as the conservation of energy. We postulated that the assumed alignment between individual, population, and species-level tradeoffs depends on the specific selective pressures and opportunities posed by the environment. This alludes to another important level of organization that is not always included in demographic models, including our own: feedback with the environment. Population modeling approaches accounting for both individual life-history mechanisms and environmental feedbacks show complex population dynamics, including alternative stable states (Persson et al., 1998; de Roos & Persson, 2013b). Crucially, such complex dynamics are usually directly dependent on individual-level processes, such as size-dependent differences in mortality rates or feeding efficiency. We already highlighted how the gains from additional mechanistic insight when accounting for individual-level complexity comes at the cost of being able to examine fewer species when we wish to examine population responses to environmental variation. This leaves the question of how to best move forward in the future. We summarise our perspective in a conceptual framework (Figure 4), listing the strengths and weaknesses of varying demographic modeling approaches using functional traits to model population responses. We find that this framework actually points towards the potential of combining different methods to address large and complex questions, such as which species are most vulnerable to environmental change. For example, we can use (1) pattern based models to characterize the different life history strategies that have evolved across species, (2) a hybrid model, which combines patterns in traits in combination with a limited set of life history tradeoffs and or processes, to identify which of these strategies and individual species show the highest sensitivity when exposed to environmental variation, and (3) a process model to study the responses of the most sensitive species to environmental change in a fuller ecological context, including feedbacks and accounting for trophic interactions. In this way, each approach acts as a focusing lens for the next one, and adds to their overall utility in addressing urgent conservation issues by combining their individual powers. We hope that this perspective can help pave the way towards a more integrative approach utilizing functional traits to understand complex demographic processes in an era of change (Salguero-Gómez et al., 2018).

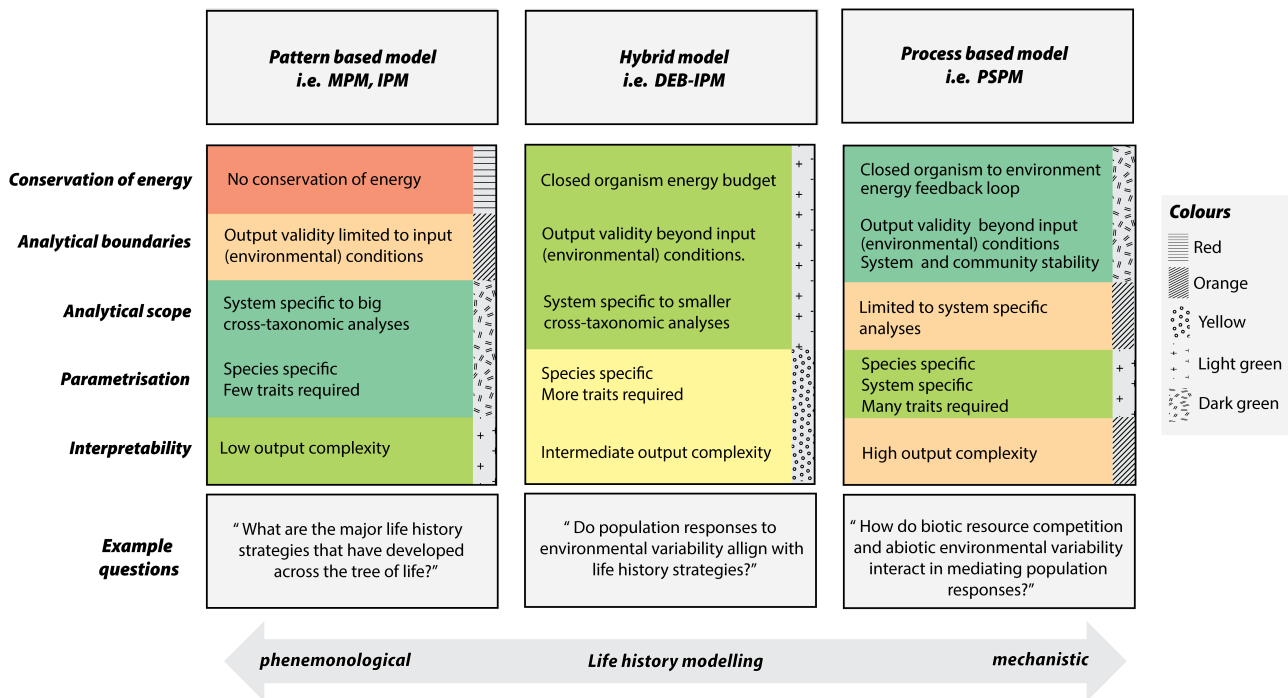


Figure 5.4: Conceptual framework highlighting the characteristics of different kinds of demographic modelling approaches in life history research. The framework can be used to identify the most appropriate approach based on research specifics. The columns list three different modelling approaches (pattern, hybrid, and process based models, respectively). The rows describe important modelling assumptions. The text in the row cells explains the limitation of each of the three modelling approaches in relation to these assumptions. This explanation is combined with both a 5-valued color scale that indicates how the different modelling approaches perform in relation to each assumption (Red: poor, Orange: bad, Yellow: average, Light green: good, Dark green: very good). Finally, the bottom row lists an example research question that each modelling approach is suited to address.

Chapter 6

Population regulation in semelparous deep-sea squid is driven by ecological conditions for paralarvae in surface waters and depth-specific predation by cetaceans

This chapter is based on:

Rademaker, M., ten Brink, H., Hoving, H.J., Visser, F., & van Leeuwen, A. (in prep). Population regulation in semelparous deep-sea squid is driven by ecological conditions for paralarvae in surface waters and depth-specific predation by cetaceans.

Abstract

Oceanic squid are the most abundant group of cephalopods inhabiting the pelagic deep-sea and form an important prey for deep-diving cetaceans. Despite the increasing number of observations on deep-sea squid life history, we still understand little about their population-level dynamics. Understanding population dynamics of deep-sea squid is key to forming a more general theory of the ecological functioning of the pelagic deep-sea across trophic levels. Such a theory is urgently needed to be better able to predict the impacts of anthropogenic activities on deep-sea ecosystems beyond benthic communities. Here we use empirical data on individual life history to develop a size-structured population model of the hyperabundant deep-sea squid *Histioteuthis reversa*. We use this model to mechanistically understand the processes underlying empirical observations on exponential-like individual growth and seasonal maturation in *H. reversa*, and examine the emergent population-level dynamics. We further analyse the population responses of *H. reversa* to depth-specific predation by two deep-diving cetacean predators. Our model shows how population regulation in deep-sea squid is primarily driven by conditions experienced as paralarvae in the upper water column. We find model predictions on individual growth align with empirical observations. Population dynamics of *H. reversa* are characterized by single-cohort cycles that lead to 'seasonal' periodicity in maturation and reproduction in the absence of any seasonality in the resource environment. We further find that predation of *H. reversa* by deep-diving cetaceans at different depths can result in emergent facilitation between predator species. Our outcomes provide fundamental new insights into the population regulation of one of the most abundant and trophically important species groups in the pelagic deep-sea.

6.1 Introduction

Cephalopod populations are increasing around the globe (Doubleday et al., 2016b), expanding their ecological niche in response to overfishing of competing species groups (fish) and climate-driven changes in the ocean environment (Rodhouse et al., 2014; Pecl & Jackson, 2008; Caddy & Rodhouse, 1998; Vecchione et al., 2009). Squid are considered the most abundant and species-rich group of cephalopods inhabiting the pelagic deep-sea (Hoving et al., 2014; Escáñez et al., 2022). Total biomass of deep-sea squid has been estimated to range between 110 - 320 million tons (Clarke, 1977; Kawakami, 1980); exceeding the total human fisheries and aquaculture production in marine and freshwater environments combined (FAO, 2022). Deep-sea squid form a key trophic link in pelagic ecosystems by foraging on nekton and functioning as a primary food source for a wide range of marine apex predators, including tuna, billfish, seals, sharks, and cetaceans (Young et al., 2013; Smale, 1996; Klages, 1996). Despite an increasing number of empirical studies on deep sea squid life history (Hoving et al., 2014), there is little to no understanding of their population dynamics. It is necessary to integrate empirical studies on deep-sea squid life history more strongly with theory to understand how individual-level observations translate into population-level regulation. Understanding population regulation in deep-sea squid is key to forming a general theory of the functioning of pelagic deep-sea ecosystems across trophic levels. There is an urgent need for such a theory to be able to better predict and mitigate the impacts of human-induced changes in the world's largest and least explored marine habitat (Stenvers et al., 2023; Ramirez-Llodra et al., 2010).

The predation of deep-sea squid by their deep-diving cetacean predators illustrates the trophic links existing between the pelagic deep-sea and surface waters. Deep-diving cetaceans are among the most elusive and enigmatic apex predators in marine systems, but their populations are threatened by anthropogenic disturbances that disrupt their foraging (Li & Rosso, 2021; Bernaldo de Quirós et al., 2019; Cholewiak et al., 2017; Moore & Barlow, 2013). The response of prey populations to predation plays an important role in predicting whether deep-diving cetacean populations will be able to persist, or go extinct, with increasing anthropogenic disturbances (Hin et al., 2021, 2023). Many deep-diving cetaceans co-occur and forage on similar deep-sea squid prey communities (Clarke, 1996; Visser et al., 2021). Rather than specializing on a particular prey species, recent empirical studies suggest co-occurring deep-diving cetacean species segregate their ecological niche by targeting distinct depth ranges (Visser et al., 2021). Trawler surveys show commonly preyed deep-sea squid species are distributed in depth in relation to size (Quetglas et al., 2010; Young, 1978). This suggests that deep-diving cetaceans impose size-selective predation mortality on their deep-sea squid prey. When size-selective predation relieves intra-specific competition between prey size-classes, this leads to increased efficiency in growth or reproduction, and increasing prey biomass (Schröder et al., 2009). This biomass overcompensation represents a positive feedback of the predator population on its own foraging success that operates through, and is dependent on, the life history of the prey (de Roos et al., 2003). In a multi-predator context, size-selective predation can result in emergent-facilitation between predator species (De Roos et al., 2008; Huss &

Nilsson, 2011), where one predator cannot persist without the size-selective predation on the shared prey imposed by other predators. The responses of deep-sea squid populations to size-selective predation by deep-diving cetaceans remain unknown. This represents a major challenge in understanding how this key trophic interaction linking the pelagic deep sea and surface waters might be expected to change in the future. However, to understand the regulation of higher trophic levels we must first better understand the life history and internal population regulation of the prey.

The deep-sea squid genus *Histioteuthis* is one of the most abundant, widely distributed, and well-studied groups of deep sea squid (Jereb & Roper, 2010), with members occurring in all the world oceans and marine seas (Boyle & Rodhouse, 2008). They are also among the most commonly reported squid prey of deep-diving cetaceans (Clarke & MR, 1980; Clarke, 1996; Visser et al., 2021). *Histioteuthis* squid are generally characterized by relatively fast growth rates, semelparous reproduction, and a short lifespan of 1-2 years (Jereb & Roper, 2010). However, the mechanisms underlying the life history processes of growth and reproduction observed in *H. reversa* remain less well understood. Growth in *Histioteuthis* and other deep-sea cephalopods tends to show an exponential pattern without an upper plateau (Mereu et al., 2011; Hoving & Robison, 2017). Exponential growth has been hypothesized to occur as a strategy in semelparous deep-sea organisms to increase fecundity by having the largest increase in size at the end of life (Herring, 2001). This hypothesis, however, does not provide a mechanistic explanation of the processes underlying accelerating growth with size. A physiological explanation for this pattern may lie in the behaviour of *Histioteuthis* species, where they tend to move to deeper ocean regions as they grow in size (Quetglas et al., 2010). Inhabiting larger depths has been shown to reduce metabolic costs in cephalopods in terms of oxygen consumption per gram biomass (Seibel et al., 1997; Seibel, 2007). This provides a relative growth advantage to individuals who move deeper, as they 'pay' less metabolic maintenance costs compared to similar-sized individuals at shallower depths. Alternatively, the lack of an upper plateau in growth could be explained by the undersampling of the largest size classes in survey data. For example, the handful of *H. reversa* females with spent gonads found at the surface have been much larger than the multitude of maturing females sampled by trawler surveys (141 -230 mm versus 45-120 mm)(Quetglas et al., 2010). Growth curves fitted to such imbalanced data likely overestimate growth rates of individuals in the upper size range. Identifying the physiological and ecological mechanisms that underly the growth patterns observed in *H. reversa* forms the starting point to understand maturation patterns, and ultimately the reproductive output of deep-sea squid populations.

Reproduction in *Histioteuthis* is thought to be seasonal as trawler surveys find clear periodical peaks in the number of individuals with mature gonads caught (Jereb & Roper, 2010; Quetglas et al., 2010). The underlying mechanism of this seasonal reproduction remains unknown, however. Individuals might achieve maturation body size earlier in the year but postpone ripening of the gonads to synchronously reproduce coinciding with optimal conditions, as observed in several fish and squid species (Asoh & Yoshikawa, 2002; Takemura et al., 2010; Van Noord, 2020). Alternatively, there might be continuous reproduction by different cohorts of squid year-round, but only a single cohort of offspring dominates

and outcompetes previous cohorts due to hatching under optimal conditions. This latter, intra-specific competition-driven phenomenon, is known as single-cohort cycles (Persson et al., 1998), and has large impacts on population regulation. Single-cohort cycle dynamics regulate the population and cause alternations between the presence of juvenile and adult individuals. This strong signature in population dynamics was described previously for fish (both in lakes and open marine systems, (De Roos et al., 2003; Murdoch et al., 2002) as well as for antarctic krill (Ryabov et al., 2017). Improving our understanding of how growth and ecological conditions affect reproduction in *Histioteuthis* is therefore key to understanding their population regulation.

Here we use available empirical data to develop a size-structured population model of the hyperabundant deep-sea squid species *H. reversa*. We use this theoretical model to mechanistically understand the causes of empirical observations on individual growth and maturation in deep-sea squid, as well as the population level dynamics emerging from these individual level processes. We additionally seek to understand how population dynamics are affected by seasonality in resource dynamics, and how prey populations of deep-sea squid respond to predation by higher trophic levels. We use the deep-diving cetaceans *Grampus griseus* and *Ziphius cavirostris* as model cetacean predators of *H. reversa*. These species co-occur and are known to forage on *H. reversa* and target distinct depth ranges (Visser et al., 2021). The outcomes from our study provide new fundamental insights into the population ecology of one of the most abundant and trophically important species groups in pelagic deep-sea ecosystems.

6.2 Material and methods

6.2.1 Model summary

We model the *H. reversa* population using a size-structured population model that describes dynamics based on the individual level processes of growth, reproduction, and mortality. (de Roos & Persson, 2013b). Our size-structured modeling approach only considers the dynamics of the females in the population. Individual *H. reversa* develop through three life stages: paralarvae, juveniles, and reproducing adults. The egg-stage of *H. reversa* is not modeled in any temporal detail, but egg mortality, and energy conversion efficiency from egg to hatchling paralarvae stage are accounted for. Paralarvae forage on zooplankton resources in the upper water column and switch to forage on nekton in the deep-scattering layer when reaching juvenile size. As juveniles increase in size they move to deeper habitats where a second nekton resource at the benthic boundary layer becomes available. During development, juveniles allocate an increasing fraction of their ingested energy to the production of gonads. Once the gonads of an individual have reached a threshold level, they transition to the reproducing adult stage and immediately release all their eggs. At this stage individuals stop feeding and reproduce only, eventually dying of starvation post-reproduction. Below, we provide a mathematical description of the life history functions in our model and the underlying biological assumptions in relation to individual growth, mortality, and reproduction. Model parameters can be found in Table 1.

6.2.2 Life history functions and assumptions

We model three life stages that are distinguished based on their body size. Paralarvae feed upon a zooplankton resource with density R_1 . Paralarvae switch to the juvenile stage at a body mass S_j . Juveniles initially forage on nekton resource R_2 , and gradually shift to foraging on nekton resource R_3 as they grow larger. After reaching a reproductive buffer mass of β_{\min} , we classify individuals as adults. We assume that adults immediately release their reproductive buffer after reaching the reproduction threshold. Due to the cessation of feeding adults die of starvation post-reproduction. Several of the life history functions are dependent on the relative depth, ρ , inhabited by an individual. This relative depth depends on individual body size s , and follows a continuous, piecewise-differentiable, sigmoid function that ranges between 0 and 1 (van Kooten et al., 2004). A ρ value of 0 indicates that an individual remains at the surface and a value of 1 indicates that individuals have reached the maximum depth.

$$\rho(s) = \begin{cases} 0, & \text{for } f(s) \leq 0, \\ \frac{1}{6}f(s)^3, & \text{for } 0 < f(s) \leq 1, \\ -\frac{3}{2}f(s) + \frac{3}{2}f(s)^2 - \frac{1}{3}f(s)^3 + \frac{1}{2}, & \text{for } 1 < f(s) \leq 2, \\ \frac{9}{2}f(s) - \frac{3}{2}f(s)^2 + \frac{1}{6}f(s)^3 - \frac{7}{2}, & \text{for } 2 < f(s) \leq 3, \\ 1, & \text{otherwise.} \end{cases} \quad (6.1)$$

Individuals start migrating at a body size of $s = S_{\text{shallow}}$, and reach half the maximum depth at a body size of $s = S_{\text{deep}}$. In this equation, the function $f(s)$ equals:

$$f(s) = \frac{3}{2} \left(\frac{s - S_{\text{shallow}}}{S_{\text{deep}} - S_{\text{shallow}}} \right) \quad (6.2)$$

Food intake

Individuals forage on multiple resources with densities R_i ($i = 1, 2, 3$) following a holling type II functional response. Paralarvae, with body mass $s < S_j$, feed upon zooplankton (R_1) only, while juveniles can feed upon two nekton resources (R_2 , and R_3) depending on their inhabited depth $\rho(s)$. We assume that adults do not feed. Mass-specific food intake, $I(s, R_1, R_2, R_3)$, equals

$$I(s, R_1, R_2, R_3) = \begin{cases} \frac{aR_1}{1 + ahR_1}, & \text{if } S_b \leq s < S_j, \\ (1 - \rho(s)) \left(\frac{aR_2}{1 + ahR_2} \right) + \rho(s) \left(\frac{aR_3}{1 + ahR_3} \right), & \text{if } S_j \leq s \text{ \& } \beta < \beta_{\min}, \\ 0, & \text{if } S_j \leq s \text{ \& } \beta \geq \beta_{\min}. \end{cases} \quad (6.3)$$

In this equation, a represents the mass-specific attack rate and parameter h the handling time.

Biomass production

Ingested food is assimilated with efficiency σ . Individuals use assimilated energy first to pay their mass-specific maintenance costs. We assume that these maintenance costs decrease proportionally with the inhabited relative depth, $\rho(s)$. The mass-specific net-biomass production rate of an individual, $\nu(s, R_1, R_2, R_3)$, is then given by the difference between energy intake and maintenance costs following

$$\nu(s, R_1, R_2, R_3) = \sigma I(s, R_1, R_2, R_3) - \tau(1 - \rho(s)) \quad (6.4)$$

We also examine the scenario in which there is no decrease in mass-specific maintenance costs with increasing inhabited relative depth, in which equation 4 reverts to $\sigma I(s, R_1, R_2, R_3) - \tau$. When energy uptake is not enough to pay maintenance costs ($\sigma I(s, R_1, R_2, R_3) < \tau(1 - \rho(s))$), individuals experience starvation mortality, μ_s , equal to $-\nu(s, R_1, R_2, R_3)$ on top of their background mortality (see section on mortality below). Note that due to our assumption of non-feeding adults, adults always starve with a per capita rate of $\tau(1 - \rho(s))s$. We use the variable ν^+ to model how mass-specific net biomass production links to energy investment in structural body mass and reproductive tissue. Because we assume individuals cannot shrink, ν^+ equals zero when mass-specific net biomass production is negative, and ν^+ equals ν when it is positive:

$$\nu^+(s, R_1, R_2, R_3) = \begin{cases} \nu(s, R_1, R_2, R_3), & \text{if } \nu(s, R_1, R_2, R_3) > 0, \\ 0, & \text{if } \nu(s, R_1, R_2, R_3) \leq 0. \end{cases} \quad (6.5)$$

As individuals transition from the paralarval to the juvenile stage and grow towards maturation, they invest a decreasing proportion, κ , of net biomass production into somatic growth, and an increasing proportion, $(1 - \kappa(s))$, into the reproductive buffer. The fraction κ is modeled as a smoothly decreasing function of body size following

$$\kappa(s) = 1 - 3\xi^2(s) + 2\xi^3(s). \quad (6.6)$$

In this equation, ξ equals

$$\xi(s) = \frac{s - S_m}{S_{\max} - S_m}, \quad (6.7)$$

where parameter S_m equals minimum maturation body size and parameter S_{\max} the theoretical maximum body size individuals can reach.

Fecundity

When the reproductive buffer of an individual reached the level β_{\min} , the reproductive storage of an individual is immediately transformed into newborn paralarvae. The number of paralarvae is given by

$$F = \frac{\beta}{S_b} \theta \quad (6.8)$$

Where θ indicates a conversion of efficiency to account for mortality during the egg stage due to predation and or disease.

Mortality

Background mortality rates for *H. reversa* are life-stage specific, with a high constant background mortality for paralarvae in the upper water column, and a lower mortality rate for juveniles. In addition to background mortality, individuals may experience starvation mortality, $\mu_s(s, R_1, R_2, R_3)$, and size-selective mortality imposed by deep-diving cetaceans. Total mortality rate is given by

$$\mu(s) = \begin{cases} \mu_b + \mu_s(s, R_1, R_2, R_3), & \text{if } S_b \leq s < S_j \\ \mu_j + \mu_s(s, R_1, R_2, R_3) + \mu_g, & \text{if } S_j \leq s < S_g \\ \mu_j + \mu_s(s, R_1, R_2, R_3) + \mu_c, & \text{if } S_g \leq s < S_c \end{cases} \quad (6.9)$$

In this equation, μ_g equals the additional predation mortality imposed by *G. griseus* and μ_c the additional mortality imposed by *Z. cavirostris*. We assume that *G. griseus* feeds upon individuals with a body mass between S_j and S_g , and *Z. cavirostris* on individuals with a body mass between S_g and S_c . Hence, the two predators are specialized on two non-overlapping size ranges.

6.2.3 Population dynamics

Since adults release all their eggs at once, all offspring produced at a reproductive event are grouped into a single cohort and assumed to experience identical environmental conditions and hence to develop at the same rate. The dynamics of each cohort $i \in \mathbb{N}$ can be followed numerically by integrating a set of three ODEs. These ODEs keep track of the number of individuals in the cohort, c_i , their body mass, s_i , and their reproductive buffer, β_i . When a cohort of adults reproduces, a new cohort of paralarvae is added to the population, which results in three additional differential equations describing the population dynamics. Cohorts pass through three life stages: the paralarval (L), juvenile (J), and adult stage (A). Transitioning between life stages is conditional on cohort size (s_i) and cohort buffer (β_i). The dynamics of the density, body mass, and reproductive buffer in paralarvae and juveniles depend on the amount of food they encounter and can be described by the following set of ODEs:

$$\begin{aligned} &\text{For } S_b \leq s_i < S_j \\ &\begin{cases} \frac{dc_i}{dt} = -\mu(s_i, R_1)c_i, \\ \frac{ds_i}{dt} = \nu^+(s_i, R_1)s_i, \\ \frac{d\beta_i}{dt} = 0. \end{cases} \end{aligned} \quad (6.10)$$

$$\begin{aligned} &\text{For } S_j \leq s_i \ \& \ \beta_i < \beta_{\min} \\ &\begin{cases} \frac{dc_i}{dt} = -\mu(s_i, R_2, R_3)c_i, \\ \frac{ds_i}{dt} = \kappa(s_i)\nu^+(s_i, R_2, R_3)s_i, \\ \frac{d\beta_i}{dt} = (1 - \kappa(s_i))\nu^+(s_i, R_2, R_3)s_i. \end{cases} \end{aligned} \quad (6.11)$$

Whenever the reproductive buffer of the oldest juvenile cohort with index $i = m$ reaches the threshold value $\beta_i = \beta_{\min}$, at time $t = t_{\text{repro}}$, a reproduction event occurs. At the moment just after a reproductive event t_{repro}^+ , this juvenile cohort becomes an adult cohort, equal in number and size to the cohort just before the reproductive event t_{repro}^- . These adults reproduce immediately and a new cohort with index 0 is formed from the biomass stored until just before reproduction t_{repro}^- . The buffer of the reproducing cohort is set to 0 and all cohorts (both reproducing and non-reproducing) are renumbered. The changes are described by the following sets of equations:

$$\begin{cases} c_0(t_{\text{repro}}^+) = \theta \frac{\beta_m(t_{\text{repro}}^-) c_m(t_{\text{repro}}^-)}{S_b}, \\ s_0(t_{\text{repro}}^+) = S_b, \\ \beta_0(t_{\text{repro}}^+) = 0. \end{cases} \quad (6.12)$$

For $i \neq m$

$$\begin{cases} c_{i+1}(t_{\text{repro}}^+) = c_i(t_{\text{repro}}^-), \\ s_{i+1}(t_{\text{repro}}^+) = s_i(t_{\text{repro}}^-), \\ \beta_{i+1}(t_{\text{repro}}^+) = \beta_i(t_{\text{repro}}^-). \end{cases} \quad (6.13)$$

For $i = m$

$$\begin{cases} c_{m+1}(t_{\text{repro}}^+) = c_m(t_{\text{repro}}^-), \\ s_{m+1}(t_{\text{repro}}^+) = s_m(t_{\text{repro}}^-), \\ \beta_{m+1}(t_{\text{repro}}^+) = 0. \end{cases} \quad (6.14)$$

The spent adults no longer feed and their dynamics are thus no longer dependent on food densities. Adults only starve and their dynamics can be described by the following set of ODEs:

$$\begin{cases} \frac{dc_i}{dt} = -\mu(s_i)c_i, \\ \frac{ds_i}{dt} = 0, \\ \frac{d\beta_i}{dt} = 0. \end{cases} \quad (6.15)$$

6.2.4 Resource dynamics

Our model includes three unstructured resources expressed in grams per unit volume. The biomass dynamics of all three resources are described by a turnover rate δ_i , maximum resource density $R_{i,\text{max}}$, and consumption by *H. reversa* life stages (eqn. 19-21). The zooplankton resource dynamics can be expressed as:

$$\frac{dR_1}{dt} = \delta_1 R_{1,\text{max}} \left(1 + \psi \sin \left(2\pi \frac{t}{365} \right) \right) - \delta_1 R_1 - \sum_{i|s_i < S_j} c_i s_i \left(\frac{aR_1}{1 + ahR_1} \right) \quad (6.16)$$

Where the summation term models the resource ingestion over all paralarval cohorts i , and the zooplankton resource productivity is seasonal and modeled through a sinusoidal function with a period of 365 days and amplitude ψ ranging from $0 < \psi < 1$. Ecologically, a ψ value of 0 means there is no seasonality and resource availability is spread evenly over the year. In contrast, ψ values ranging between $0 < \psi < 1$ indicate a range of weak to strong seasonality where peak resources are available in an increasingly narrow time window within the year. The total resource production within a year in the absence of consumers is the same irrespective of the value of ψ . The nekton resources R_2 and R_3 are assumed to be aseasonal and their dynamics can be expressed as:

$$\frac{dR_2}{dt} = \delta_2(R_{2\max} - R_2) - \sum_{i|s_i \geq S_j} c_i s_i \left(1 - \rho(s) \left(\frac{aR_2}{1 + ahR_2} \right) \right) \quad (6.17)$$

$$\frac{dR_3}{dt} = \delta_3(R_{3\max} - R_3) - \sum_{i|s_i \geq S_j} c_i s_i \rho(s) \left(\frac{aR_3}{1 + ahR_3} \right) \quad (6.18)$$

Where the summation term models the ingestion of the resource over all juvenile cohorts i .

6.2.5 Model parameterization and analysis

We parametrized the life history functions for *H. reversa* based on a review of scientific literature (Table 1). We were able to derive most life history parameters directly from published empirical studies on *H. reversa* (References in Table 1). When this information was not available, we used studies of closely related species (*H. hoylei*, *H. heteropsis*, *H. bonelli*), where possible. The life history functions and the set of ODEs describing the dynamics of *H. reversa* life stages were coded in C programming language and numerically integrated using the escalator boxcar train (EBT-train) method (De Roos et al., 1992), using the EBT-tool (de Roos, 2023). We ran time-series of *H. reversa* population dynamics over 1,000,000 time steps, where each individual time step represents one day. Each model run started with an initial 6 differently-sized cohorts each containing 100 individuals. After ensuring that the population dynamics had reached a stable attractor, we extracted the final 3,000 time-steps from the model output to visualize population level abundance, biomass dynamics, and individual (cohort) growth. We ran the model with and without depth-dependent metabolic costs to examine its effect on population dynamics and individual growth. Next, we examined how sensitive population and individual level dynamics were to changes in life history and resource parameters, by means of bifurcation analysis. To this end we ran an iterative time-series analysis with intervals of 100,000 time steps. At the start of each new iteration we systematically increased or decreased the value of the bifurcation parameter with a marginal amount (plus or minus 0.001 as step-size). We included parameters pertaining to resource productivity ($R_{1\max}$, $R_{2\max}$, $R_{3\max}$), background mortality (μ_b , μ_j), depth migration (\bar{s}), resource seasonality (ψ), and size-selective predation mortality (μ_g , μ_c), in the bifurcation analysis.

Table 6.1: Parameters and default values for the *H. reversa* model. Calculations to convert the values and units as presented in the source references to those listed in the table are presented in Supplementary Information I.

Parameter	Default value	Unit	Description	Source species & Ref.
δ_i	0.1	day ⁻¹	Resource turnover rate	Modelling assumption (1998)
$R_{1max}, R_{2max}, R_{3max}$	Variable	g · L ⁻¹	Maximum biomass density of resource 1,2, and 3	-
σ	0.42	-	Conversion efficiency	<i>I. illecebrosus</i> (1981)
a	0.6	L · g ⁻¹ · day ⁻¹	Maximum mass-specific attack rate	Modelling assumption (2017)
h	1	day	Mass-specific handling time	Modelling assumption (2017)
τ	0.1	day ⁻¹	Mass-specific maintenance rate (depth dependent)	<i>H. hoylei</i> , <i>H. heteropsis</i> (1997; 1972; 1986)
μ_b	0.028	day ⁻¹	Background mortality rate paralarvae	<i>H. reversa</i> , <i>H. bonelli</i> (1996; 2011)
μ_j	0.016	day ⁻¹	Background mortality rate juveniles & adults	<i>H. reversa</i> , <i>H. bonelli</i> (1996; 2011)
θ	0.5	-	Egg to offspring energy conversion efficiency	Modelling assumption (1998)
β_{min}	76.8	g	Minimum reproductive buffer biomass	<i>H. reversa</i> (2001)
S_b	0.0016	g	Paralarvae size at birth	<i>H. reversa</i> (2001; 2010)
S_j	2.1	g	Paralarvae to juvenile transition size	<i>H. reversa</i> (2010; 1998)
S_{max}	811	g	Maximum size	<i>H. reversa</i> (2010; 2010)
S_m	93	g	Maturation size	<i>H. reversa</i> (2010; 1998)
$S_{shallow}$	2.1	g	Size at start depth migration	<i>H. reversa</i> (2010; 1998)
S_{deep}	405	g	Size at half the maximum depth migration	<i>H. reversa</i> (2010)

6.3 Results

Our theoretical model predicts similar growth patterns and longevity as observed in empirical studies. At the population level, dynamics are characterized by cohort cycles, and dynamics are most strongly affected by paralarval mortality and seasonality while the metabolic benefit of moving deeper with increasing size has no impact at either the individual or population level in terms of growth and reproduction. Finally, we find evidence for a potential emergent allee effect between multiple deep-diving cetacean predators. We now discuss each of these findings in detail, starting from the individual level, moving to the population level, and finally discussing community-level outcomes through size-selective predation.

6.3.1 Individual growth

Individuals show an exponential-like growth curve (Fig. 1a). However, rather than a constant mass-specific growth rate as expected under true exponential growth, we find an underlying pattern of a sharp decrease in mass-specific growth early in life (paralarval stage, Fig. 1b), followed by an increase in mass-specific growth with increasing juvenile size (Fig. 1c). The sharp drop in mass-specific growth during the early life stage is due to high resource competition among paralarvae. Conversely, the sharp increase in mass-specific growth with increasing juvenile size is related to release from intraspecific competition by gaining access to the secondary nekton resource. We find that only under very extreme and limited ecological conditions the pattern of an increase of mass-specific growth at larger juvenile sizes breaks. Specifically, only a combination of high paralarval mortality, low nekton resource productivity in the deep-scattering layer, and an early switch at which juveniles start to utilize this resource results in a qualitative reversion where mass-specific growth decreases with increasing size (Supplementary Figure 2).

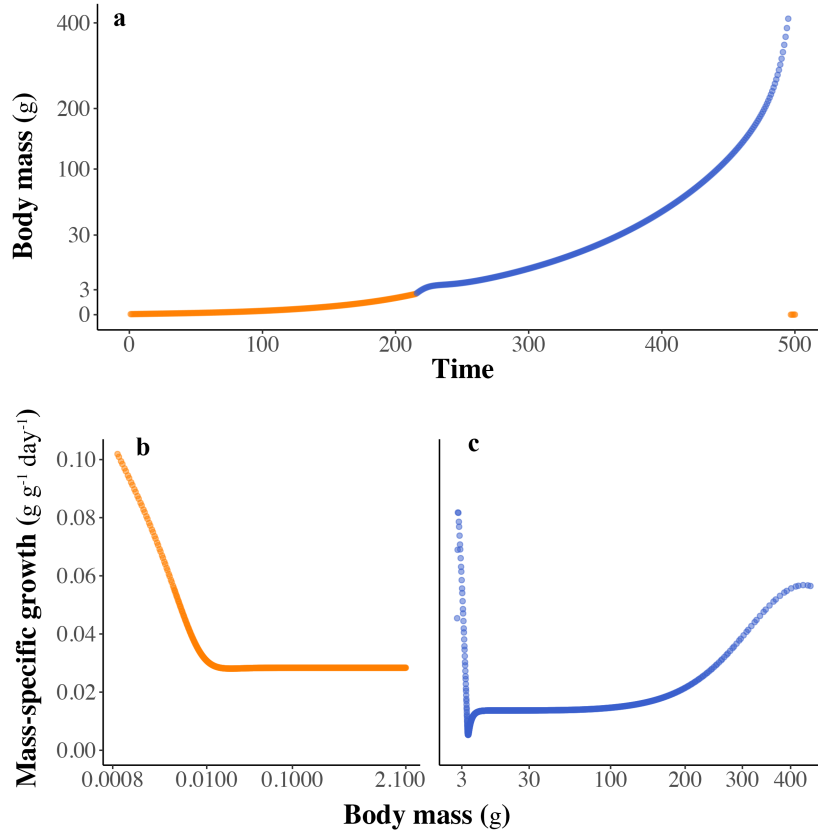


Figure 6.1: Individual growth curve (a) and mass-specific growth rate split out for paralarvae (orange, b) and juveniles (blue, c) for default parameters (Table 1). Mass-specific growth rate was calculated as the change in body mass between time steps t and $t + 1$ divided by total body mass at time t . For visualization purposes, a square root scaling was applied to the y-axis of (a), a log scaling to the x-axis of (b) and a square-root scaling to the x-axis of (c).

6.3.2 Population dynamics

Population dynamics of *H. reversa* are characterized by single cohort cycles (Fig. 2). During these cohort cycles there is a high reproductive inflow into the paralarval life stage (Fig. 2a). The high densities of paralarvae lead to intense resource competition for zooplankton (Fig. 2c) among individuals and an initially steep decline in paralarval densities due to high starvation mortality. After this period of steep decline in paralarval density the competition among remaining individuals no longer imposes starvation mortality. However, competition among remaining individuals still sufficiently suppresses the zooplankton resource density to lead to a bottleneck in the late paralarval life stage (Fig 2b,c). In a bottleneck individuals grow very slowly due to competition limiting individual energy intake. This results in population-level biomass leveling off in a certain lifestage, e.g. the periodical near horizontal orange line of paralarval biomass density in Fig. 2b. As individuals eventually transition to the juvenile life stage, they initially grow very fast (Fig 1c) due to the high density of the first nekton resource (Fig 2c), resulting in a fast increase in juvenile biomass (Fig 2b). However, the juveniles almost immediately suppress the density of the first nekton resource in the the deep scattering layer to just above the critical resource density (dotted line Fig 2c), again resulting in a bottleneck where individual growth is very slow (Fig 1c). The bottleneck is lifted once

individuals start to move deeper and gain access to the second nekton resource at the benthic boundary layer (Fig. 2b). The densities of remaining large juveniles that have made it to this stage is low (Fig. 2a), and the surviving juveniles can quickly increase in biomass until they reproduce (Fig. 2b), after which the cycle starts again. These internal, paralarvae driven cohort cycles in *H. reversa* lead to periodicity in maturation and reproduction in the absence of any seasonal cyclicality in the resource environment.

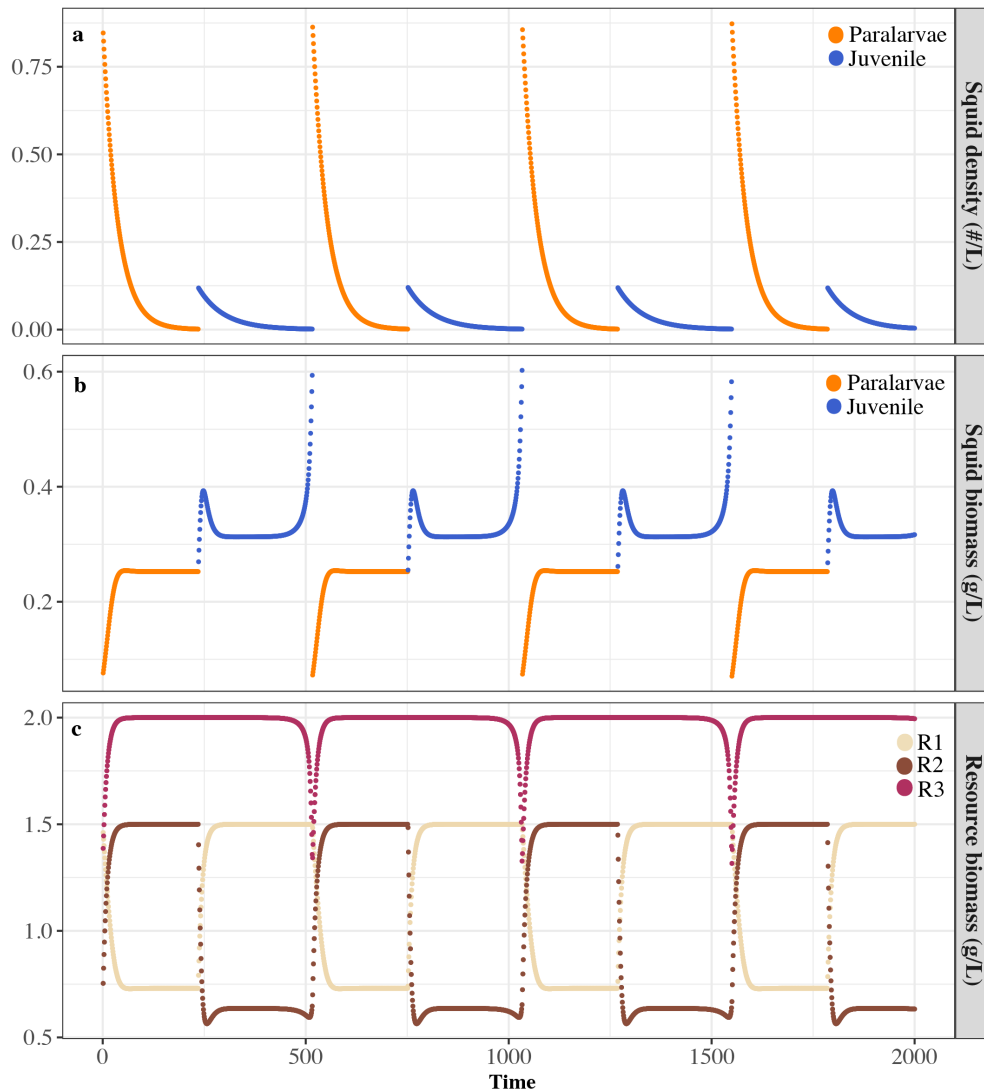


Figure 6.2: Population dynamics of squid density (a), squid biomass density (b), and resource biomass density (c). Population dynamics are characterized by single cohort cycles with bottlenecks in the paralarval stage and early juvenile stage due to resource competition. Juvenile cohorts (blue line(Fig. 2b) suppress the first nekton resource (brown line Fig. 2c) to just above the critical energy density required to cover metabolic costs (black dotted line). The bottleneck is lifted once juveniles gain access to the secondary nekton resource (red line Fig. 3c).

The formation of single cohort cycles in *H. reversa* is driven by intense resource competition in the early life stage following the high reproductive inflow into the population. In the initial transient conditions of our time-series there are multiple overlapping cohorts

(results not shown). However, as the reproductive output of the population is very high, intermediate cohorts suppress the resource density to below the levels to cover their own energetic costs. Over time these cohorts 'outcompete' themselves, gradually decreasing in density due to starvation mortality until the population reaches stable attractor dynamics in which these intermediate cohorts disappear and there is only a single dominant cohort remaining.

Increasing paralarval mortality in *H. reversa* decreases paralarval biomass density and leads to initial increases in juvenile biomass density (Fig. 3a). This is because increased paralarval mortality reduces competition among paralarvae, leading to faster development and earlier transition to the juvenile life stage (Fig. 3b). As fewer individuals transition to the juvenile life stage, juveniles can grow faster and age at maturation is reduced (Fig. 3b). At the population level, the reproductive output is increased (Fig. 3c), but this effect is not sufficient to compensate for the decreasing population biomass density under increased paralarval mortality.

Assuming that metabolic costs decrease with increasing depth does not affect the population dynamics of *H. reversa*. (Supplementary Figure 5). Similarly, individual growth curves are similar in both situations (Supplementary Figure S5). This suggests that ecological conditions experienced between different life stages, and or different depths within a life stage, such as differences in mortality or resource feedbacks, are more important in shaping the population-level dynamics of *H. reversa* than individual-level physiological responses to depth. This provides evidence that the large increase in size near the end of life is due to access to new resources rather than to reduced metabolic maintenance.

6.3.3 Effects of seasonality in zooplankton production in surface waters on population dynamics

We find that strong seasonality in zooplankton resource productivity in surface waters has a high impact on the population biomass in *H. reversa* life stages (Fig. 4a). Under strong seasonality ($0.5 < \phi < 0.9$), the population biomass switches from being juvenile to paralarvae dominated, with an overall decrease in total population biomass. The high seasonality in zooplankton productivity results in high mortality of paralarvae born outside peak zooplankton conditions. This strongly reduces the competition between remaining paralarvae, leading to fast growth and strong reduction in time spent in the paralarval stage (Fig. 4b). However, reduced competition between paralarvae now leads to strong resource competition among larger juveniles. The increased competition between larger juveniles increases age at maturation (4c), and reduces the reproductive output of the population (4d). Time series comparisons of aseasonal and seasonal population dynamics are shown in Supplementary Figure 6.

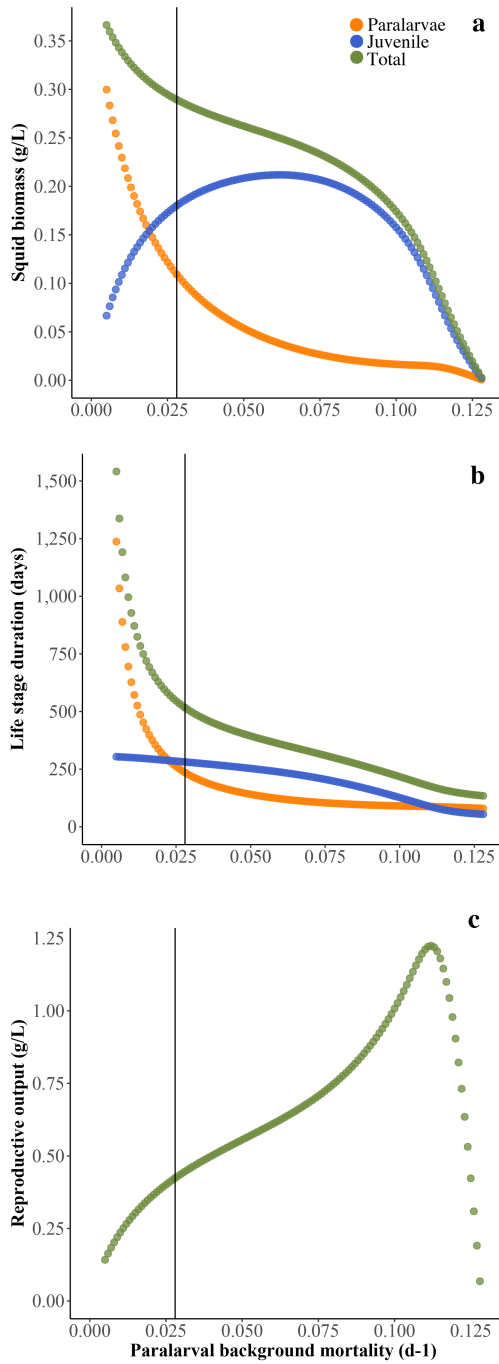


Figure 6.3: Average biomass of the three life stages (panel a), duration of each life stage (b), and reproductive output (c) as a function of the background mortality rate of paralarvae. The vertical line in each panel indicates the default background paralarvae mortality rate. Apart from changing paralarval mortality all other default parameters were kept the same (table 1).

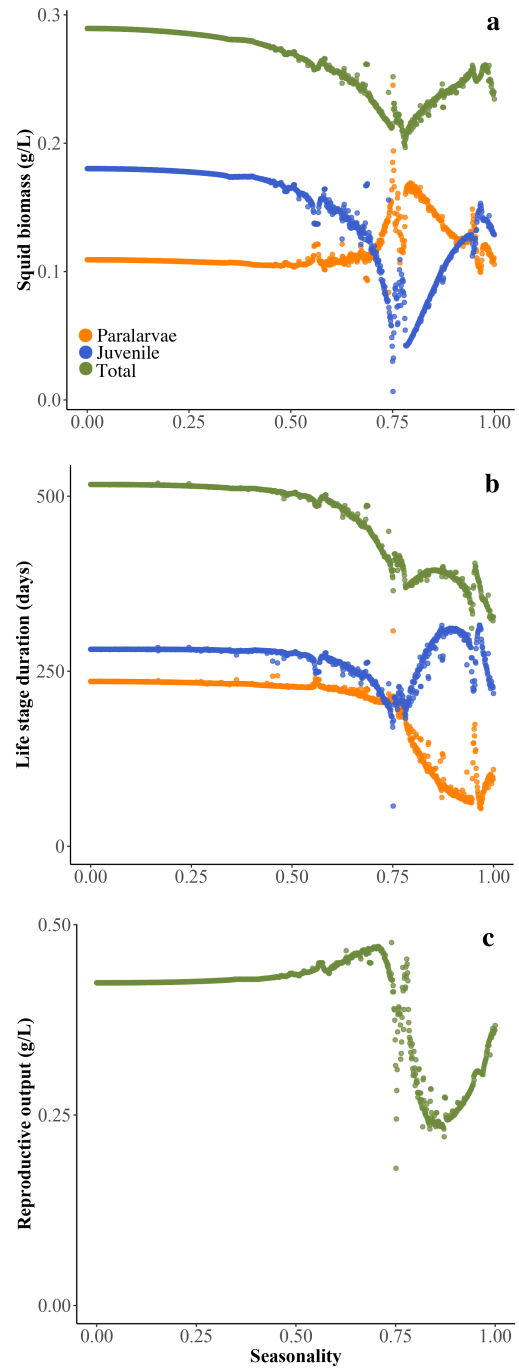


Figure 6.4: Average biomass of the three life stages (panel a), duration of each life stage (b), and reproductive output (c) as a function of seasonality in paralarvae resource productivity. The vertical line in each panel indicates the default background paralarvae mortality rate. Apart from changing paralarval mortality all other default parameters were kept the same (table 1).

6.3.4 Effects of depth-selective predation on population dynamics and predator diversity

Size-selective predation can result in emergent facilitation between deep-diving cetacean predators (Fig. 5). The effects of size-selective predation and the potential for emergent facilitation between predators are consistent across seasonal and aseasonal environments. Predation by *Z. cavirostris* on large juvenile *H. reversa* at larger depths leads to increases in the biomass of smaller juvenile *H. reversa* inhabiting shallower depths targeted by *G. griseus*. This positive effect persists over a large range of *Z. cavirostris* predation pressure. In contrast, the biomass of large juveniles is directly suppressed by increased size-selective predation by *Z. cavirostris* (Fig. 5a, orange line). As a result, fewer large individuals are maturing and reproducing, and there is less biomass inflow into the paralarval stage (Supplementary figure 6). The lower competition experienced in the paralarval stage relieves the bottleneck experienced in the paralarval life stage, resulting in faster growth and earlier transition to the juvenile stage. Now biomass accumulates in the small juvenile stage, resulting in a competition bottleneck. Due to the high biomass of small juveniles, growth slows down, resulting in a longer period in this size-range. Predators such as *G. griseus* foraging on this size class will therefore have more prey available.

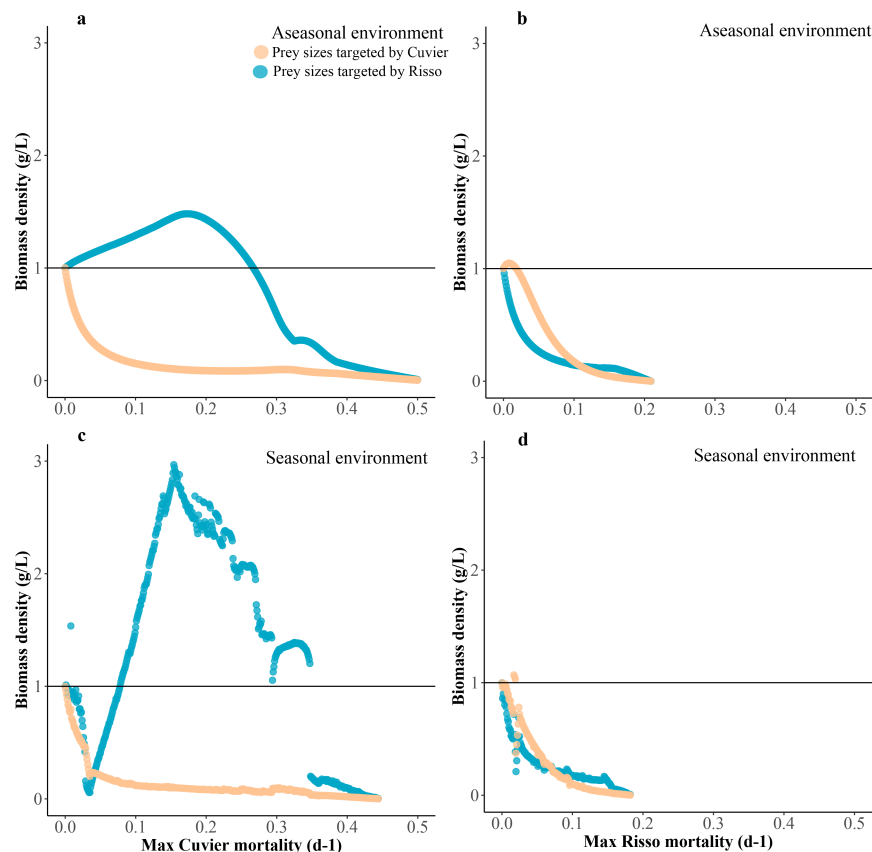


Figure 6.5: Scaled average biomass density of squid prey size classes preferred by Cuvier’s beaked whale (orange-pink) and Risso’s dolphin (blue), as a function of predation pressure of either predator in aseasonal (a,b) and seasonal (c,d) resource environments. The scaling of average prey biomass density is relative to the average prey biomass density when there is no predation by either predator (horizontal line at 1.0 on the y-axis). Emergent allee effects occur when prey-biomass density exceeds 1.0 for a predator as a function of increased predation pressure by another predator.

The scope for emergent facilitation by *G. griseus* of *Z. cavirostris* is limited to a small parameter range. Low predation pressure on small juvenile *H. reversa* by *G. griseus* at shallower depths leads to a small increase in the biomass of large juvenile *H. reversa* at deeper depths (Fig. 5b). Thus, in this limited range emergent facilitation of *Z. cavirostris* by *G. griseus* can occur. However, this positive effect on large juvenile *H. reversa* biomass density quickly becomes negative when the predation pressure by *G. griseus* increases. Biomass density of small-juvenile *H. reversa* is directly suppressed by size-selective predation by *G. griseus*. As a result, there are less small juvenile *H. reversa* surviving and growing to maturation size, but they reach this size faster than in the absence of *G. griseus* predation. As reproductive output by large juvenile *H. reversa* is maintained the size-selective predation on small juvenile *H. reversa* instead increases the existing competition bottleneck in the paralarval life stage (Supplementary figure 7). This results in an overall reduction of total population biomass compared to the scenario where there is no size-selective predation by *G. griseus*.

6.4 Discussion

We show that population regulation in the hyperabundant semelparous deep-sea squid *H. reversa* is primarily driven by conditions experienced in the paralarval stage in the upper water column (research aim i). Our model predictions align with empirical observations for the individual-level exponential growth curve and increasing mass-specific growth with increasing size (research aim ii). The exponential like growth curves can be explained by changes in mass-specific growth in relation to resource feedbacks. As a result of these resource feedbacks, cohort cycles emerge at the population-level with an apparent seasonal periodicity in maturation. These cohort cycles are fully driven by internal dynamics rather than seasonality in the resource environment. We further find that resource feedbacks overrule individual physiological benefits of depth migration in shaping the growth of individuals and emergent population dynamics. Finally, seasonality and size-specific predation can alter population regulation in *H. reversa* by relieving bottlenecks in the paralarval life-stage. Size-selective predation can further lead to emergent facilitation between multiple predator species.

The single cohort cycles we find in *H. reversa* typically occur in ecological systems where organisms share a single resource throughout the life-cycle and foraging efficiency scales with body size (Persson et al., 1998). Classic examples from empirical systems include freshwater lake systems such as zooplanktivorous *Cisco* fish (Jarvi, 1930; Salojaervi, 1987; Hamrin & Persson, 1986; Helminen & Sarvala, 1994), and phytoplanktivorous *Daphnia* (McCauley & Murdoch, 1987; McCauley et al., 1988; McCauley, 1993; Murdoch & McCauley, 1985). In *Cisco* fish, small recruits entering the population suppress the zooplankton resource to a level where older cohorts of larger *Cisco* can no longer take in sufficient resources to cover their energetic costs for metabolic maintenance (Persson et al., 1998). This leads to the starvation of older cohorts due to asymmetric competition and the rapid growth and emergence of a single dominant cohort (De Roos et al., 2003). The life history of *H. reversa* in this study is simpler than in these classic studies because we have no scaling in foraging efficiency with body size, but it is also more complex

as *H. reversa* undergo multiple ontogenetic diet shifts over their life history. Therefore we find a slightly different origin for the emergence of single-cohort cycles. When multiple cohorts of *H. reversa* are present in the population, the 'intermediate' cohorts gradually outcompete themselves by suppressing the resource density to below the critical level required to cover their energetic maintenance costs. This process continues until a single dominant cohort remains. It therefore seems that single-cohort cycles, rather than multi-cohort cycles, emerge, because *H. reversa* populations fall victim to their own reproductive productivity.

The life-stage specific bottlenecks we describe for *H. reversa* are a typical outcome of size-structured population models of species with ontogenetic niche shifts (de Roos & Persson, 2013b). Most animal species undergo some form of ontogenetic niche shifts, in which individuals specialize on different diets or habitats during their development to limit intraspecific competition between life stages (Werner & Gilliam, 1984; Nakazawa, 2015). Examples include discrete changes in morphology and resource use following metamorphosis in insects and amphibians (Ten Brink et al., 2019), or gradual changes in resource use with increasing body size in fish and reptiles (Anaya-Rojas et al., 2023; Aresco et al., 2015; Briones et al., 2012; Renones et al., 2002; Wallace & Leslie, 2008). The population growth of species undergoing ontogenetic niche-shifts is limited by one of two processes (1) the development of early life-stages, or (2) the suppression of reproduction in later life stages (Schreiber & Rudolf, 2008; Guill, 2009). These two forms of population regulation are referred to as 'development control' and 'reproduction control', respectively (de Roos & Persson, 2013b). The bottleneck we describe for paralarval *H. reversa* is typical for populations that are regulated through development control. Under development control resource availability in the early life stage is relatively low compared to later life stages, resulting in slow growth and long development times (Sun & de Roos, 2015). This fits the condition in our study where paralarvae have access to a single resource and juveniles have access to multiple resources. By imposing strong seasonality, the relative resource availability between paralarvae and juveniles changes while paralarval mortality increases. As a result, the system switches to being regulated by 'reproduction control' with a bottleneck in the juvenile stage. Size-selective predation on large maturing juveniles also switches the system to being regulated by reproduction control by limiting the number of reproducing individuals while simultaneously reducing the competition between newborn cohorts of paralarvae. The reproductive output of *H. reversa* is generally so high that only increasing paralarval mortality or maximum paralarval resource density does not switch the population regulation in the system (Fig 3a, Supplementary Figure 3a). These processes must be affected simultaneously for switches in population regulation to occur.

The responses of deep-sea squid populations to size-selective predation offer fundamental insights into the intricate trophic dynamics shaping species communities in the pelagic deep-sea. Our findings further carry distinct applied importance in evaluating the potential effects of anthropogenic activities on deep-sea ecosystems. Previous studies have demonstrated that biomass overcompensation in prey populations, as a response to predation, is crucial for the persistence of populations of deep-diving cetaceans under

increasing anthropogenic disturbances (Hin et al., 2023, 2021). While our study confirms that biomass overcompensation in preferred prey size classes can occur, it does so only indirectly through the presence of a second deep-diving cetacean predator targeting a second squid size class. This emergent facilitation between deep-diving cetaceans highlights the importance of maintaining diverse communities of apex predators in the pelagic deep-sea. Research has consistently shown that diverse communities of apex predators are key to maintaining ecosystem functioning, productivity, and diversity across trophic levels (Finke & Denno, 2004; Finke & Snyder, 2010; Ceulemans et al., 2021). Understanding the functioning of pelagic deep-sea ecosystems across trophic levels is urgently needed to predict the impacts of current and future anthropogenic activities. Most research on anthropogenic activities in the pelagic deep-sea has focused on the responses of seafloor organisms to deep-sea mining (Robison, 2009; Webb et al., 2010). However, a recent study by Stenvers et al. (Stenvers et al., 2023) demonstrates that organisms in the water column, such as deep-sea jellyfish, can also be negatively affected by mining plumes. Similarly, the noise associated with mining activities might reasonably be expected to negatively affect the foraging of deep-diving cetaceans. This illustrates the need to broaden the discussion on the impacts of anthropogenic activities on pelagic deep-sea ecosystems beyond the immediate effects on the seafloor (Drazen et al., 2020). Our study contributes important new insights in this context by mechanistically highlighting the links existing between ecological processes in the pelagic deep-sea and surface waters. These links are exemplified by the internal population regulation of deep-sea squid being driven by conditions experienced as paralarva in the upper water column. Additionally, the trophic interactions between deep-sea squid and their surface-breathing apex predators are crucial for the latter's long-term persistence under anthropogenic disturbance. We conclude that extending our approach to multiple trophic levels in future research will help pave the way to forming a general theory of the functioning of pelagic deep-sea ecosystems in an era of global change.

Chapter 7

General discussion

7.1 General discussion

“The most merciful thing in the world, I think, is the inability of the human mind to correlate all its contents. We live on a placid island of ignorance in the midst of black seas of infinity, and it was not meant that we should voyage far. The sciences, each straining in its own direction, have hitherto harmed us little; but some day the piecing together of dissociated knowledge will open up such terrifying vistas of reality, and of our frightful position therein, that we shall either go mad from the revelation or flee from the light into the peace and safety of a new dark age”, H.P. Lovecraft, The Call of Cthulhu (1928).

The paths to achieving generality in ecology have been argued to be as diverse as the organisms and systems under study (Fox, 2019). In the general introduction of this thesis, I outlined a diverse gradient of approaches, ranging from pattern-to process-based models, to achieve a general understanding of how and why marine populations fluctuate over time. The past decades have seen rapid developments mainly at the pattern side of this gradient. These developments have been fueled by the popularization of data-driven approaches for scientific discovery in an era of ‘big data’ (Callebaut, 2012). The promise is that data-driven approaches, such as machine learning models, will ultimately disentangle the entirety of correlative interdependencies ‘hidden’ in the vast sets of big data that characterize modern society and science. That such a ‘complete’ understanding of the interdependencies in the world has fascinated and frightened people long before the concepts of big-data or machine-learning existed is nicely illustrated by the opening lines of H.P. Lovecrafts horror tale, quoted at the start of this chapter. However, there are other questions that arise. For example, what would we ‘know’ about the world given the identification of the entirety of correlative interdependencies in data? Particularly when data is but an imperfect reflection of the world. In marine population ecology, would knowing all correlative interdependencies lead to a better understanding of how and why marine populations fluctuate over time? Would it allow us to better understand population responses to the rapid changes observed in the global environment? What are the roles of the other approaches that make up the pattern to process gradient in this respect, and how might they be improved? This issue is broad and complex, but highly relevant given the large dependency of human societies across the globe on marine populations for their nutrition and livelihoods. To guide the exploration of this issue, I formulated the following main research question.

How to best move forward to the goal of understanding how and why marine populations fluctuate over time in an era of big data and global change?

In the following sections, I will try to answer this question based on the outcomes of a range of studies conducted within the context of this PhD thesis. These studies cover both the gradient of modelling approaches, from fully data-driven to process-based, and different levels of biological organization, from the individual organismal level to the population and community level.

7.2 Data-driven discovery in marine population ecology

Part of the ‘big data’ in marine population ecology is formed by large, curated databases of multidecadal monitoring programs. These datasets typically contain the population abundance and biomass data of many different species populations and abiotic variables. This high dimensionality makes them an ideal testing ground for data-driven approaches to detect novel interdependencies. In chapter two and chapter three of this thesis I used two data-driven approaches to identify novel (a)biotic relationships in large monitoring datasets of benthic invertebrates and marine fish. In box 1, I then examined how to validate the outcomes of such data-driven discovery.

The outcomes of chapters two and three corroborate the suitability of machine-learning models to identify novel interactions in large ecological datasets. Chapter two further shows how machine-learning approaches can act as a precursor to formal hypothesis testing. For example, the deep-learning species distribution model (dl-sdm) developed in chapter two was able to tease apart different types of interspecific interactions between benthic invertebrate species in the Wadden Sea, while simultaneously accounting for the abiotic relationships of each species, and spatial autocorrelation. Before this study, abiotic preferences and interspecific interactions of benthic invertebrates in the Wadden Sea had only been studied in detail for a handful of well-known species. Furthermore, the effects of interspecific interactions, abiotic variables, and spatial autocorrelation tended to be studied separately, whereas the dl-sdm could account for all these variables simultaneously. Perhaps the most interesting outcome was the predicted patterns in the community level structuring of interspecific interactions, which suggested the community should be stable. We were subsequently able to confirm this hypothesis through formal statistical testing. In short, the modelled interactions provided new information on the correlative interdependencies between benthic invertebrates, while the structuring of these interactions yielded testable hypotheses on community stability.

Despite the ability to detect novel interdependencies in the datasets, it must be recognized that the actual ecological insights gained from the machine-learning models used in chapter two and three was very limited. Inferences remained at the level of correlative interdependencies between population trends of species and (a)biotic variables, without a clear link to the underlying mechanisms. We were, for example, unable to pinpoint whether negative interdependencies modelled between different benthic invertebrate populations were due to trophic interactions such as predation, or due to competitive exclusion. This is an important counterpoint to the argument that functional relationships are ‘embodied’ in the fitted machine-learning models (Yu et al., 2021). In contrast to our expectations, using further data-driven analysis to link the modelled interdependencies to species functional traits also did not yield these kinds of insights. The mismatch between the scale of the data collected in monitoring surveys and the level of desired inference could not be overcome by simply linking it to more different types of big data, i.e. large functional trait databases. Our outcomes show targeted experiments are still required to elucidate

underlying mechanisms and improve understanding of the functioning of complex species communities.

Peters et al. (2014) argue that when data-driven approaches feed into ‘classic’ scientific approaches for hypothesis testing this represents the fastest way towards ecological knowledge discovery in an era of big data. Chapter two is an example where data-driven approaches were combined with more classic statistical hypothesis testing. The next step in completing such a framework according to Peters et al. is to use the outcomes to guide future data-collection efforts. Thus, creating a feedback loop where newly collected data enters the data-driven model and the cycle repeats itself. However, there is an inherent risk in such data-driven feedback frameworks leading to biased decision making. For example, due to biases in input data. Such bias will propagate itself through the feedback loop and ‘infect’ the hypothesis testing, theory refinement and future data collection.

Biases in spatiotemporal resolution of population and environmental big data are a major challenge in marine systems. In terrestrial systems, population survey data can increasingly be matched with high resolution remote sensing data of key ecosystem variables such as precipitation, temperature, vegetation health, and vegetation density (Dobson et al., 2023). In marine systems there is less availability of such key environmental data at a global scale. Instead, studies are forced to rely more on oceanographic models and the long-term monitoring of water temperatures, salinity, and productivity collected by national research institutes or governments (Robison, 2009; Scales et al., 2017). Moreover, data on other potentially important variables, such as wave action, sediment transport, bed shear stress, and benthic habitats are generally not part of long-term monitoring. Typically, such information is sporadically produced for specific research projects and study sites. This means that often there is a disconnect between the temporal representation of the environmental data and the population data. This leads to biases in modelled interdependencies (Abdulwahab et al., 2022; Pacifici et al., 2019). Biases can be present in species population data too. For example, global databases of marine biodiversity show a lack of spatial accuracy in marine mammal observation data (Moudrý & Devillers, 2020). The combination of biases in global population and environmental data can lead to temporal and spatial mismatches when linking biotic and abiotic observations, creating biased datasets that will in turn affect modelled interdependencies. When data-driven approaches are used in a feedback loop this could lead to biased decision-making.

The consequences of data bias for data-driven decision making have been studied best in a socioeconomic context (Rudin, 2019). For example, bias in big data leads data-driven algorithms of lending firms and banks to charge higher interest rates for loans depending on gender, ethnicity, and zip-code (Alesina et al., 2013; Alliance NFH, 2014; Bertrand & Weill, 2021; O’neil, 2017). Higher interest rates in turn increase the probability of defaulting on loans, creating a negative feedback loop that will further strengthen existing bias. In the context of marine population ecology, data bias could equally lead to poor decision making. For example, data-driven approaches such as species distribution models are used for marine protected area planning and management (Ferrari et al., 2018;

Sánchez-Carnero et al., 2016; Guisan et al., 2013), projecting changes in the suitability of species habitats under climate change (Hazen et al., 2013; Willis-Norton et al., 2015) and reducing conflict between humans and marine wildlife along shipping routes (Redfern et al., 2013). Data bias could thus unintentionally lead to the prioritization of the wrong areas and habitats in efforts to conserve marine populations.

The inherent bias in data strengthens the need to validate modelled interdependencies by fully data-driven approaches. This runs counter to traditional thinking in data-driven research. Ideally, there should be as little a priori assumptions as possible on which variables to include and how to represent them. Given sufficient big data, the model should be able to extract the relevant dependencies from the large number of inputs and ‘transform’ them for bias correction, as the most unbiased representation maximizes predictive power. One way in which data-driven model outcomes are validated is by using local explanatory algorithms approximating modelled relationships. These algorithms typically apply a permutation design to approximate the contribution of each input variable to modelled predictions (Ribeiro et al., 2016), and some can reconstruct the shape of modelled interdependencies (Lundberg & Lee, 2017b). This means that modelled relationships of the data-driven approach can be compared to those ‘known’ based on scientific literature for validation. For example, in Chapter 2 the relationships between species abundance and abiotic variables such as sediment size and grain size corresponded with what was expected based on existing scientific literature. Therefore, there is more ‘trust’ in the newly modelled and previously unknown interdependencies identified by the model too.

A better approach, however, is to test the ‘robustness’ of modelled dependencies in machine-learning models through a sensitivity analysis in which input values are slightly perturbed (Hancox-Li, 2020). Unfortunately, it turns out that although the predictive performance of machine-learning models vary little when input data is slightly perturbed, the variable importance identified by explanatory algorithms varies greatly (Alvarez-Melis & Jaakkola, 2018). As noted by Hancox-Li 2020 this is disturbing because “*data is collected from the world with finite precision, and we should allow for that by ensuring that the uncertainty involved in those measurements does not drastically affect the decisions we make. However, it appears that this uncertainty could drastically affect the explanations we use to explain our results*”. This links closely to the broader issue posed by the ‘Rashomon effect’, where for a given set of data many different models can be developed that have equally high performance but differ greatly in their explanations (Breiman, 2001; Hancox-Li, 2020; Perretti et al., 2012). Dong & Rudin 2020 show how different data-driven models all perform well but find different important variables while using the same datasets. The lack of robustness in modelled relationships of data-driven approaches should be viewed as a warning against the promise they hold in terms of predictive power. This has led to calls against the use of data-driven approaches for societally important decision making (Rudin, 2019). In the context of this thesis, it could equally apply against calls to ‘infuse’ the scientific method with machine-learning to transform ecology.

Concluding, this section showed that data-driven approaches can be a useful tool for identi-

fying novel interdependencies in large, highly dimensional ecological datasets. However, I also showed how the dependencies modelled by data-driven approaches are difficult to validate and sensitive to data bias. Furthermore, the outcomes of the data-driven approaches used in chapters 1 and 2 provided limited insight to the mechanisms shaping observed patterns in marine populations. Data-driven approaches therefore provide limited scope towards achieving a better understanding of how and why marine populations fluctuate over time in an era of big data and global change.

7.3 Life history complexity and understanding population responses to global change

Scientists commonly use matrix population models as a ‘hybrid’ approach to understand generalities in population responses using big data (Logofet & Salguero-Gómez, 2021b). The big data component is provided by large functional trait databases that can be used to parametrize population matrices for hundreds of different plant and animal taxa (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016a). The parametrized matrix models then project population-level dynamics for each of these taxa by extrapolating the outcomes of biological functions on survival, growth, and reproduction up to some desired future time point.

The use of big datasets of functional traits has yielded some surprising general outcomes. For example, studies repeatedly find the variation in life history traits across different plant and animal species structure along a similar continuum (Gaillard et al., 1989; Salguero-Gómez et al., 2016b; Capdevila et al., 2020). This fast-slow continuum is made up of fast-growing, short-lived species with high fecundity at one extreme, and slow-growing, long-lived species with low fecundity at the other. Studies combining functional traits with matrix population models have found that the position of a species along the fast-slow continuum is correlated to their projected population responses to environmental change (Morris et al., 2008; Paniw et al., 2018). Species with fast life histories were found to be more sensitive to environmental change than species with slow life histories. These outcomes suggest that matrix population models parametrized using big sets of functional traits can provide a highly generalizable framework to understand how and why populations fluctuate in response to global change. The outcomes also indicate functional trait databases can help inform decision-making. The idea is that a limited set of key functional traits can be used to make informed decisions on which populations are most at risk from environmental change, and should therefore be prioritized in management (Kissling et al., 2018b).

Scientists do not know the mechanisms underlying the generality in structuring of life history traits along a fast-slow continuum and population responses to environmental change. It is thought these are ultimately shaped by ‘universal’ life history tradeoffs faced by each individual organism. Well-known examples of such life history tradeoffs include tradeoffs in energy allocation and future versus current reproduction. However, these individual-level dimensions are typically not represented in matrix population models.

As noted by Del Giudice 2020, the important implicit assumption underlying most current studies is that the structure of individual differences in life history traits aligns with the structure of variation across populations and species. If this assumption holds true, matrix population projections based on ‘average type traits’ are sufficient to understand population responses, and no representation of individual-level complexity is required. I have sought to address this question in chapter 5. I used a recently developed matrix population modelling framework that can account for individual-level tradeoffs in energy allocation (Smallegange et al., 2017). I then extended this model so that it also accounts for tradeoffs in investing in future versus current reproduction. Thus, I was able to examine the assumption that individual-level tradeoffs shape general patterns in population-level trait structuring and responses to environmental change. The answer is no. Introducing individual-level tradeoffs removes the classical relationship observed between life history strategies and projected population responses to environmental change. The outcomes instead suggested population responses to be idiosyncratic. Unfortunately, this also means general cross-taxonomical patterns in traits are likely a poor indicator of population responses for conservation decision-making; trait patterns do not necessarily inform on population processes.

The outcomes of chapter 5 are part of a broader perspective shift in life history studies that has been gaining ground during the past two decades. This ‘counter-perspective’ highlights the importance of accounting for the dimensions of variation between individuals, populations, or even taxa, over ignoring this variation and relying on one dimensional representations to achieve cross-taxonomical generality. To my knowledge, Jeschke & Kokko 2009 first showed that the occurrence and character of the fast-slow continuum across taxa might be less general than previously thought. Their study showed that the number and type of functional traits making up the fast-slow continuum can differ within taxa such as mammals, fish, and birds depending on the data-corrections applied. Furthermore, Jeschke and Kokko show important variation in key trait values between taxa, despite occupying similar positions on the fast-slow continuum. For example, mammals and birds with slow life histories have lowered fecundity, whereas this pattern is the opposite for fish species with slow life histories. This example illustrates that accounting for variation between species erodes evidence of cross-taxonomical generality.

Around the same time, questions started to arise on the generality of life history strategies within species. Nilsen et al. 2009 parametrized multiple matrix population models with population-specific monitoring data of roe deer. Surprisingly, the life history strategies of roe deer populations differed strongly across a gradient of environmental conditions and predation pressure. Generation time was particularly variable between populations, meaning that some populations could be categorized as having a fast life history, while others were slow. A recent study by Gamelon et al. 2021 similarly found such intraspecific differences in life history strategies of European wild boar. Although not examined in the context of matrix population modelling, it is well known that fish species can similarly display highly varying life history strategies. For example, species containing both resident and diadromous migratory populations (Fleming, 1996). These examples illustrate accounting for within species variation erodes evidence of species-level and

cross-taxonomical generality in life history strategies.

Finally, there is the question of individual-level variation. A recent study by Van de Walle et al. 2023b addressed this issue using demographic data drawn from populations of 17 different bird and mammal species. Using averaged (one-dimensional) data they could detect a general structuring of traits along a fast-slow continuum across species. However, there was no such structuring present between individuals within populations of a species. This outcome is important as it falsifies the previously introduced working assumption that *‘the structure of individual differences in life history traits resembles in important ways the structure of variation across species’* (Del Giudice, 2020). If this is not the case, individual level variation and complexity are important, and accounting for it may lead to very different outcomes than the generality observed under standard matrix models ignoring this. Chapter 5, together with the preceding studies by (Smallegange & Berg, 2019; Smallegange et al., 2020), shows this to indeed be the case. Accounting for individual-level variation and complexity in life history erodes evidence of cross-taxonomical generality in life history strategies and responses to environmental change.

Moving forward, matrix model projections of population responses to global change will need to move away from one-dimensional representations of life histories and better account for the variation observed across taxa, species, populations, and individuals. Big functional trait databases will remain a very important part in this process for initial model parametrization. However, within matrix population modelling frameworks these initial values should be more mechanistically translated to ‘realized’ values by individuals in the population. This increased complexity and biological realism will lead to less generalizable patterns, but at the benefit of better-informed decision-making on which populations to prioritize in management. The interspecific variation in life histories observed in the studies discussed serve both as an inspiring testament to the adaptive capacity and plasticity of species presented with different (changing) environments, but also as a warning. The capacity to adapt life histories while maintaining viable populations will not be present for many taxa given the sheer intensity of current anthropogenic pressures (Ceballos & Ehrlich, 2023).

7.4 Process-based discovery of population and trophic regulation

Although the field of marine population ecology has embraced big data, there are many marine systems for which little information remains available. A good example is the pelagic deep-sea, which forms the world’s largest and least explored marine habitat (Robison, 2009; Webb et al., 2010). Scientific understanding of the pelagic deep sea has evolved over the past century from that of a biologically devoid abyss to an environment that is highly diverse in species and habitats (Hessler & Sanders, 1967; Grassle & Maciolek, 1992; Snelgrove & Smith, 2002; Ramirez-Llodra et al., 2010). However, most studies on deep-sea ecology have focused on the diversity of seafloor organisms, e.g. Simon-Lledó et al. 2023, with less attention for the ecology of the open water column

that represents $\sim 90\%$ of this system (Drazen et al., 2020). Taxa such as jellyfish, fish, and squid play key trophic roles in this part of the deep-sea (Hays et al., 2018; Hoving et al., 2014), with estimated biomasses dwarfing global harvests of human fisheries across marine and freshwater systems (Clarke, 1977; Kawakami, 1980; Irigoien et al., 2014). It is important to form an understanding what might drive the population dynamics of these key trophic species groups. Especially because the effects of anthropogenic activities in pelagic-deep sea systems are preceding our ability to monitor their impacts (Drazen et al., 2020). Chapter 6 of this thesis presented a process-based approach to enhance our understanding of population regulation in understudied systems and species. Specifically, using a theoretical, size-structured population model, to examine population regulation and the impacts of trophic interactions on semelparous deep-sea squid.

The outcomes of chapter 6 highlight important differences in the inferential capacity between pattern, hybrid, and process-based approaches. For deep-sea squid, life history data is generally limited to sparse observations of individuals collected at depth using towed cameras or trawler surveys (Hoving et al., 2014). From these surveys we know size ranges, reproductive strategies, fecundity, diets and growth patterns of several hyperabundant species (Jereb & Roper, 2010). As discussed in section 7.2, data-driven approaches proved unable to generate inferences on ecological function beyond the level of organization at which data has been collected. This means data-driven approaches are unsuitable to gain insights into the population-level regulation of deep-sea squid. Hybrid approaches such as matrix population models accounting for individual life history complexity (section 7.3) already present a better option. Such models will be able to translate observations made at the individual level to projected population-level responses. Population responses could further be projected for all deep-sea squid species for which sufficient information is available. This could provide a somewhat ‘general’ overview of population dynamics that might be expected across this group. However, the downside of using this kind of matrix population model is that there is no feedback between the individual and its resources. As a result, there can be no emergent population-level dynamics that are the outcome of density-dependent processes such as resource competition we know might occur. Ultimately, such matrix population models would therefore yield limited insights into the mechanisms that shape population regulation in semelparous deep-sea squid. Thus, formal theory-based approaches in this case represent the best option for moving towards better population-level understanding of this understudied species group. It allowed me to translate individual-level observations to population-level dynamics based on first principles and examine the effect of density-dependent feedback on mechanisms of population regulation. Finally, it allowed me to examine under which range of conditions we might expect these mechanisms to hold. This makes process-based approaches highly suitable to gain a mechanistic understanding of how and why populations might show certain responses to global change. However, the additional insights gained from process-based approaches come at a tradeoff of being able to examine fewer species compared to hybrid approaches due to increased complexity.

There is a general hesitancy in modern-day ecology towards the use and funding of formal theoretical approaches in research projects (Lomnicki, 1988; Marquet et al., 2014;

Courchamp et al., 2015; Rossberg et al., 2019). This is partly fed by the false assumption that more mathematical models by default cannot be as representative of real-world processes as data-driven models. An (unscientific) thought experiment illustrating the current schism between theory and empiricism in ecology is to imagine a room full of ecologists asked to raise their hand in agreement to the following statement: “By and large theoretical ecologists focus on proving meta-level ideas using abstract models that bear little resemblance to real natural communities, while empiricists do most of the actual work of capturing and proving how real-world ecosystems operate through experimental data.” What proportion of people would you, as a reader, expect to lift their hands? The core of this hyperbole is the false dilemma presented between focusing on ‘unreal’ theory and ‘real’ empiricism. The key is that theoretical and empirical approaches represent two sides of the same scientific coin, aimed at gaining a general understanding of how real-world ecological systems operate. Consequently, most inferential power can be gained when empirical and theoretical work are combined in research and feed into each other. A testament to this is that the majority of the 100 most influential papers in ecology published by the British Ecological Society involved formal theory (Grubb & Whittaker, 2013). The need for a tight integration between empirical and theoretical work within research projects provides a good step towards answering the general aim of this thesis.

7.5 Conclusion: Striking a balance across the pattern-to-process gradient

This thesis attempted to answer how to best move forward in understanding how and why marine populations fluctuate over time in an era of big data and global change. Big data has undeniably positively affected the way scientists can study marine communities and populations. The capacity to identify novel correlative interdependencies from highly dimensional datasets serves as a positive stimulus for scientific enquiry. However, I argue that despite the vast changes in the scale of data, this does not change the role of the data itself in the process of scientific inference. Big data should remain a precursor, not a solution, to gaining a formal understanding of how and why marine populations fluctuate in response to global change. An overreliance on data-driven approaches will likely not ‘transform ecological learning’ but result in a skewed and biased view of community and population responses. A view, in which pattern might be mistaken for process and the propagation of bias might further entrench false patterns, unintentionally stifling fundamental scientific enquiry. The outcomes of this thesis support the statement that ‘*Big data needs big theory too*’ (Coveney et al., 2016b). In the discussion of chapter 5, I attempted to generate a roadmap that might lead to a tighter integration between big data and theory in future research. The goal of this roadmap was to gain the most benefits of each approach along the pattern-to-process gradient within the context of a single research project. Here, each approach acts as a focusing lens for the next one: (1) data-driven approaches serve to characterize the correlative interdependencies in the data at a certain level of biological organization, (2) hybrid approaches can use these patterns and provide insights into the expected responses at other levels of biological organization

under an ‘idealized’ scenario across many species or systems, finally (3) process-based approaches can be used for gaining a better understanding of how particular populations, communities or systems of interest might behave in a fuller ecological context accounting for feedbacks across trophic levels. Utilizing such roadmaps might foster collaboration and discussion between research groups with different specializations along the pattern-to-process-gradient. Hopefully, this discussion can lessen the current ‘schism’ between empirical and theoretical approaches in marine population ecology; promising a better understanding of how and why marine populations fluctuate in an era of big data and global change.

Box 2

Unlocking the Potential of Data-Driven Approaches in Understanding Marine Population Dynamics

Abstract

This counterargument aims to challenge the conclusions drawn by Rademaker in his 2023 PhD thesis, which posits that the potential for fundamental insights into the regulation of marine populations using fully data-driven approaches is limited. While we acknowledge the challenges raised by Rademaker, we contend that data-driven approaches have the capacity to provide crucial and innovative insights into the complex dynamics of marine populations. In this discussion, we will explore the strengths and limitations of data-driven methods, address Rademaker's concerns, and present evidence supporting the assertion that these approaches can indeed uncover valuable information beyond the biological level of data collection.

Introduction

Rademaker's skepticism about the potential of data-driven approaches in marine population studies raises important questions about the applicability and reliability of such methods. However, it is crucial to recognize the evolving landscape of data science and emphasize that advancements in technology and methodologies warrant a reconsideration of his conclusions.

Strengths of Data-Driven Approaches

- a. **Holistic Understanding:** One of the key strengths of data-driven approaches lies in their ability to capture and analyze vast amounts of diverse data sources. By amalgamating information from environmental sensors, satellite imagery, and ecological surveys, these methods can provide a more comprehensive view of marine ecosystems than traditional, hypothesis-driven approaches.
- b. **Complex Pattern Recognition:** Data-driven approaches, particularly machine learning algorithms, excel in identifying intricate patterns within large datasets. This capability allows for the detection of subtle relationships and non-linear dynamics that may be

overlooked by more traditional statistical methods.

c. **Real-time Monitoring:** The dynamic nature of marine environments requires real-time monitoring to understand population fluctuations. Data-driven approaches, when coupled with advanced sensor technologies, enable continuous data collection and analysis, offering a more up-to-date perspective on the factors influencing marine populations.

Addressing Rademaker's Concerns

a. **Limitations of Biological Inference:** While Rademaker rightly points out the challenge of making inferences beyond the biological level of data collection, it is essential to recognize that the biological perspective is foundational. Data-driven approaches can complement traditional biological methods by providing insights into the underlying processes driving observed patterns.

b. **Validation Challenges:** Rademaker's inability to validate outcomes, even with synthetic data, raises concerns about the reliability of data-driven approaches. However, recent advancements in validation techniques, such as cross-validation and bootstrapping, demonstrate improved accuracy and reliability in model predictions. Additionally, ongoing research in explainable AI ensures transparency in model outcomes.

Evidence Supporting Data-Driven Insights

a. **Case Studies in Marine Ecology:** Numerous case studies demonstrate the successful application of data-driven approaches in marine ecology. For example, studies using machine learning algorithms have identified previously unknown relationships between environmental variables and fish population dynamics, contributing to a more nuanced understanding of ecosystem interactions.

b. **Predictive Modeling for Fisheries Management:** Data-driven models have proven effective in predicting fishery yields and optimizing management strategies. These models consider a multitude of variables, including climate, oceanography, and human activities, providing a more holistic and accurate prediction of population dynamics.

Conclusion

In conclusion, while Rademaker's concerns about the limitations of data-driven approaches are valid, it is essential to recognize the transformative potential of these methods in advancing our understanding of marine population dynamics. By embracing the strengths of data-driven approaches and addressing existing challenges through ongoing research and technological advancements, we can harness these tools to unlock fundamental insights into the regulation of marine populations. The integration of data-driven approaches with traditional biological methods can usher in a new era of interdisciplinary research, fostering a more holistic and nuanced understanding of the complex marine ecosystems.

Author note

This box was written by a data-driven large-language model (Chat-GPT 3.5) on 7 January 2024, 15:22, to provide a counterargument against the critique on data-driven approaches in this thesis, based on the following input prompt: "Rademaker, in his PhD thesis (2023), argues that the potential for fundamental insights into the regulation of marine populations using fully data-driven approaches is very limited. His main argument is based on the observation that data-driven approaches in his research could not generate inferences beyond the biological level of the organisation at which the data was collected. Furthermore, he was unable to validate the outcomes of data-driven approaches, even when using synthetic data with known underlying relationships. Based on these arguments, Rademaker concludes that data-driven approaches should only be used as a precursor to formal scientific inference. Please provide a 1000-word counterargument to Rademaker, including references, explaining why and how data-driven approaches can provide fundamental new insights into what is driving the observed fluctuations of marine populations".

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Summary

Human-induced changes in the global environment have led to major changes in the structuring of marine communities. At the same time, the amount of information available to study the responses of marine communities to global change has increased by orders of magnitude through the advent of big data. These developments have reignited a century old scientific debate on how to best understand what is driving the observed fluctuations of marine populations; a debate between scientific inference based on **pattern** versus **process**. This PhD synthesis integrates the findings from five studies, representing a gradient of pattern-to-process based approaches, and different marine systems, in an attempt to answer the main research question:

How to best move forward to the goal of understanding how and why marine populations fluctuate over time in an era of big data and global change?

Data-driven inference

The thesis starts at the pattern side of the gradient, with a focus on the ecological insights that can be gained from fully data-driven, machine-learning approaches. In chapter 2, I developed and used a deep-learning species distribution model (DL-SDM) to explore the community-wide structuring of interspecific interactions between benthic invertebrates in a 2400 km² intertidal ecosystem. The dataset consisted of > 30 000 (a)biotic samples collected between 2008-2020 as part of the Synoptic Intertidal Benthic Survey (SIBES). Our data-driven approach showed that populations of benthic invertebrates in the Wadden Sea form a network in which each individual species engages in relatively few strong interactions embedded in a larger network of weak interactions. We could use these outcomes and combine them with more formal methods of statistical inference to show interaction network structure affirms existing stability-connectivity theories. We could further statistically link the number of interspecific interactions of a species to certain functional traits. However, the biological interpretation of these links remains open. Rather than posing a catch-all solution for ecological inference, the data-driven DL-SDM provides a baseline mapping tool and starting point for more targeted experiments to elucidate underlying mechanisms.

Chapter 3 and Box 1 examined the potential of more causality-oriented data-driven approaches to understand the drivers of observed population responses. These approaches were applied to both observational and to synthetic time-series datasets of marine-fish biomass. The observational dataset consisted of 41 years of systematic monitoring data derived from the International North-Sea Bottom Trawl Survey (NS-IBTS). Although the NS-IBTS represents huge spatial effort and coverage, temporal resolution is relatively low as it can only be undertaken quarterly or twice annually. This makes it uncertain how data-driven approaches handle this type of ‘big’ ecological dataset. I spatially aggregated the NS-IBTS data by dividing the North Sea into 10 distinct zones based on seabed morphology, called seascapes. The resulting spatial time-series data consisted of the average annual fish biomass densities per seascape. Next, I examined whether any causal interdependencies existed between these time-series at different time-lags using a causal association network. I found that the network was able to identify time-lagged interdependencies in fish biomass density between different seascapes, and that these dependencies could be systematically grouped across different fish species. These findings underscored the importance of abiotic bottom-up processes, such as seafloor structure, in shaping temporal patterns in observed population-level biomass densities. It further highlighted the capacity of causality-based data-driven approaches in identifying lagged dependencies in time-series datasets with a high spatial, but low temporal resolution. However, this outcome immediately also gave rise to questions on how to validate the relationships identified by such data-driven approaches. We therefore designed a simulation experiment using a stage-structured population model with known interdependencies between biomass of different marine fish. The stage-structured model described the life-stage specific trophic interactions between a consumer (sprat) and predator (cod) population, of which the latter was subjected to additional human fishing pressure. We then analyzed a range of scenarios concerning different temporal resolutions and signal to noise ratios, to approximate different kinds of observational datasets. Surprisingly, the specific causality-based framework applied was unable to identify underlying dependencies across all simulated scenarios. This suggests it will be difficult to validate the relationships inferred on observational datasets in which underlying dependencies are unknown. Future studies should repeat this experiment across different ‘causal’ data-driven approaches and types of synthetic ecological datasets, to better pinpoint whether this represents a model-specific, or general issue concerning outcome validation.

In contrast to large regional monitoring surveys (such as the NS-IBTS), local surveys of marine populations can maintain a much higher temporal sampling resolution. These local, high-temporal resolution surveys might therefore actually be more suitable for gaining a general understanding of what is driving observed fluctuations in marine fish populations in response to environmental change. In chapter 4 of this thesis, I used a local survey that represents the longest, highest-resolution, time series of marine fish abundance in Northern Europe, to examine changes in the population trends of herring between 1982-2021. Using a non-linear statistical model (GAM), I was able to show in detail how the phenology of herring moving between the North Sea and the Wadden Sea has shifted forwards during the past decades. The observed dynamics were mostly driven by small juveniles (5-15cm) and could be best explained by changes in North Sea water

temperatures. Next, I checked how likely it would be to detect these effects in larger-scaled surveys with lower temporal resolution. I found that reducing the temporal resolution of the data drastically reduces the chances of detecting phenological shifts and can result into a hundredfold reduction in estimated effect sizes. The outcomes of chapter 4 are important, as they show that local, long-term, high-resolution time-series are essential to gain a more general understanding of the responses of marine fish populations to climate warming.

Hybrid approaches to inference

Another type of big data in marine population ecology is formed by big trait databases. These datasets contain information on key life history traits, such as average individual growth rates, fecundity and maximum body sizes, across a vast range of taxonomic groups. In chapter 5 of this thesis, I examined correlative patterns in the structuring of variation in life history traits across ray-finned fish, and how this links to population-level responses to environmental change. The existence of a link between patterns in traits and population-level responses holds great applied promise. It would allow marine scientists to make informed inferences on which species might be most sensitive to future climate change based on limited information, i.e. key traits. Scientist usually study this question by projecting population responses across hundreds of different taxa using matrix population models parametrized using big trait databases. The outcomes of these matrix population modelling studies showed that populations of species categorized as having slow life history strategies (low fecundity, longevity, high adult survival) are less sensitive to environmental change than species with fast life histories (high fecundity, short-lived, high adult mortality). However, the matrix population models used typically do not account for individual-level life history complexity, such as tradeoffs in energy allocation and reproduction faced by each organism. Furthermore, most matrix modelling approaches make the link between the population and environmental conditions indirectly. This is done, for example, by slightly changing the value of the average growth-rate at each time-step to mimic variation in realized growth under different environmental conditions. In chapter 5, I examine what happens to projected population responses, when explicitly accounting for individual-level complexity and tradeoffs in matrix population models. The outcomes of chapter 5 show that the classical association between fast-and-slow life history strategies and population responses to environmental change disappear when accounting for individual-level complexity. Our outcomes highlight the idiosyncrasy of projected population responses to environmental change. Unfortunately, this also indicates no meaningful inferences on the sensitivity of populations to climate change can be made based on a limited set of traits. Future large, cross-taxonomical studies of population responses to environmental change using matrix population models and big trait databases will have to take into account individual-level life history complexity.

Process-based inference

The final chapter of this thesis examined the role of formal theory in gaining a general understanding of the drivers of population dynamics in marine communities. Especially for understudied marine systems. I used deep-sea squid as a model system because they play a key trophic role in the worlds oceans but are extremely difficult to study. Most

of our knowledge on deep-sea squid life history is gathered from sparse observations on live individuals made at depth by camera surveys, as well as specimens collected from trawler surveys. I used available empirical information to develop and parametrize a theoretical size-structured population model of a hyperabundant species of deep-sea squid (*Histioteuthis reversa*). By using a theoretical size-structured population model I was able to translate the available individual level observations to expected population level dynamics based on first principles. At the individual level, the growth pattern predicted by the size-structured population model aligned with empirical observations. The emergent population level dynamics were characterized by single-cohort cycles that lead to ‘seasonal’ patterns in maturation and reproduction, without there being any seasonality in the environment. The formation of these single-cohort cycles could be traced back to the high resource competition between paralarvae. Finally, the outcomes showed that the presence of multiple deep-sea squid predators foraging at different depths can result in emergent facilitation between predator species. In this scenario the squid biomass density in the size-class preferred by one predator increases as a result of predation of another size class at a different depth by a second predator. The outcomes of chapter 6 provide fundamental new insights into the population regulation of one of the most trophically important, but understudied, species groups in the pelagic deep-sea.

Conclusion

The outcomes of chapters 2-6 illustrate the difference in inferential capacity between pattern, hybrid and process-based approaches in understanding what is driving observed population responses in marine communities. On the pattern side of the gradient, big data enables the identification of many new correlative interdependencies in large and high-dimensional datasets. However, based on the outcomes of this thesis I argue that the role of data-driven work should not start to outweigh that of formal theory when generating inferences on underlying mechanisms. An overreliance on data-driven ‘discovery’ will lead to a skewed understanding of the functioning of marine communities and their responses to global change; with outcomes that can be unrobust and difficult to validate. In chapter 5 and the global synthesis of this study I discuss a roadmap to reconcile the different approaches across the pattern-to-process gradient. As part of this perspective, I argue that most insight is gained when these different approaches are combined within single research projects. To achieve this, better collaboration is required between research groups with different specializations along the pattern-to-process-gradient. Hopefully, this might also lessen the current ‘schism’ between empirical and theoretical approaches in marine population ecology. I argue that such an approach will lead to a better understanding of how and why marine populations fluctuate in an era of big data and global change.

Appendix

7.6 Supplementary Information Chapter 2

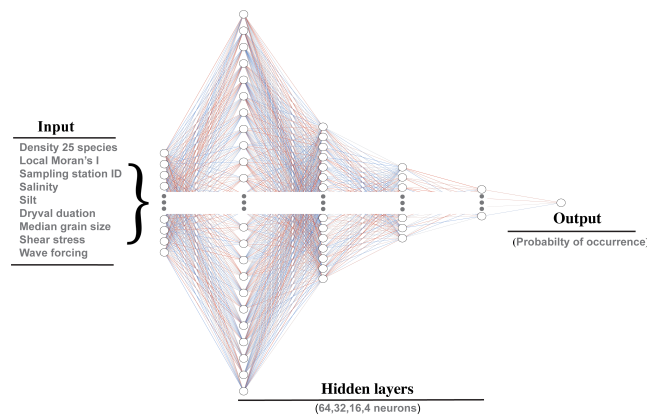


Figure 7.6.1: Schematic representation of model architecture. Red and blue lines exemplify potential negative and positive weights between neurons in adjacent layers, respectively.

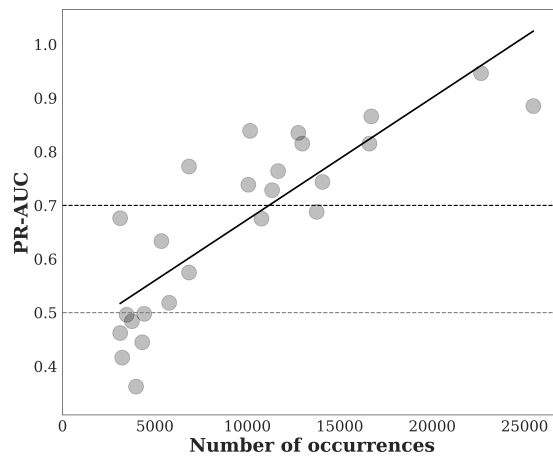


Figure 7.6.2: Model performance score (PR-AUC) as a function of the number of occurrences of species in the dataset.

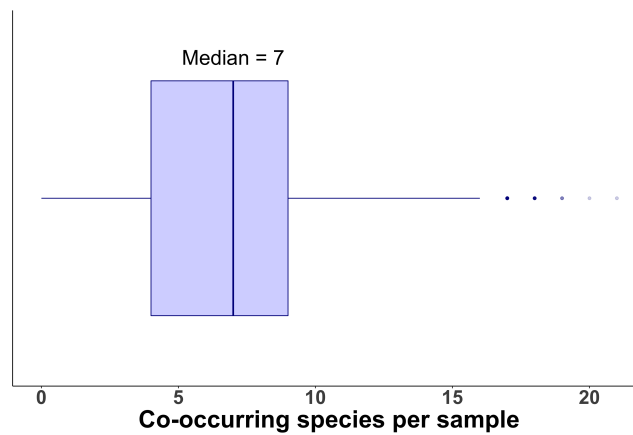


Figure 7.6.3: Median number of co-occurring species in the dataset.

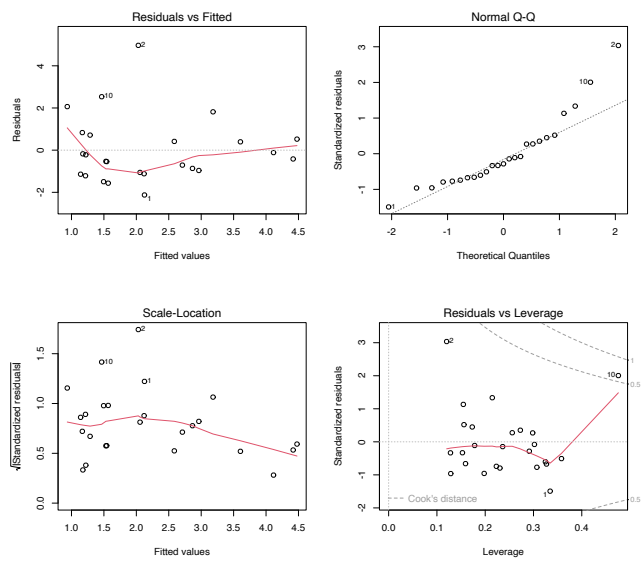


Figure 7.6.4: Multivariate linear regression diagnostic plots of data including *A. marioni*

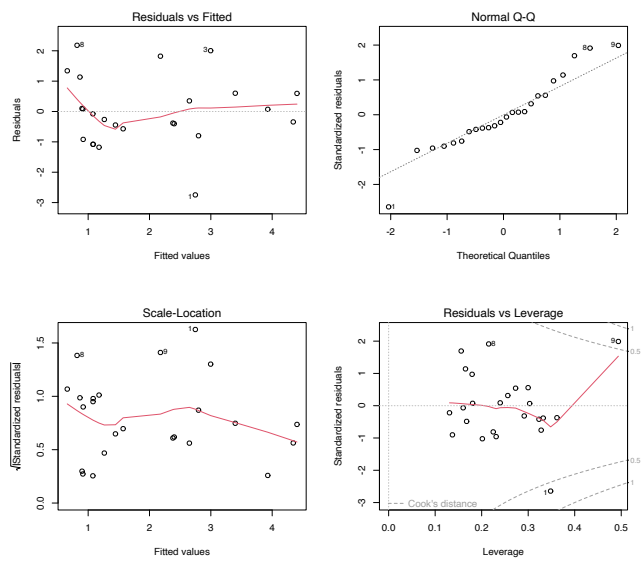


Figure 7.6.5: Multivariate linear regression diagnostic plots of data excluding *A. marioni*

Table 7.1: Interannual variability in the occupancy rates of model species. High variation and differences between mean and median could be indicative of recruitment events skewing the distribution of non-zero abundance entries.

Species	Min(%)	Max(%)	Range (%)	Mean (%)	Median (%)	St.dev. (%)
<i>Allita succinea</i>	5.21	11.97	6.76	8.29	8.29	2.23
<i>Aphelochaeta marioni</i>	37.23	52.03	14.81	45.84	46.99	5.01
<i>Arenicola marina</i>	19.55	40.03	20.48	31.09	31.29	4.69
<i>Capitella capitata</i>	11.39	53.67	42.28	38.81	42.14	12.4
<i>Carcinus maenas</i>	5.19	15.31	10.12	8.58	8.56	2.56
<i>Cerastoderma edule</i>	18.48	39.53	21.05	26.73	25.77	5.88
<i>Corophiidae</i>	0.88	24.57	23.69	13.23	10.98	7.79
<i>Ensis leei</i>	4.25	37.92	33.67	12.9	11.14	8.55
<i>Eteone longa</i>	16.21	59.87	43.76	37.08	37.93	10.79
<i>Hediste diversicolor</i>	30.2	44.46	14.26	36.02	35.49	4.17
<i>Heteromastus filiformis</i>	15.97	61.41	45.44	33.56	28.72	14.32
<i>Laniche conchilega</i>	8.57	33.29	24.72	20.76	19.7	6.19
<i>Limecola balthica</i>	29.54	58.38	28.85	44.89	46.2	9.37
<i>Marenzelleria viridis</i>	12.06	56.65	44.59	30.41	27.74	13.92
<i>Mya arenaria</i>	6.29	39.88	33.59	13.17	11.19	8.14
<i>Nephtys hombergii</i>	5.89	22.16	16.27	10.48	10.34	4.28
<i>Nereididae</i>	2.93	24.74	21.80	11.78	10.49	7.85
<i>Oligochaeta</i>	24.14	40.28	16.14	34.90	35.65	3.85
<i>Peringia ulvae</i>	7.00	27.39	20.39	17.34	16.24	6.09
<i>Phyllodoce mucosa</i>	2.0	28.85	26.84	15.30	13.53	7.13
<i>Polydora cornuta</i>	4.2	16.0	11.81	9.73	9.91	3.88
<i>Pygospio elegans</i>	42.96	85.18	42.22	69.83	69.54	10.47
<i>Scoloplos armiger</i>	53.94	72.39	18.45	63.12	62.16	4.33
<i>Spio martinensis</i>	4.47	16.5	12.03	9.78	9.45	4.14
<i>Urothoe poseidonis</i>	22.83	31.55	8.73	28.55	28.93	2.26

7.7 Supplementary Information Chapter 4

Table 7.2: Six-point scale used to determine gonadal ripeness of individuals subsampled for dissection (N=480).

Gonadal ripeness	Male description	Female description
1 - Immature	Testes undeveloped or very thin line	Ovaries undeveloped or empty
2 - Maturing / Recovering	Testes slightly thickened on one side	Eggs visible as small points in ovaries
3 - Maturing / Recovering	Testes thickened and coloring white	Ovaries color orange, eggs well visible
4 - Mature / prespawning	Testes thick and white, but no release of milt	Eggs swelling, but no release
5 - Spawning	Milt secretion when pressure is applied	Eggs released when light pressure is applied
6 - Spent	Testes flabby	Ovaries bloodshot and flabby.

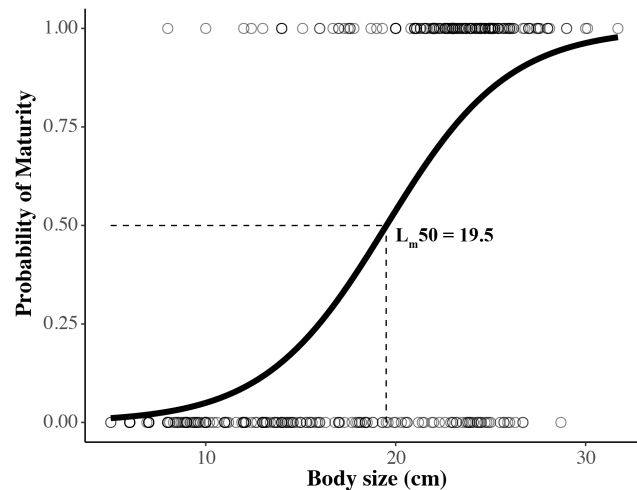


Figure 7.7.1: Logistic regression to determine the size in cm at which 50% of all dissected individuals subsampled from the kom-fyke catches reach maturity ($L_m 50 = 19.5$ cm, N=480). Individuals with Gonadal ripeness scores of 1 were classified as immature juveniles and individuals with gonadal ripeness scores > 1 as mature (see table S1).

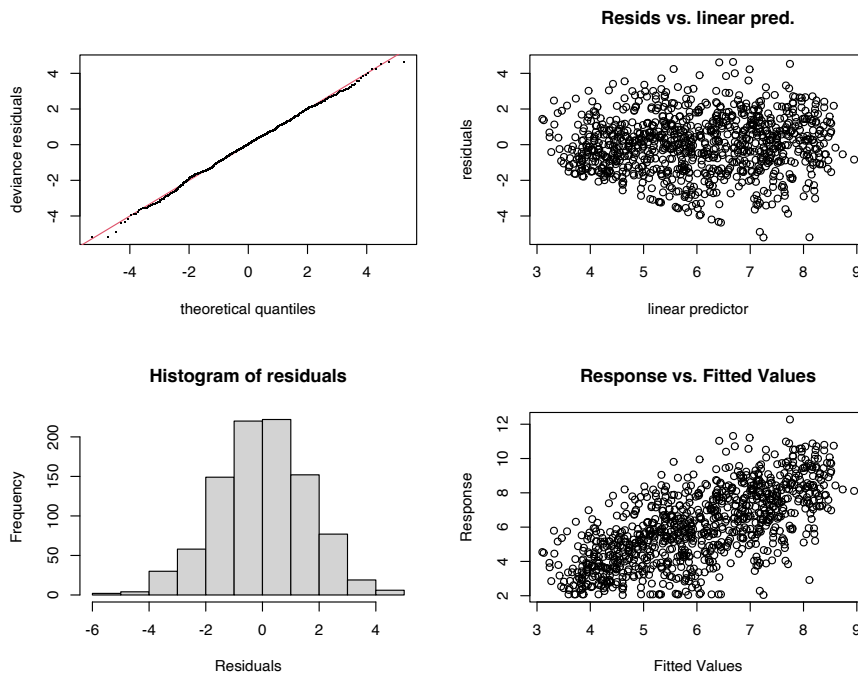


Figure 7.7.2: Diagnostic plots for the additive model, clockwise: qqplot, residuals vs linear predictors, residuals histogram, and response vs fitted values.

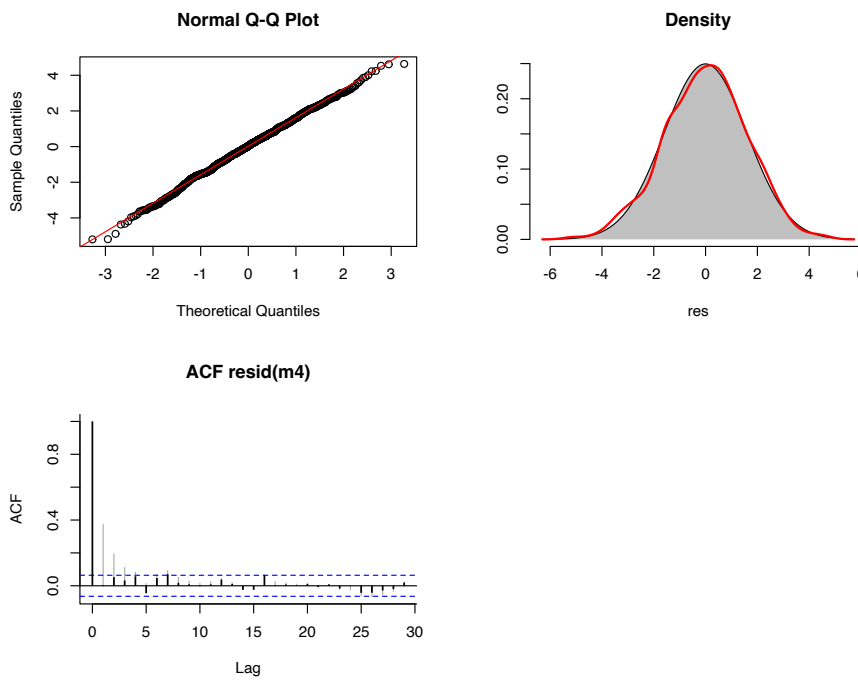


Figure 7.7.3: Diagnostic plots for the additive model, clockwise: qqplot, residual density plot, and residual autocorrelation.

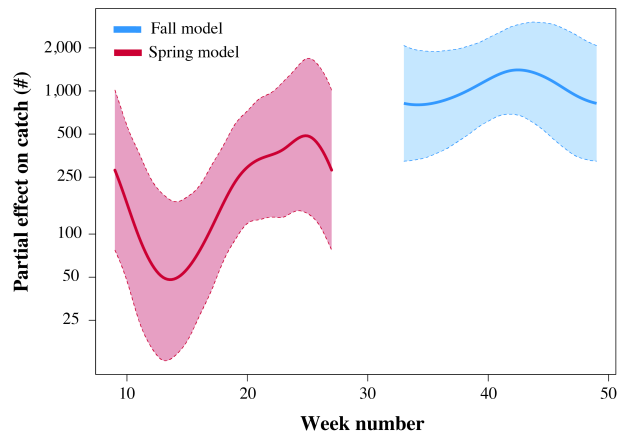


Figure 7.7.4: Partial interaction effect of week number on weekly standardized herring catches in the spring data (red line) and fall data (blue line) models used to compare against full data model in Fig.3a of the manuscript. Shaded area represents the pointwise 95% CI.

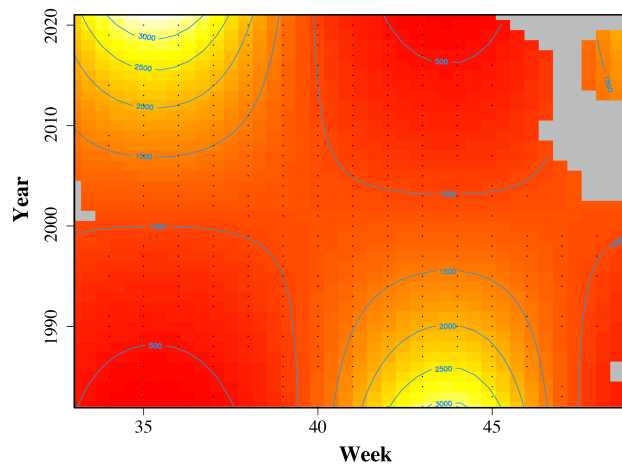


Figure 7.7.5: Partial interaction effect of the week and year on weekly standardized herring catches in the fall data model used to compare against the full data model in Fig. 3b of the manuscript.

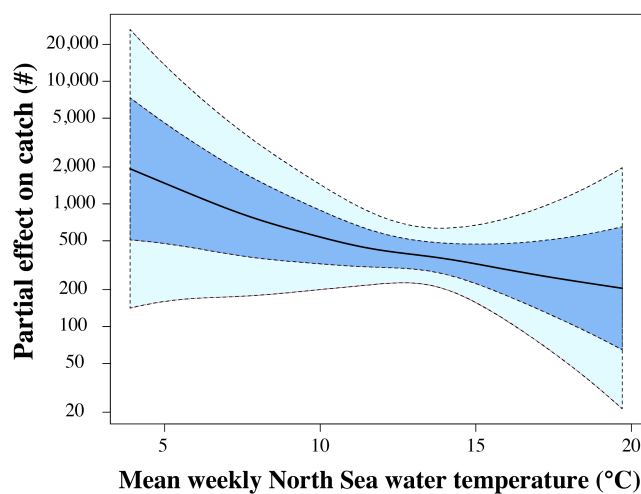


Figure 7.7.6: Partial effect of North Sea water temperatures on weekly standardized herring catches in the full data model. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the pointwise 95% CI.

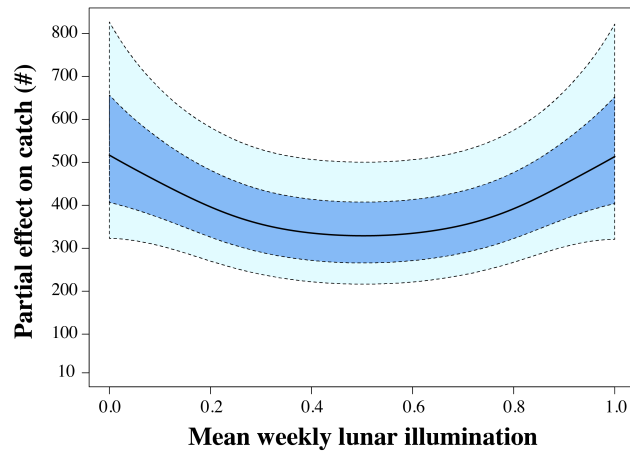


Figure 7.7.7: Partial effect of lunar illumination on weekly standardized herring catches in the full data model. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the pointwise 95% CI.

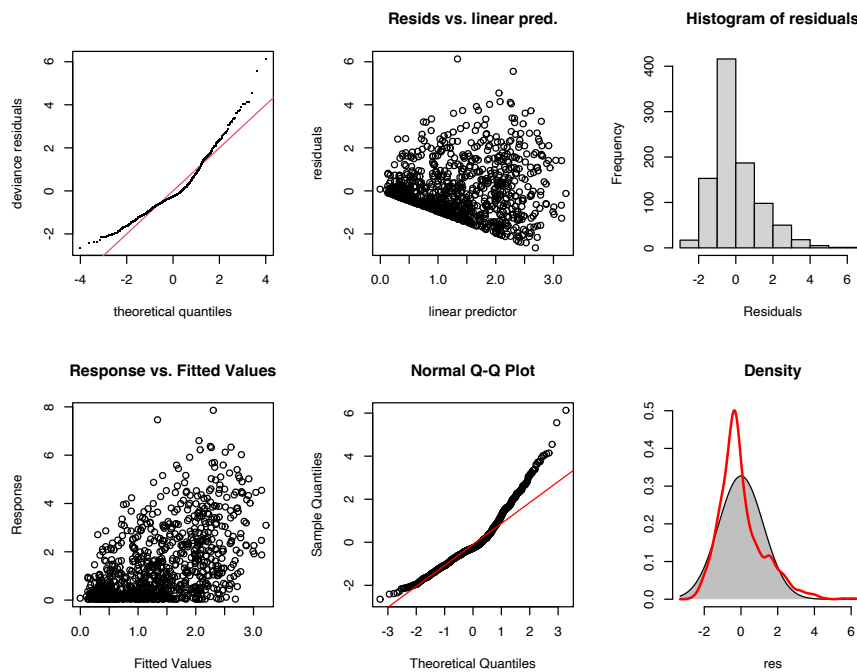


Figure 7.7.8: Diagnostic plots for the weekly sampled additive model, clockwise: qqplot, residuals vs linear predictors, residuals histogram, and response vs fitted values.

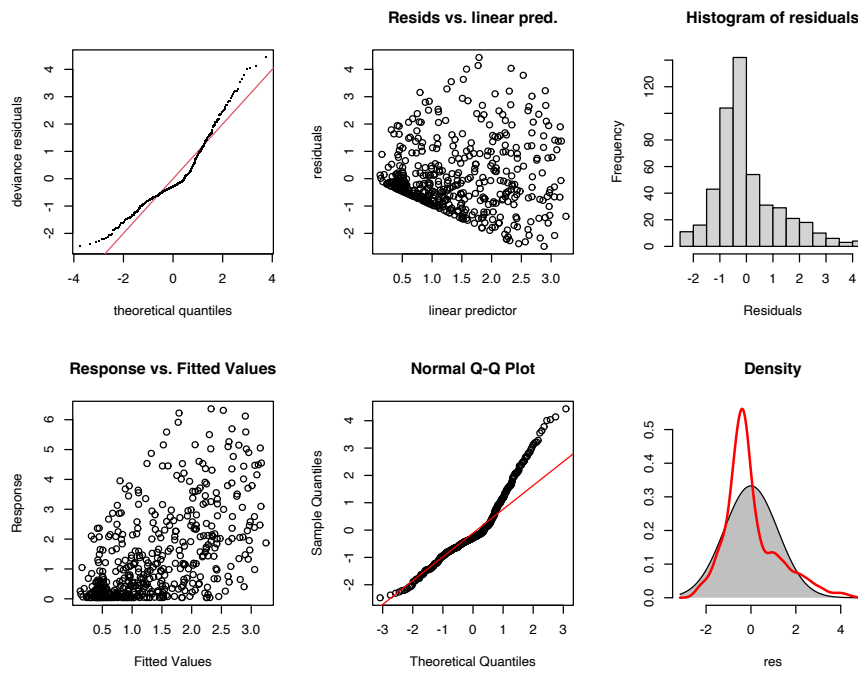


Figure 7.7.9: Diagnostic plots for the biweekly sampled additive model, clockwise: qqplot, residuals vs linear predictors, residuals histogram, and response vs fitted values.

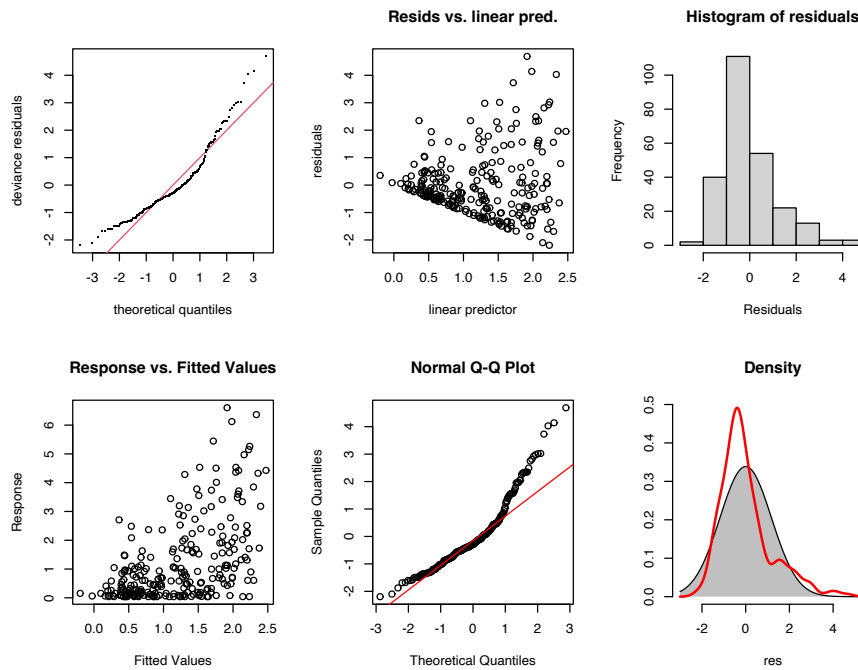


Figure 7.7.10: Diagnostic plots for the monthly sampled additive model, clockwise: qqplot, residuals vs linear predictors, residuals histogram, and response vs fitted values.

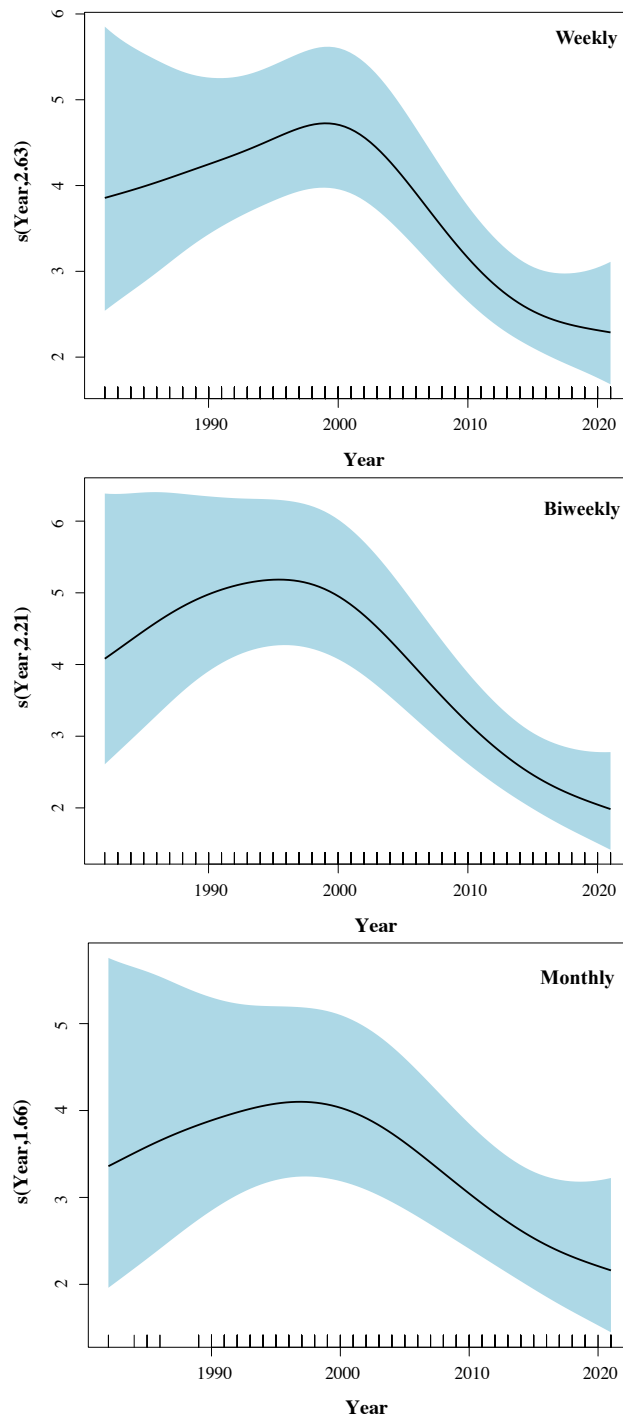


Figure 7.7.11: Partial effect of year on standardized herring catches when sampling once per week, biweekly, or month, respectively.

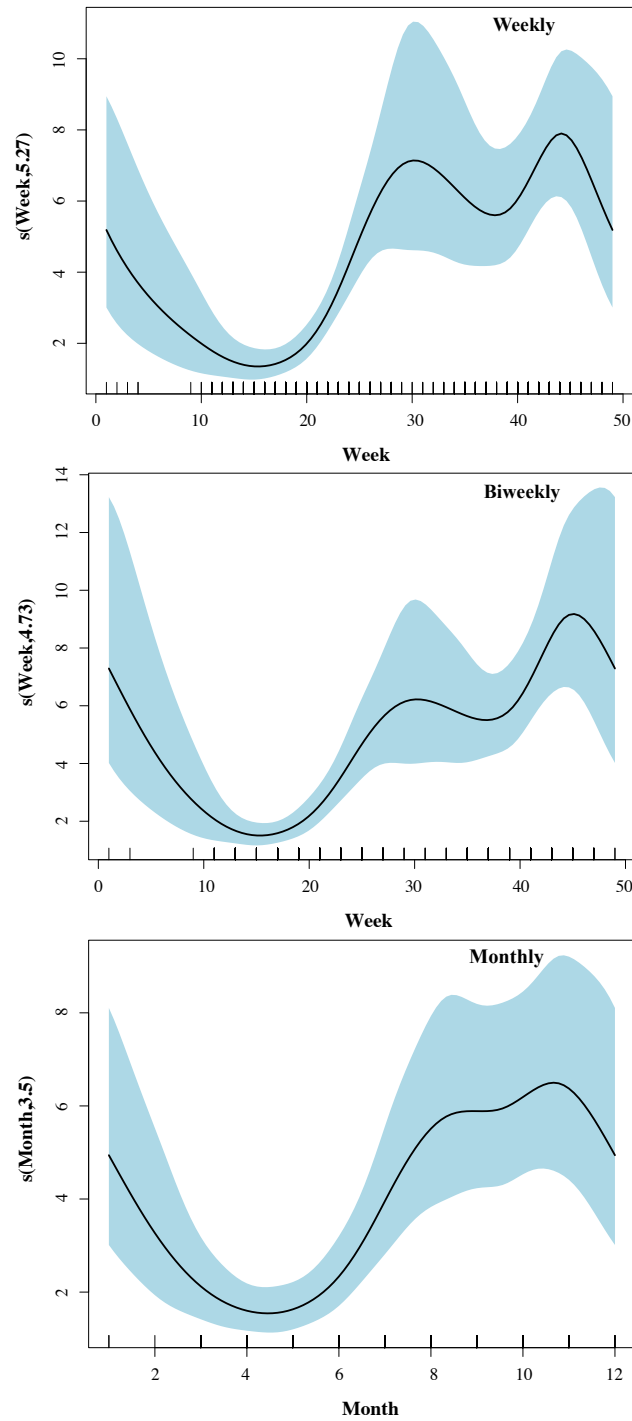


Figure 7.7.12: Partial effect of season on standardized herring catches when sampling once per week, biweekly, or month, respectively.

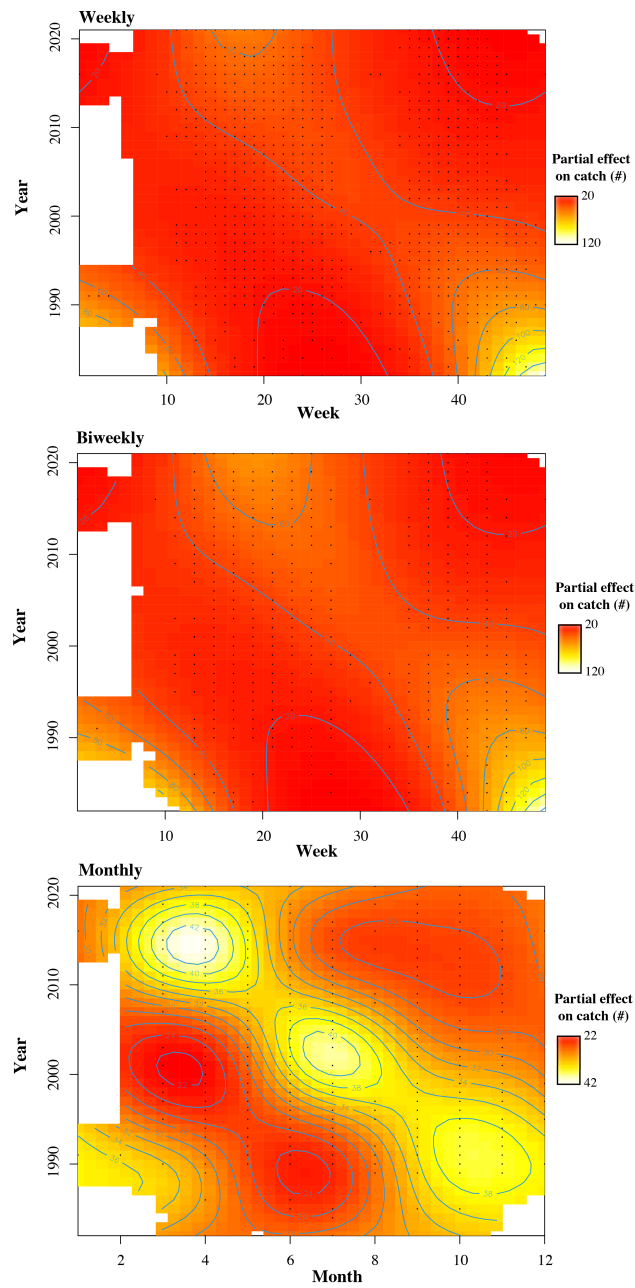


Figure 7.7.13: Partial interaction effect of season and year on standardized herring catches when sampling once per week, biweekly, or month, respectively.

7.8 Supplementary Information Chapter 5

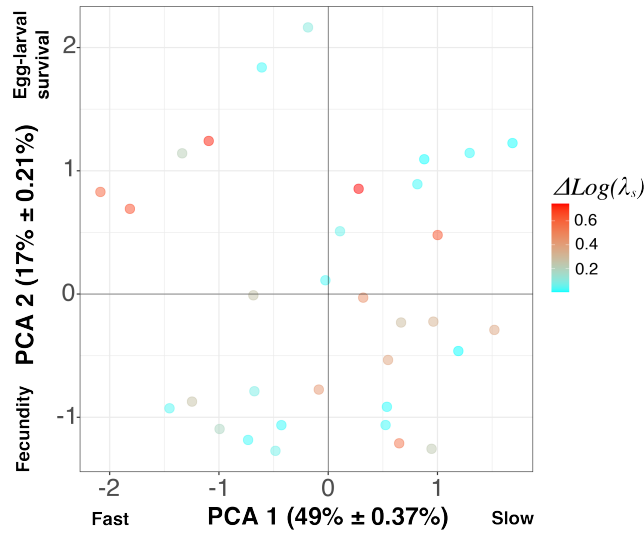


Figure 7.8.1: Distribution of species sensitivity values $\Delta(\log(\lambda_s))$ over the fast-slow and reproductive strategy axes.

Sensitivity and individual traits

We found no significant (non)linear relationships between sensitivity and log-transformed trait values (Table S1: Pearson correlation, Distance correlation). When examining the distribution of sensitivity values across species, we observed a clear separation between species that did and did not show any sensitivity to shifts in environmental autocorrelation (Fig. S2). We therefore split the data into two categories (sensitive vs. insensitive species) and compared the distribution of log-transformed trait values between these two categories using the Kolmogorov-Smirnov test. However these distributions did not differ from each other significantly for any of the traits considered. Finally, we also split data into three classes (low, middle, high sensitivity) and used these values to check for potential differences in sensitivity using Fisher's exact test (Table S1: Fisher's exact test, dotted lines in Fig. S3).

Table 7.3: Linear and non-linear test statistics of the relationship between $\Delta \log(\lambda_s)$ and log transformed life history traits. For the Kolmogorov-Smirnov test, distributions of trait values were compared between species classified as sensitive and insensitive. For Fischer's exact test, the trait values of species were classified into three quantile groups (low, medium and high values). Supporting plots for data grouping into classes and quantile groups are provided in Supplementary information III. There is no indication of significance, since none of these measures showed a significant correlation.

Life history traits	Pearson correlation	Distance correlation	Kolmogorov-smirnov test	Fischer's exact test
1. $\log_{10}(\mu_p)$	$r = 0.162, p = 0.366$	$dCor = 0.293, p = 0.285$	$D = 0.169, p = 0.972$	$p = 0.490$
2. $\log_{10}(L_p)$	$r = 0.139, p = 0.422$	$dCor = 0.282, p = 0.335$	$D = 0.287, p = 0.507$	$p = 0.240$
3. $\log_{10}(\phi)$	$r = 0.262, p = 0.140$	$dCor = 0.358, p = 0.076$	$D = 0.224, p = 0.801$	$p = 1.000$
4. $\log_{10}(r_B)$	$r = 0.250, p = 0.163$	$dCor = 0.328, p = 0.176$	$D = 0.290, p = 0.490$	$p = 0.092$
5. $\log_{10}(\sigma_{L_B})$	$r = 0.168, p = 0.431$	$dCor = 0.246, p = 0.467$	$D = 0.268, p = 0.593$	$p = 0.469$
6. $\log_{10}(R_m)$	$r = -0.042, p = 0.815$	$dCor = 0.279, p = 0.318$	$D = 0.290, p = 0.490$	$p = 0.735$
7. $\log_{10}(L_b)$	$r = 0.021, p = 0.909$	$dCor = 0.199, p = 0.880$	$D = 0.232, p = 0.768$	$p = 0.853$
8. $\log_{10}(L_m)$	$r = -0.145, p = 0.419$	$dCor = 0.259, p = 0.395$	$D = 0.235, p = 0.751$	$p = 0.295$

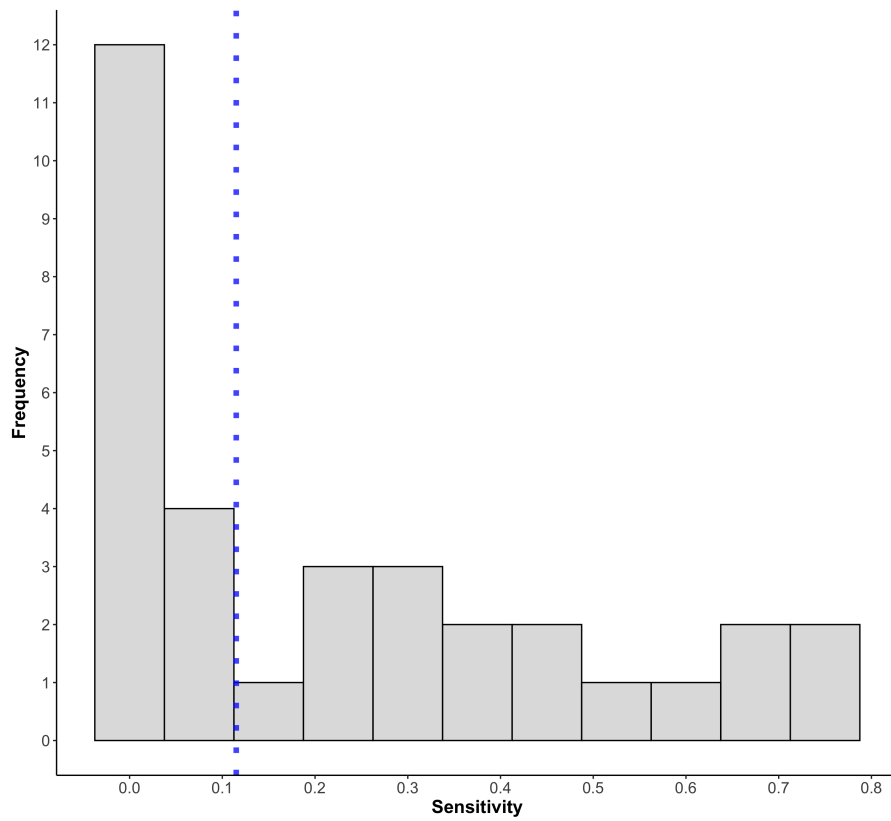


Figure 7.8.2: Histogram showing the distribution of sensitivity values across species. Blue line indicates separation between species classified as insensitive and sensitive to shifts in environmental autocorrelation

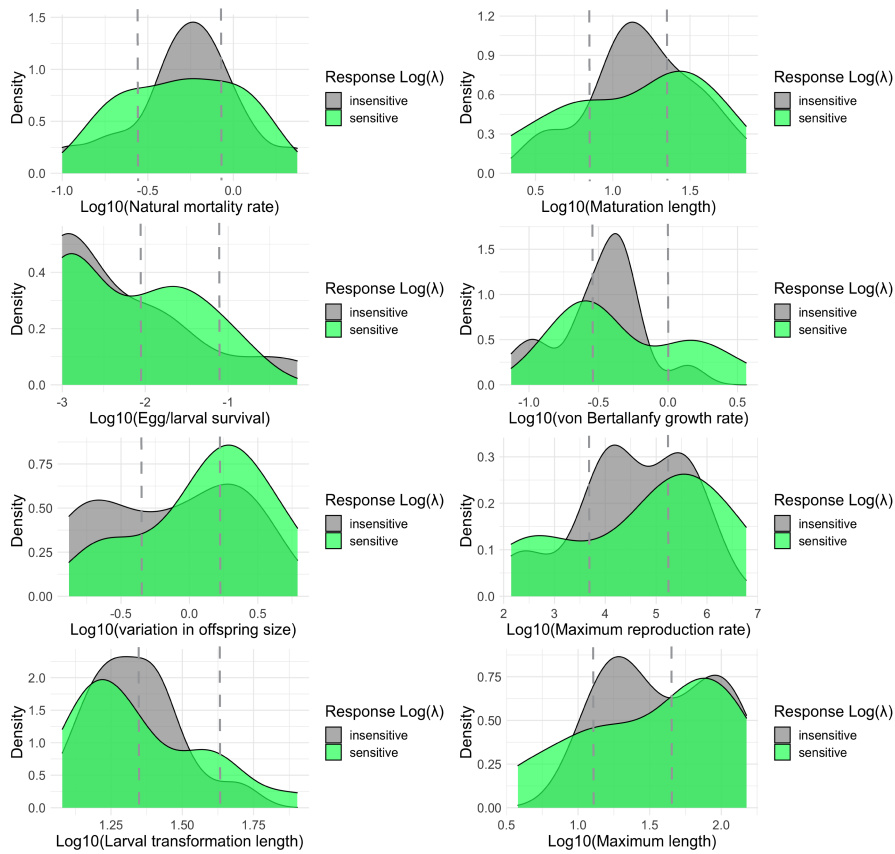


Figure 7.8.3: Distribution of log-transformed trait values between species classified as sensitive or insensitive to shifts in environmental autocorrelation used for Kolmogorov-smirnov test. Dotted lines indicated alternative classification into three groups (low, middle, high sensitivity) used for Fisher's exact test.

7.9 Supplementary Information Chapter 6

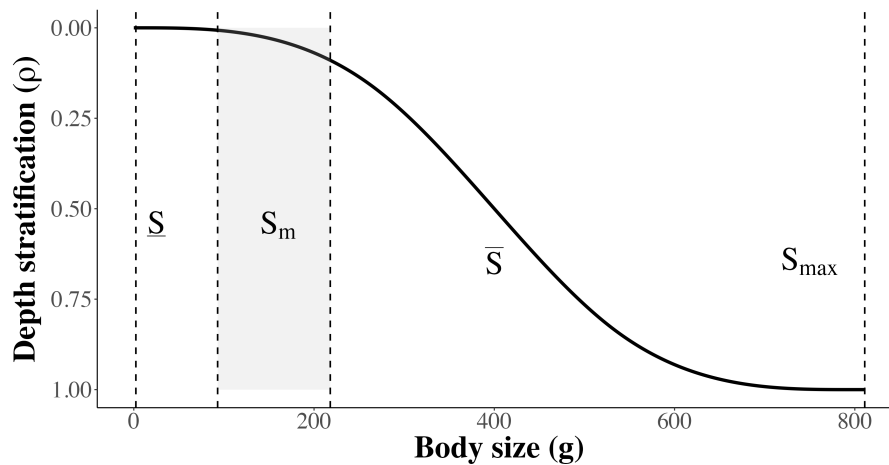


Figure 7.9.1: The depth inhabited by individual *H. reversa* as a function of body size. Where \underline{s} is the size at which individuals start depth migration, the shaded area represents the observed range of maturation sizes s_m , \bar{s} is the size at half the maximum depth migration, and s_{max} is maximum body size.

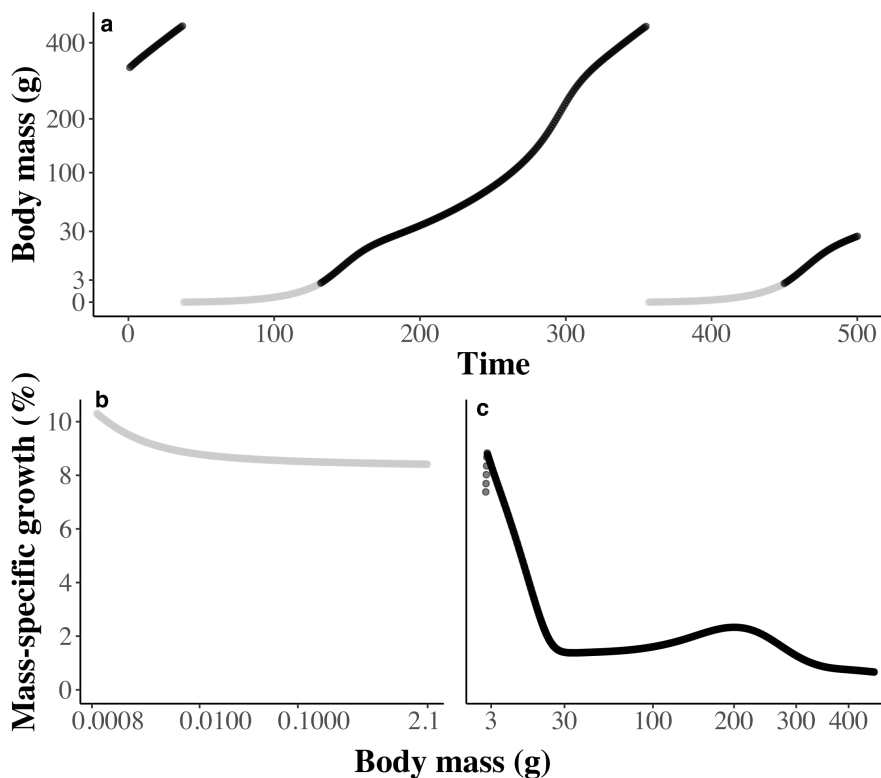


Figure 7.9.2: Extreme ecological conditions (low R3 resource productivity, high paralarvae mortality, direct switch to benthic resource feeding as juveniles) resulting in a qualitative reversion where growth trajectories become more linear (a) and mass-specific growth decreases with increasing size (b,c).

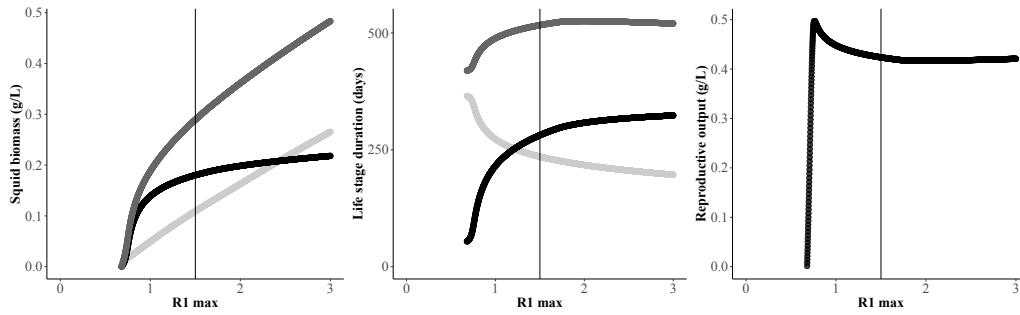


Figure 7.9.3: Equilibrium biomass (a), equilibrium life-stage duration (b), and equilibrium reproductive output (c), as an emergent outcome of changing zooplankton resource productivity (R_1).

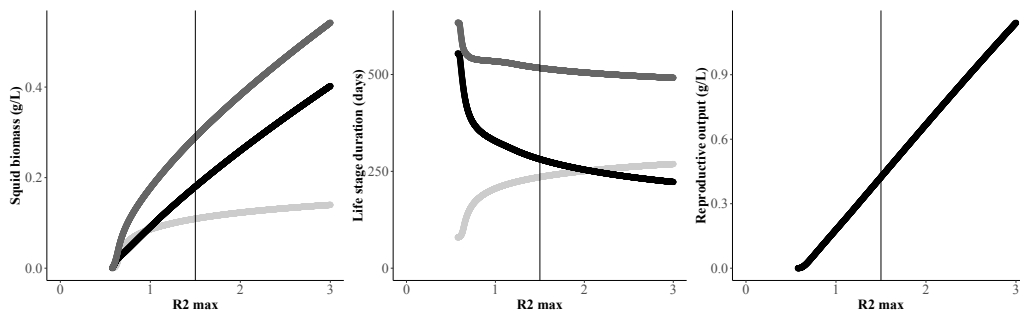


Figure 7.9.4: Equilibrium biomass (a), equilibrium life-stage duration (b), and equilibrium reproductive output (c), as an emergent outcome of changing nekton resource productivity (R_2).

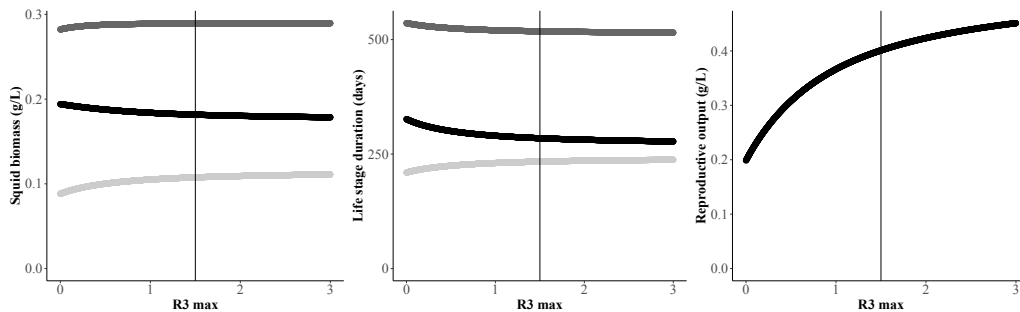


Figure 7.9.5: Equilibrium biomass (a), equilibrium life-stage duration (b), and equilibrium reproductive output (c), as an emergent outcome of changing zooplankton resource productivity (R_3).

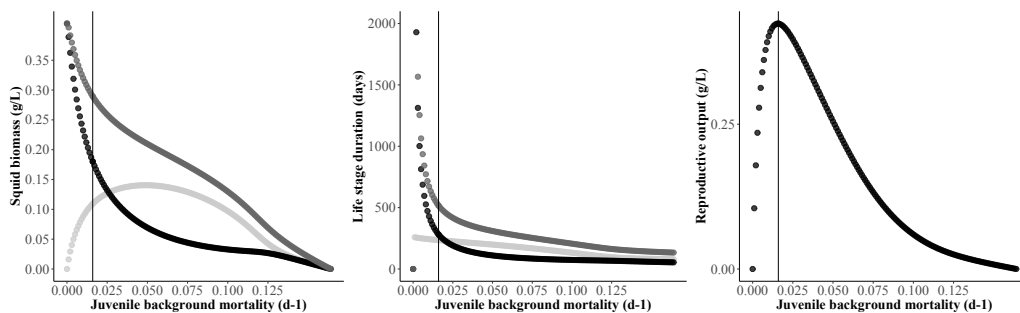


Figure 7.9.6: Equilibrium biomass (a), equilibrium life-stage duration (b), and equilibrium reproductive output (c), as an emergent outcome of changing juvenile background mortality

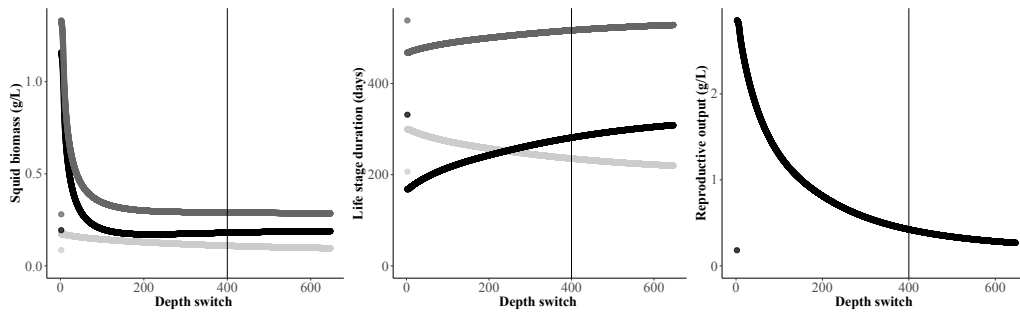


Figure 7.9.7: Equilibrium biomass (a), equilibrium life-stage duration (b), and equilibrium reproductive output (c), as an emergent outcome of changing depth switch

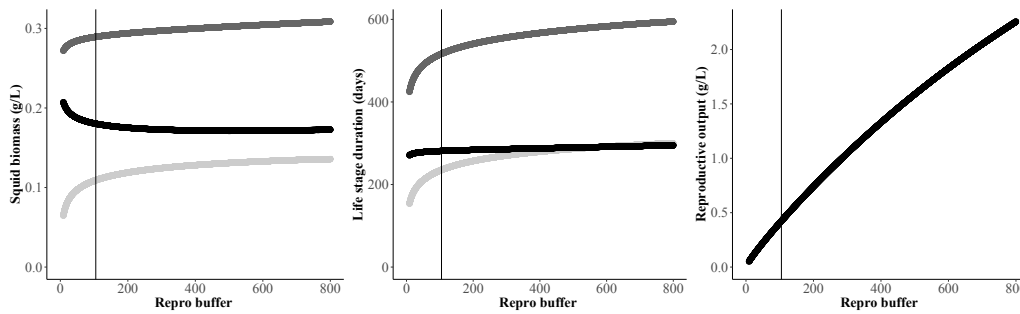


Figure 7.9.8: Equilibrium biomass (a), equilibrium life-stage duration (b), and equilibrium reproductive output (c), as an emergent outcome of changing reproductive buffer mass

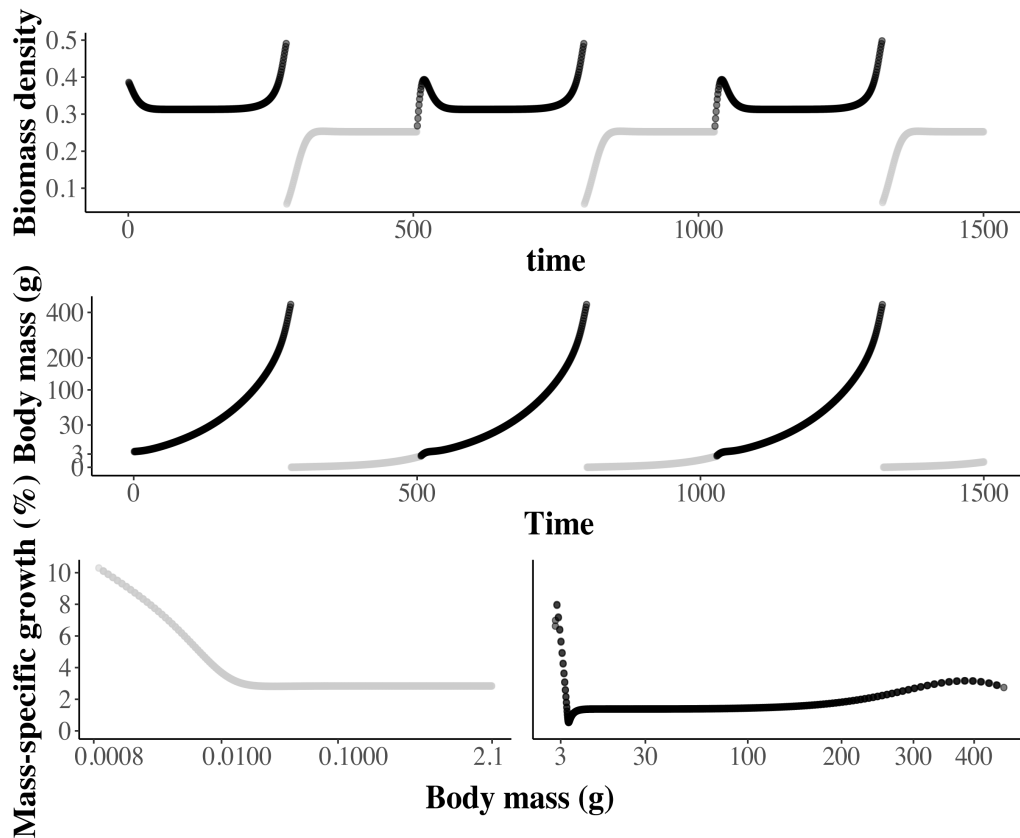
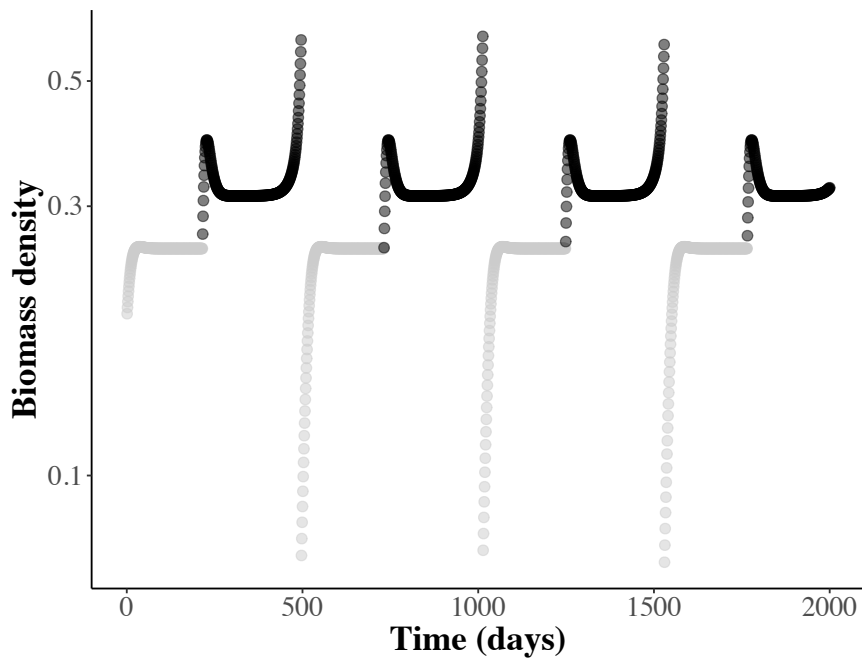
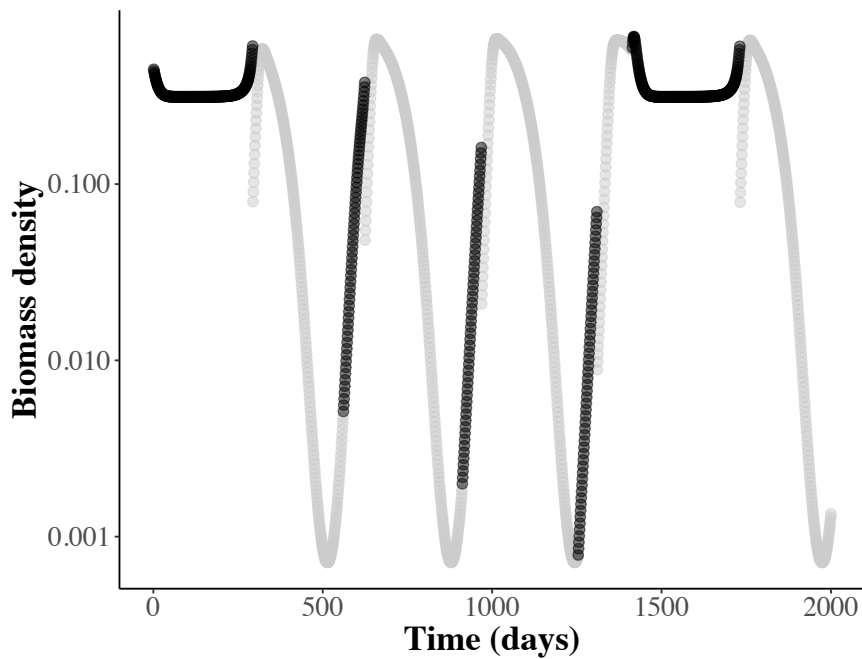


Figure 7.9.9: Time series population dynamics and individual growth curves without depth specific decreases in metabolic maintenance.



(a)



(b)

Figure 7.9.10: (Top) Time series population dynamics with low zooplankton resource seasonality ($\phi = 0$) and high zooplankton resource seasonality ($\phi = 0.8$). Total population biomass is reduced with high seasonality. The average population biomass is highest in the juvenile stage (black line) in aseasonal environments and highest in the paralarval lifestage (light grey line) in seasonal environments. In both cases dynamics are characterized by single cohort cycles, but in seasonal environments the bottleneck in the paralarval lifestage is lifted.

About the author

Mark Rademaker was born on the 8th of June 1993 in the agricultural municipality of the Noordoostpolder, the Netherlands. He spent the first years of his life growing up with his parents and older brother on the family farm near the village of Nagele. After finishing primary school, he gradually moved his way up through the Dutch secondary and tertiary educational system; starting with completing four years at the vmbo-tl at the Bonifatius Mavo college (2005-2009), followed by two more years of havo at the Zuyderzee college (2009-2011), both in the town of Emmeloord.

He went on to study a bachelor's in Animal Management with a major in Wildlife Management at Van Hall University of Applied Sciences in Leeuwarden (2011-2015). Multiple research internships working with endangered species on the island of Java during this time made him question how to examine population sizes. He therefore designed a research project to provide the first population estimation of the Bawean warty pig. Ultimately, this turned into a multi-year conservation project (BEKI) combining camera trap research with community outreach programs and capacity building of local forestry rangers. It also led to membership of the IUCN/SSC Wild Pig Specialist Group. In this role, he wrote the first Red List Assessment of the species. The conflicts between wildlife and agricultural development motivated him to move on and study Agricultural Business Management at Gadjah Mada University in Jogjakarta (2015-2017); concluding with a thesis on the financial feasibility of establishing cooperative farming to limit illegal grazing inside Baluran National Park.

The years abroad left him with the sense that regional (power) political issues dominate conservation and make it unethical to study and advise ways to manifest bottom-up change while not bearing any of the risks as a foreign academic. The difficult decision was made to move back to the Netherlands and re-establish a scientific life there. Back in the Netherlands, Mark completed a second master's degree in Forest & Nature Conservation at Wageningen University (2017-2019). Within the master's program he took as many specializations in (statistical) modelling as possible, combined with an internship on developing deep-learning species distribution models at Naturalis Natural History Museum in Leiden. With a lengthy educational experience under his belt, he finally felt confident enough to apply for a PhD position. Four years of hard work later, the outcomes of this PhD are presented in the booklet laying before you today.

Acknowledgements

A little over four years ago I bought a small book called ‘How to get a PhD’ by Estelle Phillips and Derek Pugh. At the time, I was about to graduate in Wageningen and doubting whether a PhD would be the best next step in life. The first few chapters of the book taught me doctorate studies have an uncanny ability to change one’s perspective upon (academic) life; for better or worse. Worryingly, a large part of this experience can be outside of your own control: subjected to the opaque world of academic procedures and the power inequalities between the PhD student, their supervisors, and institutional regulations. All this combines with subpar payment, and the (unscientific) fact that not a single PhD in history has been able to explain what they do and why it matters to close relatives. However, the book also showed me that many of the positive experiences that can be gained from a PhD are within your own control: treating a PhD as a job, not a lifestyle, exploring new interests outside of academia, and being wary of (older) peers who scamper upon ‘unmotivated students’ as ‘they only work office hours and hardly get burnouts anymore’. Ultimately, I realized that a PhD is similar to other challenges in life—rewarding in the right environment and challenging to potentially horrible in the wrong one. I’m grateful for the supportive environment created by all those around me during my PhD, both inside and outside of work. I can wholeheartedly say that doing a PhD has been an amazing experience thanks to all of you!

First of all, I would like to thank my primary supervisor Anieke van Leeuwen, as well as my co-promotor Isabel Smallegange, for having the trust (and guts!) to select a student with no background or experience in marine ecology for this PhD project. Our collaboration felt smooth from the start, and our discussions always made me feel supported in exploring the different areas of research that have formed this broad research. I remember how a certain global pandemic forced us to change quite a bit of the original research planning. Gradually, we moved away from empirical studies on fish ecology to broader issues in marine population ecology. The confidence and calm you radiated meant that even through these unusual times the PhD project never felt loose, and I never felt lost as to what we were striving for. Apart from the great day-to-day supervision, I would further like to thank you Anieke, for providing me with the opportunity to practice and gain confidence in formal theoretical ecology. I would also like to thank you Isabel for taking over the role of primary supervisor during the second year; impromptu coming up with a research idea that might have become my favorite chapter of this thesis! I would also

like to thank Tinka Murk and Myron Peck for their willingness to join the project as promoters so late in the PhD, and Tinka a very big thank you for all your help in sorting out the transfer to WIAS and processing the final bureaucratic steps in Hora Finita. It would all have taken much longer without you. I would also like to thank the other members of the ‘Lions Lab’ throughout the years (Bass Dye, Hanna ten Brink, Roeland Bom) and all the students, for the informal lunch meetings and general good working group vibe. I’m further indebted to you, Bass, for sharing the burden of the challenging whiteboard mathematics sessions designed by Anieke and Hanna. These sessions were marked by a peculiar blend of existential angst and struggle when forced to work through sets of equations before an audience, which was later replaced by the empowering and exhilarating sensation of successfully solving the problems.

From the ‘old’ PhD/COS guard I would particularly like to thank Carlijn, Clea, Jeras, Selin, Zoë, Bas, Eileen, Jeroen and Amin for making it such an easy transition moving to the island and establishing a social life there. Communal dinners, beach-breaks, gaming, potvis bar dancing, stargazing, and leisurely strolls; there was never a shortage of social activities. Carlijn and Jeras, I do miss the slightly competitive vibe we established in learning to play the piano. It was a great distraction during that long covid hiatus spent locked up inside the Potvis. Selin, you were the best officemate I could have hoped for as a new PhD, and I miss the BBQs that you and Nino would organize. I also have to thank you Selin, and Eileen (and of course Willie Nelson and Dante), for showing me that a PhD can be combined with responsible dog-ownership! Jon and Maryann, you two were a gift from heaven. Not only because your later BBQ sessions in Den Burg became a tasty tradition in their own right, but also by offering a safe new place for Tiago the half-tail hound when the situation became untenable for me. Speaking of dogs and their owners, there are some other colourful pairs that deserve mentioning here: Katharina (human) and rambunctious Tomke (dog), the only dog I know that growls when he wants to play. Lia, Byron (humans), and purebred alpha Bokkie (dog), the little * putting all the castrated studs in their place. Sterre, Michel (humans) and Lil’ Boef (dog), all-round sweetheart as long as there are treats around. Stanley (human) and floating butterfly Moochi (dog?), I think the question mark there says it all. You guys and furballs made the Potvis such a nice and lively place to live. Furthermore, you provided the ideal community for my own floofball Nanook (dog) to grow up in, although he might have never mastered growing up in the end. Nanook, it has truly been an awesome time since I found. Your enthusiastic greeting rituals ensure that I can’t help but to start every day with a smile, followed by picking all the hairs of my clothes. Also, don’t get too comfortable on the couch.

As fieldwork is not a given when you focus on data and models, I would also like to thank the following people for their receptiveness towards taking a ‘modeller’ aboard. The NIOZ fyke crew, particularly Siem, Marco, Bas, Robert, Luc, Dennis, and Anne; for their boating skills, their knowledge of the intricacies of setting up and removing a fyke, species identification, and sharing a memorable Dakar-style truck ride through the dunes at de Hors (too bad the shovel got stuck in the swamp). I would further like to thank Fleur, Machiel and Marie for the opportunity to join fieldwork expeditions to the Azores despite my inexperience in the field of cetaceans. Who knew observing pods of

whales all day from land or following them by boat through crystal clear waters could be so much fun? Just kidding, it is literally every marine ecologist's dream! Standing on the back of a shaking boat after a successful sperm whale tagging event followed by a big tail slap remains etched in my memory, as do all the breaches and amazing species diversity observed. Apart from fieldwork you have also been a great office and surftrip buddy Marie, and I thank you for always making sure there was plenty of chocolate or homemade brownies to go around. Evy and Allert, thanks for letting me join on the Navicula trip to catch and tag waders on Griend. Even if it was just for a few windy days, the memories of holding a knot in my hands and nighttime boat rides with the waters lighting up from all the noctiluca was amazing!

There are different groups to thank as well, with some overlap in their composition. The NIOZ Futsal team in all its weekly varying, but (almost) always competitive compositions (Tim, Matthijs, Allert, Michel, Jan-Dirk, Koen, Paul). Then there is the weekly COS bootcamp crew (Jena, Bram, Carlijn, Clea, Marie, Jan, Geert, Eva, Léon), and of course thank you Wilma as head of the bootcamp for keeping us all fit and balanced! During covid, the humbly named Original Beasts groups emerged (Misha, Nino, Amin). Thanks guys, for keeping up the workouts during these challenging times. I would also like to thank the more recent weekend trail-running group (Jon, Maryann, Charlotte, Léon, Rosa, Carlijn, Clea, Jan, Eva), and of course, the Potvis surf group (Bass, Tim, Floris, Clea, Matthijs, Paul). It was a delight to share the waves with you guys. I still think we should claim paal 15 as 'our' local spot and have NIOZ sponsor our wetsuits. Since I count birding as a sport, I would also like to thank Evy, Tom, and Tim for our sessions touring around the island. It is always nice when other people share the excitement of seeing a drably colored curlew sandpiper, tundra bean goose, or a fleeting glimpse of a nightjar. In the non-sporting section, I would like to extend a thanks to all the members joining the art-night group, whether weekly or briefly (Carlijn, Jena, Katharina, Marie, Evy). It was cool to see everyone working on their own piece, using their own medium, side-by-side, while sipping tea. Keep up the creative work!

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via de kabel kon kijken (toen die kanalen nog wat voorstelde), was dat zaadje van een carrière als natuurvorser misschien nooit geplant!

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MARK RADEMAKER