Planktivorous fish and environmental change: using mechanistic modelling to explore the underpinnings and general validity of expected responses

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Thesis for the degree of Philosophiae Doctor (PhD)
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Scientific environment

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Summary

The living conditions of marine and terrestrial organisms are currently changing at a rapid pace due to human activities. To predict how this will affect them, and hence to develop appropriate management and conservation strategies, we need to identify the fundamental drivers of their ecology and hence the mechanisms that underlie observed spatial and temporal patterns. Present-day climate change is associated with three universal ecological responses: shifts in distribution, shifts in phenology, and declining body size. In this PhD thesis I use mechanistic modelling to investigate the underpinnings and general validity of these three expectations for planktivorous fishes. In aquatic systems, planktivores constitute the link between lower and higher trophic levels. Hence, understanding the impacts on this group is crucial for reliable prediction of consequences of environmental change for marine ecosystems.

This PhD thesis contains three papers in addition to this synthesis. In the first two papers I develop different models to produce explanatory predictions of optimal **spawning time** and **body size,** and validate these predictions with observations from real life. I then explore the influence of environmental variation and discuss the implications of my findings for forecasting responses of planktivorous fishes to environmental change. In the third paper I use two models that reproduce observed patterns to forecast the influence of ocean warming on **spatial redistributions**. This work resulted in several unintuitive findings that can improve our understanding and prediction of environmental influences on planktivorous fishes.

The first paper shows that seasonality in the resource environments of both parents and their offspring is important for spawning time phenology, but that the relative importance of high offspring fitness (match between birth and conditions that maximize offspring survival) depends on resource dynamics at the feeding grounds of adults. Mismatches between spawning and optimal offspring conditions resulted from parents choosing to breed earlier or later to maximize their fecundity. Hence, our findings suggest that timing of spawning, as well as interannual and intraspecific variability in this trait,

could result from stronger selection on parents to optimize their annual routine to a different seasonal resource regime. Phenological traits have complex origins. Thus, to better understand and predict changes in phenology and their consequences in marine systems, I advocate for incorporation of both the parental and offspring perspective, for considering changes at different locations, and for modelling optimal annual routines, which describe how annual periodicity affects optimal activity schedules within the annual cycle.

Latitudinal variation in body size and recent body size declines in response to climate change are typically linked to gradients and changes in temperature and food abundance. In the second paper, we show that for planktivores that forage through vision, factors that affect the accessibility of prey are much more important for optimal body size and surplus energy. Their feeding rates are limited by the distance at which prey can be detected, hence prey size was the most influential environmental factor, and light availability was also important. This suggests that larger zooplankton and longer days in spring and summer at higher latitudes contribute to a latitudinal size cline in visually foraging planktivores. It also suggests that inferences based on temperature and prey abundance, or biomass, are likely to have limited predictive ability, and future work should prioritize research to improve predictions of body size shifts in this group.

The third paper explores how accounting for increasing light seasonality with latitude affects predictions of poleward shifts and redistributions of visual foragers under global warming. Using two planktivorous fishes with different lifestyles as examples: one that occupies the sunlit epipelagic zone, and one that that performs diel vertical migrations in and out of the dim to dark mesopelagic zone, we illustrate that shifts from lower to higher latitudes may be constrained by the long and dark winters at higher latitudes, and by increased predation risk. Contrary to the common expectation, our findings also suggest that ocean warming could lead to shifts towards the equator, and that the optimal direction of shift may vary between the seasons and among individuals of different body sizes. In the paper, we discuss the implications of our findings for predicting warming-driven redistributions in visual foragers.

In conclusion, even though the models in this PhD work are simple, they highlight several features that are likely to be important for reliable forecasting of responses of planktivorous fishes to climate change, and to environmental change in general. They also point to research that should be prioritized to improve future models, by indicating important drivers and sensitive parameters for which accuracy, and hence data collection and reliable prediction, is key.

List of publications

PAPER I

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PAPER II

Ljungström G, Claireaux, M, Fiksen Ø, Jørgensen C. Body size and climate change: zooplankton community is more important than temperature or food abundance in planktivore fish model. *Marine Ecology Progress Series*.

(in review)

PAPER III

Ljungström G, Langbehn, T, Jørgensen C. Increasing light seasonality with latitude: implications for forecasting of warming-driven redistributions in visual foragers

(manuscript)

Contents

INTRODUCTION

1. Organisms and their environment

Across the globe, marine and terrestrial environments are currently changing at a rapid pace due to human activities (Crutzen, 2002). This includes changes in climate regimes, fragmentation and destruction of habitats, and alterations of habitat quality due to chemical and nutrient release. Effects of these changes can already be seen at all levels of biological organization, from genes to individuals, to populations, communities, and ecosystems (Scheffers *et al.*, 2016). In order to develop appropriate management and conservation strategies, we need to anticipate how organisms will respond to forecasted environmental changes (Bonebrake *et al.*, 2018). This requires an understanding of the fundamental drivers of their ecology and hence of the mechanisms that underlie observed spatial and temporal patterns (Mouquet *et al.*, 2015).

Organisms are a product of their environment. The way they look, function, and behave have been shaped by natural selection through differential survival and reproductive success. To maintain its life, grow, and produce new life an organism has to acquire energy, but it must also avoid becoming food itself. Food availability and predation risk are therefore central in shaping organism form, function, and behaviour (Roff, 1992; Stearns, 1992). However, the amount of energy that an organism has at its disposal is not a simple function of food abundance, but is modulated by its own ability to acquire food, by competition from individuals of the same and other species, by the risk of being predated, and by abiotic factors such as light, temperature, and oxygen.

For visual foragers, light availability affects foraging rates (Aksnes and Utne, 1997), and more daylight hours in spring and summer thus lead to increased opportunities, while the darker winters restrict feeding. In poikilotherms, whose internal temperature varies with the ambient temperature, temperature influences nearly all biochemical rates and thereby the rate at which energy is taken up (digested) and lost (by metabolism) (Jobling, 1994; Brown *et al.*, 2004). This effect is stronger in aquatic than terrestrial environments, since organisms on land have greater physiological and behavioural flexibility with which to adjust their internal temperature. Temperature also affects oxygen uptake, and oxygen sets a limit to how much energy can be used through aerobic metabolism (Schmidt-Nielsen, 1997a). In addition to these factors, all life has to deal with the physical laws pertaining to the medium in which they live, set up by forces such as gravity and drag, and buoyancy in water but not in air (Schmidt-Nielsen, 1984).

Considering the multitude of factors that influence organisms, disentangling their relative effects on observed patterns may seem like an impossible task. One way to deal with this is to adopt a mechanistic approach, whereby potential processes that may account for observations are specifically defined and tested (Denny & Benedetti-Cecchi, 2012). Present-day climate change is observed and predicted to lead to three universal ecological responses: shifts in distribution, shifts in phenology, and declining body size (Pörtner *et al.*, 2014). In this PhD thesis I use a mechanistic approach to investigate the underpinnings and general validity of these three expectations for planktivorous fishes.

Planktivores play a central role in aquatic systems by determining the flux of energy from lower to higher trophic levels (Alder *et al.*, 2008). Hence, understanding impacts on this group is crucial for predicting consequences of environmental change for marine ecosystems. More specifically, I use mechanistic models to identify the drivers and underlying mechanisms of optimal strategies that maximize individual fitness in terms of reproductive phenology (**Paper I**), body size (**Paper II**), and distribution dynamics (**Paper III**). I then discuss the implications of my findings for forecasting responses of planktivorous fishes to environmental change. In the next sections I introduce the general frameworks that the work in this PhD thesis is based on (1.1, 1.2, and 1.3). I then move on to present the three universal responses to climate change in more detail (2.1, 2.2, 2.3), discuss when and why mathematical models can be useful (3), and introduce the organisms and systems that are used in the analyses (4).

1.1 Life history theory

"How should an individual allocate time and resources to growth, reproduction, and survival over its lifetime?" This is the general life history problem (Schaffer, 1983) and life-history theory seeks to explain how external and internal constraints and opportunities impact survival and reproduction at different stages, and thereby affect how such strategies evolve (Roff, 1992; Stearns, 1992). Spatial and temporal variation in resources and mortality impose external constraints on an organism, whereas the connection between traits and how they can vary lead to internal trade-offs, such as investment in reproduction versus growth, and in current versus future reproduction and survival (Stearns, 2000). A classic problem from life history theory, which also illustrates its difficulties, is the optimal allocation of energy into current and future reproduction under different levels of mortality. When the prospects of survival and hence future reproduction are low, life-history theory predicts that individuals that grow fast, mature early, and invest a large proportion of their energy into each reproductive event have a higher reproductive success than individuals with the opposite strategy (Michod, 1979; Roff, 1981). Conversely, a higher energy investment in growth and later maturation is predicted when the risk of mortality is low, allowing for an increase in fecundity. This may appear straightforward but several factors complicate these predictions. For example, the risk of predation typically decreases with increasing size (Roff, 1992; Charlesworth, 1994), and fast growth often leads to increased mortality (higher foraging-related predation risk; Billerbeck et al., 2001; Lankford et al., 2001; Arnott et al., 2006; Jørgensen et al., 2014). In addition, seasonality in resource availability and mortality risk, and state-dependent variation, lead to complex trade-offs between when and how to invest time and energy in growth, reproduction, and survival (Varpe, 2017).

1.2 Life in seasonal environments

Life in seasonal environments is challenging: the year typically consists of a productive and an unproductive season and organisms need to schedule their activities according to the challenges that these seasons present. During the productive part of the year, energy has to be acquired and allocated to fundamental processes such as growth and reproduction (to immediate reproduction for income breeders, or as stores for capital breeders; Jönsson, 1997), and energy reserves are often needed to survive the unproductive season. Since both body size and stores are typically associated with survival and reproductive success (Peters, 1983; Ejsmond *et al.*, 2015), this leads to many life-history trade-offs. Seasonal variation in predation risk may further constrain how organisms time their activities. Thus, in seasonal environments future consequences of alternative actions become particularly important (e.g. Ejsmond *et al.*, 2010; Varpe, 2017). Given their close link to fitness, it is reasonable to assume that natural selection has found optimal solutions to these trade-offs, and hence, that the way organisms time their activities over the year maximizes their lifetime reproductive success (Stearns, 1992; McNamara & Houston, 2008). This is captured by the concept of **optimal annual routines**, which describes how annual periodicity affects optimal activity schedules within the annual cycle (Feró *et al.*, 2008; McNamara & Houston, 2008; Barta, 2016).

In seasonal environments optimal behavioural and energy allocation decisions do not only depend on time of the year, but typically also on individual characteristics, such as energy reserves or body size (McNamara & Houston, 2008). Moreover, the reproductive success of a parent hinges on the success of its offspring. When both parental and offspring needs vary over the annual cycle, what is optimal from an offspring's perspective may differ from that of its parent, resulting in a parent-offspring conflict (Trivers, 1974). The outcome of such a conflict can have important implications for fitness by compromising optimality for either one, or both parties (Drent & Daan, 1980; Rowe *et al.*, 1994; Varpe *et al.*, 2007). All these non-linearities and feedbacks make verbal predictions destined to fail and quantitative analysis necessary. A useful tool for dealing with this type of complexity is **state-dependent life-history models** that use dynamic programming to find optimal strategies by maximizing lifetime reproductive success, taking both internal and external trade-offs into account (Houston & McNamara, 1999; Clark & Mangel, 2000).

1.3 Local adaptation and phenotypic plasticity

Populations of the same species that live at different latitudes experience different seasonal regimes. This may translate into variation in life-history traits and behaviours, but there can also be selection to homogenize such differences (countergradient variation; Conover and Present, 1990; Conover and Schultz, 1995). Intraspecific variation can have a variety of underpinnings, which may in turn affect how a population responds to, and is affected by, environmental change. In spatially heterogeneous environments, resident populations may be better adapted to their local environment than foreign populations. If this is the result of divergent selection, i.e. a genotype-by-environment interaction for fitness, it is referred to as a local adaptation (Williams, 1966). Temporal variation in selection may counteract local adaptation and instead promote the evolution of adaptive phenotypic plasticity, whereby a genotype that adjusts across multiple environments may be favoured over single genotypes that are superior in each environment (Stearns, 1992; Scheiner, 1993; Via *et al.*, 1995). While adaptive phenotypic plasticity may allow a population to perform well under environmental fluctuations as long as these are within the normal range of variation (DeWitt *et al.*, 1998; Ghalambor *et al.*, 2007), local adaptation can be thought of as specialization to one environment that may lead to costs in other environments (Kawecki & Ebert, 2004). However, plastic responses to environmental variation are not always adaptive. For example, environmental conditions that fall outside of the historically experienced range often induce non-adaptive plasticity as a passive consequence of environmental stress (Ghalambor *et al.*, 2007; Snell-Rood *et al.*, 2018).

Whether phenotypic plasticity facilitates or constrains evolution is a subject of much debate (see Fox *et al.*, 2019, and references therein for a recent review). In a novel environment, adaptive plasticity could assist evolution by allowing a population to persist long enough for selection to act on standing genetic variation (Price *et al.*, 2003; Ghalambor *et al.*, 2007). Conversely, by weakening selection adaptive plasticity could also constrain evolution, and non-adaptive plasticity has been shown to potentiate evolution by increasing the strength of selection (Ghalambor *et al.*, 2015). In addition, environmental conditions that fall outside of the generally experienced range may reveal cryptic genetic variation, exposing novel phenotypes to selection and increasing genetic variation (Hoffmann & Merilä, 1999; Ledon-Rettig *et al.*, 2014). Identifying the processes that underlie variation in traits and behaviours is thus important for understanding how traits evolve, and how evolution influences and is influenced by plasticity. Ultimately, such insights are also required to predict responses of populations and species to environmental change (Ghalambor *et al.*, 2007; Visser, 2008; Chevin *et al.*, 2010; Snell-Rood *et al.*, 2018).

2. Universal ecological responses to climate change

Since the industrial revolution the Earth-Atmosphere system has accumulated heat at a rapid pace, and from 1971-2001 about 93% of this heat was absorbed by the ocean (Rhein *et al.*, 2013). This has led to a rise in water temperature in the upper 75 m of 0.11°C per decade and of 0.015°C per decade at 700 m depth. However, there is considerable spatial variation and high latitudes have warmed the most, especially the North Atlantic (Rhein *et al.*, 2013). By the end of the 21st century, temperatures in the upper 100 m of the ocean are predicted to rise by 0.6°C (RCP2.6) to 2.0°C (RCP8.5), but these changes will not be regionally uniform (Collins *et al.*, 2013). In combination with altered wind and precipitation patterns and more frequent extreme events (Collins *et al.*, 2013), warmer temperatures can influence the ocean in several ways. This includes changes in circulation patterns, stratification and mixing, dissolved oxygen concentrations, turbidity, and sea level rise (Rhein *et al.*, 2013). Moreover, a higher atmospheric CO_2 concentration is leading to a decrease in ocean pH (Rhein *et al.*, 2013). This is influencing marine ecosystems at all levels, from direct effects on individual physiology and behaviour, to changes in population productivity, species interactions, and the structure and function of communities (Rijnsdorp *et al.*, 2009; Doney *et al.*, 2012). Out of these changes three general patterns have emerged: shifts in 1) distribution and 2) phenology, and 3) declining body size.

2.1 Shifts in distribution

The most frequently observed response of marine organisms to climate change is shifts in distribution, and the general direction is towards higher latitudes and greater depths (Poloczanska *et al.*, 2013, 2016; Garciá Molinos *et al.*, 2017). Terrestrial species are also moving, but poleward range expansions are much faster in the ocean than on land (ocean: 7.2 ± 1.35 km yr^{-1}, Poloczanska *et al.*, 2013; 5.92 ± 0.94, Lenoir *et al.*, 2019; land: 1.76 ± 0.29, Chen *et al.*, 2011; 1.11 ± 0.96, Lenoir *et al.*, 2019), presumably due to the high rates of propagule production and dispersal typical of marine organisms (Poloczanska *et al.*, 2013). Correspondingly, highly mobile and dispersive pelagic organisms, including phytoplankton, bony fish, and invertebrate zooplankton show the fastest expansions (Poloczanska *et al.*, 2013). Furthermore, whereas leading-edge expansions are faster than trailing-edge contractions in terrestrial taxa, both range edges of marine taxa appear equally responsive to warming (Sunday *et al.*, 2012; Lenoir *et al.*, 2019). This has been explained by a closer correspondence between thermal tolerances and latitudinal ranges in marine than terrestrial organisms (Sunday *et al.*, 2012). However, longitudinal and equatorward shifts are also observed and local climate velocities, describing the geographic movement of temperature isotherms over time (Loarie *et al.*, 2009; Burrows *et al.*, 2011), better predict rates and directions of distributional shifts in the ocean than the general assumption of poleward movement (Pinsky *et al.*, 2013; Burrows *et al.*, 2014; Sunday *et al.*, 2015). Marine climate velocities are fastest in equatorial and Arctic regions (Burrows *et al.*, 2011), and global models predict major losses of diversity and biomass in the tropics and the highest invasion rates for the Arctic (Cheung *et al.*, 2009; García Molinos *et al.*, 2015; Jones & Cheung, 2015). In fact, boreal fish communities are already expanding into the Arctic, causing changes in community structure and ecological interactions (Fossheim *et al.*, 2015; Kortsch *et al.*, 2015).

Since the early 1990s, climate change-driven species redistribution has been a rapidly growing research field (Bonebrake *et al.*, 2018). The vast majority of publications within the field has documented patterns of change (discussed in Bates *et al.*, 2014, and

Bonebrake *et al.*, 2018) and focused on thermal tolerances or niches (e.g. Buckley & Kingsolver, 2012; Sunday *et al.*, 2012, 2014; Hiddink *et al.*, 2015), and recently also on traits (Angert *et al.*, 2011; Pinsky *et al.*, 2013; Pacifici *et al.*, 2015; Sunday *et al.*, 2015), to understand these patterns. Recently, well-developed theories have also been put forward to explain how climate change leads to range shifts by affecting range expansion and contraction dynamics (Bates *et al.*, 2014; Lenoir & Svenning, 2015; Donelson *et al.*, 2019). To predict such processes, the authors of these studies highlight the need for a mechanistic and process-based understanding of how climate change affects the performance of individuals and populations across latitudes.

2.2 Shifts in phenology

Marine organisms are also shifting their phenologies in response to seasonal changes in temperature (Poloczanska *et al.*, 2013). From 1960-2009 spring temperatures arrived earlier by 2.08 and 2.52 days per decade in the Northern and Southern Hemisphere, respectively, and colder fall temperatures were delayed by 1.73 and 2.28 days per decade (Burrows *et al.*, 2011). In a seminal study, Poloczanska and colleagues (2013) estimated changes in phenology for 52 marine taxonomic or functional groups across the globe. They found that overall spring and summer phenology had advanced by approximately 4.4 days per decade, but that there was great variation among groups. For example, while phytoplankton blooms occurred about 6.3 days earlier per decade, invertebrate zooplankton and larval bony fish had advanced their spring phenology by more than 11 days per decade. In contrast, phyto- and zooplankton showed a slower but similar advancement in summer, of about 4.6 days per decade (Poloczanska *et al.*, 2013). These variable responses suggest that climate change is affecting trophic interactions, which may have consequences for population dynamics, and for the structure and function of communities and ecosystems (Stenseth *et al.*, 2002; Durant *et al.*, 2007; Thackeray *et al.*, 2010).

At a finer scale, all organisms do not show advances in phenology. For example, across 66 plankton taxa in the North Sea (including seasonal fish and invertebrate larvae;

1958–2002) spring- and summer-peaking plankton peaked earlier, while autumn- and winter-peaking species showed a delay (Edwards & Richardson, 2004). Intraspecific differences, some populations spawning earlier and some later, have also been observed in molluscs and fish (Edwards & Richardson, 2004; Moore *et al.*, 2011; Asch, 2015). Moreover, an altered timing of annual migrations to feeding and breeding grounds has been reported for several seabirds, as well as for some migratory fish (reviewed by Poloczanska *et al.*, 2016).

2.3 Body size declines

Reductions in body size have been suggested to be the third universal response to climate change (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011; Cheung *et al.*, 2013). This trend is particularly strong in aquatic environments (Forster *et al.*, 2012; Horne *et al.*, 2015), and although harvesting is likely partly responsible, current rates of decline are faster than expected from fishing alone (Baudron *et al.*, 2011; Audzijonyte *et al.*, 2013). Several explanations have been put forward, including Bergmann's rule (Bergmann, 1847), which relates body size to thermoregulatory capacity in endotherms, and the temperature-size rule (Atkinson, 1994, Angilletta and Dunham, 2003; Kingsolver and Huey, 2008), describing the effect of temperature on growth and maturation in ectotherms. In aquatic habitats, warming-related constraints on aerobic respiration have been proposed to cause size reductions in species that breathe with gills or similar structures (Pauly, 1981; Atkinson *et al.*, 2006; Cheung *et al.*, 2011; Verberk *et al.*, 2011; Forster *et al.*, 2012), but this hypothesis has received criticism (e.g. Brander *et al.*, 2013; Lefevre *et al.*, 2017; summarized in Audzijonyte *et al.*, 2019). However, it is unclear whether rising temperatures is a universal driver of recent body size declines; changes in food availability and quality could also be an explanation (Gardner *et al.*, 2011). What is also unclear is by what mechanisms temperature and food are acting and interacting to produce smaller body sizes (see reviews by Sheridan and Bickford, 2011; Teplitsky and Millien, 2014; Audzijonyte *et al.*, 2019).

3. Understanding the world through mechanistic modelling

In order to make reliable predictions of how organisms will respond to future environmental change, we need a mechanistic and process-based understanding of the causes of observed patterns (Angilletta & Sears, 2011; McMahon *et al.*, 2011; Mouquet *et al.*, 2015; Urban *et al.*, 2016). However, since many environmental factors are correlated and some are changing in parallel over time without a causal link between them, disentangling their relative effects on adaptive and non-adaptive trait variation is easier said than done. Field studies can be good for detecting patterns, but they only offer a snapshot in time and space, and observations are influenced by many confounding factors. To be able to assess causality, experimental studies are needed. However, these also have their limitations, including practical, ethical, and legal issues. Within this PhD research I use another method, mathematical modelling, to identify drivers and underlying mechanisms of adaptations in zooplanktivorous fishes. I then use my findings as a basis for exploring expected responses of this group to environmental change, and climate change in particular.

Mathematical models are good for dealing with questions that would otherwise be difficult to assess. They can be seen as virtual laboratories and allow for integration of multiple interacting processes, non-linearity, and stochastic dynamics. As such, mathematical models can be used to explore effects of different drivers in isolation, or in combination with one another. Furthermore, by connecting processes at one level to responses at another, models that build on functional relationships (mechanistic models) allow for investigation of the mechanisms underlying observed and potentially observable patterns. Since this is key for making reliable forecasts, it is concerning that most models that have been used to predict ecological responses to climate change to date ignore mechanisms and instead extrapolate current and past statistical correlations into the future, especially since novel combinations of abiotic and biotic factors are likely in the future (Norberg *et al.*, 2012; Urban *et al.*, 2012; Bocedi *et al.*, 2013).

Models do however not stand on their own but form an integral part of the scientific method, together with field- and lab-work (Hilborn & Mangel, 1997; Angilletta & Sears, 2011). Ideally, a model should be defined to describe one or several mechanisms that could explain an observation, and should generate **explanatory predictions**, i.e. predictions about what should be expected if the theory underlying the model is correct, that can be validated with data from the field or the lab. By estimating parameter sensitivities, better measurement of sensitive parameters can be targeted. Through an iterative process of prediction, validation, and revision (*sensu* Platt, 1964) the predictive accuracy and precision of the model can then be improved. When predictions and observations agree, one may conclude that a mechanistic link between a variable and a response has been established. This process is important for making reliable **anticipatory predictions** of what the world will be like under different scenarios of environmental change (Mouquet *et al.*, 2015; Urban *et al.*, 2016). Moreover, models can help generate new hypotheses and thus guide sampling and experiments in the field and in the lab.

4. Model species and systems

Planktivorous fishes, generally referred to as forage fish, play a central role in aquatic systems by determining the flow of energy from lower to higher trophic levels (Alder *et al.*, 2008). They are highly specialized for feeding on small zooplankton and are key prey for larger fish, sea birds, and marine mammals. Thus, to predict the consequences of environmental change for marine ecosystems, it is crucial to understand the impacts on this group. Herring is a widely distributed zooplanktivore that occupies the upper sunlit part of the water column, the epipelagic zone. The Atlantic herring *Clupea harengus* is found across the North Atlantic from Spitsbergen in the north to the northern Bay of Biscay in the south, and from the west coast of Europe to the east coast of Canada and the United States (Whitehead, 1985). On the north Pacific side, Pacific herring *Clupea palasii* are distributed in the east from the Beaufort Sea, Alaska, to northern Baja California, Mexico, and from the Arctic Ocean in Russia to Japan and the Yellow Sea, Korea, in the west (Hay *et al.*, 2008). This wide distribution makes herring highly suited for studying environmental influences on geographic trait patterns.

Many pelagic fish populations, including herring, perform annual horizontal migrations. This includes feeding migrations to take advantage of the increase of surface plankton in spring, and of longer days and thus improved foraging opportunities (Varpe & Fiksen, 2010). Spawning migrations to areas where conditions are favourable for spawning (suitable habitat and availability of partners) and larval survival are also common, and so is overwintering in areas that seem to promote energy saving and reduced predation (Harden Jones, 1968; but see Huse *et al.* (2010) for an argument for why overwintering locations are not nessesarily optimal).

Herring is the main study species in this PhD thesis, but in **Paper III** we also include a mesopelagic planktivorous fish to explore how different life styles affect our predictions. Mesopelagic fish occupy the dim to dark twilight zone and are the most abundant fish on Earth, estimated to ca. 15 billion tons, or 10-20 times the combined biomass of all other fish (Irigoien *et al.*, 2014). We study an ecotype that performs diel vertical migrations, the most prevalent migration pattern in the ocean (Hays, 2003). The eyes of mesopelagic fish are adapted to low light levels (De Busserolles & Marshall, 2017). Thus, by migrating to greater depths during the day and rising to the surface at night, they seem to track preferred light intensities (Røstad *et al.*, 2016a, 2016b), possibly representing their "antipredation window" (Langbehn *et al.*, 2019), i.e. the range of light intensities where they have an advantage over their predators because they can feed at lower light intensity than the predator can efficiently find them (Clark & Levy, 1988; Scheuerell & Schindler, 2003). We use myctophids and the species *Benthosema glaciale* to parameterize our model, the most numerous species in the Norwegian Sea and belonging to the most well-studied group of mesopelagic planktivores.

THESIS APPROACH AND AIMS

In this PhD thesis I use mechanistic modelling to identify the drivers and underlying mechanisms of **optimal reproductive phenology**, **body size** and **distribution** in planktivorous fishes. Focusing on optimal strategies, i.e. trait values and behaviours that maximize individual fitness allows me to explore several **general questions** about current and future spatial and temporal patterns, such as:

1. What are drivers of an observed life-history strategy or behaviour?
2. Do intraspecific differences represent local adaptation?
3. What environments promote local adaptation versus adaptive phenotypic plasticity?
4. What are the drivers of an observed change in a life-history strategy or behaviour?
5. What type of responses would be adaptive under different scenarios of environmental change, and what are the consequences for individual and population performance?
6. And last but not least, what are the mechanisms that underlie current and forecasted patterns?

The **specific aims** of my thesis are to:

1. Point to possible drivers of evolved patterns in **spawning time** in migratory fish populations, and assess the potential magnitude of their effects on spawning time variability and change (**Paper I**).
2. Point to possible drivers of evolved patterns in **body size** in visually foraging planktivores, and assess the likely influence environmental change on optimal body size and surplus energy (**Paper II**).
3. Explore how increasing seasonality in light availability with latitude may affect energy budgets and survival, and thereby **spatial redistributions** of planktivorous fish under ocean warming (**Paper III**).

In **papers I** and **II** I use different modelling frameworks to produce explanatory predictions about optimal **spawning time** and **body size**, and validate these predictions with observations from real life. I then explore the influence of environmental variation and discuss the implications of my findings for making anticipatory predictions of responses of planktivorous fish to environmental change. In **Paper III** I use two models that reproduce observed patterns to forecast how ocean warming will influence **spatial redistributions**. All models are mechanistic, i.e. they build on functional relationships, but they vary in detail, which in turn affects the detail with which conclusions about underlying processes can be made.

In **Paper I** we use state-dependent life-history theory by stochastic dynamic programming (Houston & McNamara, 1999; Clark & Mangel, 2000) to explore potential drivers of optimal spawning time, and of spawning time variability within and among populations of migratory fish. To incorporate both the adult and offspring perspective, we investigate how conditions that affect only parents (food availability and survival at adult feeding grounds) influence optimal reproductive timing, while accounting for seasonality in offspring recruitment probability. We apply our model to migratory Pacific herring spawning in Puget Sound, WA, USA, to give a potential explanation for why 20 subpopulations of herring spawn consistently at this location, but at different times of the year, and why their spawning times have shifted in recent years.

In **Paper II** we use a model that incorporates explicit mechanisms for vision-based feeding and physiology to investigate the influence on optimal body size from several biotic (prey size, prey energy content, and prey abundance) and abiotic factors (temperature, latitude, and water clarity) known to affect foraging rates and bioenergetics in planktivorous fishes. In visual planktivores, feeding rate is size-dependent: both visual range and swimming speed increase with size and larger fish therefore have a greater encounter rate with prey. However, handling prey takes time which limits the rate at which prey can be ingested, and this ceiling is relatively insensitive to size. Further, internal constraints set by digestive capacity determine how much food can be digested and this capacity also increases with size, as well as with temperature. Hence, one of these processes always limits the processing capacity of food. Moreover, metabolic rate determines how much energy is lost and this rate also increases with size and temperature, resulting in potential surplus energy first increasing then decreasing with size. It is needless to say that understanding and predicting how all these factors come together to determine optimal body size under different environmental conditions would be difficult without a model. We apply our model to herring in the Norwegian Sea and North Sea to identify underlying drivers of the difference in body size observed between herring in these two neighbouring systems.

Paper III is set out to explore how accounting for increasing light seasonality with latitude affects predictions of poleward shifts and redistributions of visual foragers under global warming. Since warmer temperature affects the performance of individuals and populations through its direct effect on individual physiology, and the modulating effect of predators, we decompose the problem. We use the model from **Paper II** to quantify the effect of warming on overwinter energy stores and on the annual energy budget of an epipelagic planktivore. Using a state-dependent dynamic optimization model that includes predation pressure, we also predict the combined effect of warming and predation risk on optimal behavioural strategies and population performance in a mesopelagic planktivore that performs diurnal vertical migrations. Both analyses are run across a latitudinal gradient and with ocean warming, such that we can explore the impact of warmer temperature on performance at different latitudes. In the paper, we discuss the implications of our findings for predicting warming-driven redistributions in visual foragers.

Before moving on to the discussion I will justify why I have chosen to omit oxygen as a potential driver of changes in traits and behaviours of our model organisms under ocean warming. Since the solubility of oxygen in water decreases with increasing temperature, a warming-driven decline in oxygen concentration is projected for the future ocean (Hoegh-Guldberg *et al.*, 2014). This could constrain oxygen budgeting and so could a warming-driven increase in metabolic oxygen demand. The potential implications of this for marine life have been discussed and debated at length, and I will not reiterate those discussions here (e.g. see Pörtner, 2010; Lefevre *et al.*, 2017, 2018; Audzijonyte *et al.*, 2019). In summary, this is likely to affect some marine organisms more than others and will depend on things like stage and style of life, habitat, and geographic location. For example, surface waters are constantly supplied with oxygen through air-sea gas exchange and from photosynthesizers, while deeper waters rely on mixing and circulation. This makes demersal fish generally more vulnerable to reduced oxygen levels than pelagic fish (Wu, 2002). Moreover, coastal waters are more prone to deoxygenation than open waters; they are typically more stratified and exposed to eutrophication (Diaz & Rosenberg, 2008). Our primary model species, herring, occupy the epipelagic zone in relatively cold waters, and the majority of herring populations forage in the open ocean. Moreover, they feed on zooplankton that graze on oxygen-producing phytoplankton during the bloom. Thus, other factors are likely to be more important as constraints on the biology of adult herring than oxygen, and presumably also on that of other adult planktivorous fishes that feed in the epipelagic zone of open oceans. Nevertheless, oxygen could be a constraint during other life stages or periods of time, such as during overwintering in coastal waters or in fjords (Óskarsson *et al.*, 2018). Oxygen is presumably more important for mesopelagic fishes, and some studies have connected their migration depth with distribution of dissolved oxygen (Bianchi *et al.*, 2013; Netburn & Koslow, 2015). However, mesopelagic fish are also found in oxygen-depleted waters (Tont, 1976; Klevjer *et al.*, 2016; Aksnes *et al.*, 2017), suggesting that they may not be that sensitive to variation in oxygen.

DISCUSSION

Mechanistic modelling may reveal unintuitive effects

Mechanistic models can help us explore simple as well as complicated questions about the real world. By building on functional relationships, they can fill in missing links and processes, and thereby advance our understanding of how systems work. In fact, the greatest advances in science often occur when theoretical predictions do not fit with intuitive assumptions or observations (Hilborn & Mangel, 1997). This PhD work resulted in several unintuitive findings.

Phenology

Most research on spawning phenology in fish focus on offspring (Wright & Trippel, 2009). This is natural, since timing of birth is crucial for offspring fitness in many species, and particularly in seasonal environments (Reznick *et al.*, 2006; Varpe *et al.*, 2007; Varpe, 2017). **Paper I** shows that resource dynamics at the feeding grounds of adults can influence optimal timing of reproduction, even when the environmental conditions that maximize offspring survival are kept constant. We also show that a mismatch between spawning and optimal offspring conditions could be the optimal outcome of selection on parents given consequences for their offspring, and may result from a parent choosing to spawn earlier or later to maximize its fecundity. These are both unintuitive results. Ever since Johan Hjort presented his famous "critical period" hypothesis (Hjort, 1914) to explain recruitment variability in fish populations, one of the most common assumptions in fisheries science is that spawning time has evolved so that offspring encounter conditions that promote their survival, and that a poor temporal match between the peaks of offspring food demand and supply leads to recruitment failure (reviewed in Houde 2008). Our findings suggest that timing of spawning, as well as interannual and intraspecific variability in this trait, could be driven by stronger selection on parents to optimize their annual routine to a different seasonal resource regime. Moreover, since fecundity and recruitment are positively correlated in many fish populations (Lambert, 2008), they also suggest that high adult fecundity could benefit recruitment even when there is a suboptimal match between timing of birth and conditions that maximize offspring survival.

Body size

One of the most well-studied biogeographic patterns is the tendency of organisms to be smaller at higher temperatures and lower latitudes, and larger at lower temperatures and higher latitudes, and biologists have long been trying to explain the underlying mechanism (discussed in Blackburn *et al.*, 1999; Angilletta *et al.*, 2004; Millien *et al.*, 2006; Teplitsky and Millien, 2014). The two most common hypotheses: Bergmann's rule (Bergmann, 1847) and the temperature-size rule (Atkinson, 1994, Angilletta and Dunham, 2003; Kingsolver and Huey, 2008), link size differences directly to a latitudinal gradient in temperature. Others suggest that increasing seasonality in food abundance and quality with latitude is the primary cause (reviewed in McNab, 2010; Watt *et al.*, 2010; Teplitsky and Millien, 2014; Vinarski, 2014). In **Paper II** we show that for a planktivore fish that forages through vision, temperature and food abundance cannot predict body size differences between two populations that occupy different latitudes. Rather, the model suggests that it is differences in the size-structure of their zooplankton communities that is the primary cause. For visual foragers the size of prey is important for the distance at which they can detect their prey and hence prey size is a limiting factor for feeding rates.

The availability of light also modifies prey detection distance, and more light, both on a daily (higher latitude) and hourly (higher water clarity) scale, allowed for higher consumption and therefore a larger optimal size. This suggests that longer days in spring and summer at higher latitudes contribute to a latitudinal size cline in visually foraging planktivores. Furthermore, since larger zooplankton are typically found at higher latitudes (Beaugrand *et al.*, 2002; San Martin *et al.*, 2006), this could also contribute. In agreement with the temperature-size rule, warmer temperatures were associated with smaller optimal sizes. This was the result of faster digestion, leading to prey encounter- or handling time-limitation and thus surplus energy maximization at a smaller size. This mechanism is different from those previously proposed to cause the temperature-size rule (Atkinson, 1994; Angilletta & Dunham, 2003; reviewed by Audzijonyte *et al.*, 2019). Moreover, contrary to the intuitive result of a more constrained energy budget with higher temperature, the level of surplus energy was not affected, suggesting that a temperature-size relationship could arise even with a conserved energy budget.

Distribution

In **Paper III** we show that increasing light seasonality with latitude has important implications for energy budgeting and safe foraging in visual foragers. This is not a new insight (e.g. Kaartvedt 2008, Varpe & Fiksen 2010, Sundby et al. 2016), but some of our findings are. In our analysis of an epipelagic planktivore, latitude had an inconsistent effect on individuals of different sizes. At lower latitudes, small individuals were predicted to have the highest performance, while large individuals did best at higher latitudes (Fig. XX B1). This resulted from different mechanisms limiting energy intake: small individuals were digestion-limited and profited from faster digestion in warmer waters (see Q4 for a discussion of this result), whereas large individuals were limited by handling time or encounter rate and benefitted from a lower metabolic cost in colder waters and increased foraging opportunities with more daylight hours (Fig. B). According to these findings, we should expect maximum body size in planktivorous fishes to increase with latitude due to a selective advantage of being small further south and large further north.

This extends the findings from **Paper II**, which are based on the analysis of separate effects of variation in environmental factors, at one latitude alone. In **Paper III** we investigate the combined effect of latitudinal variation in the seasonality of light, temperature, and prey availability. In the warming scenario, the optimal body size at any latitude became smaller; larger individuals that were handling- or encounter-limited suffered from a higher metabolic cost, while smaller individuals that were digestion-limited benefitted. Thus, according to our predictions, smaller individuals can maintain their current level of performance *in situ* under ocean warming, suggesting that they will not have to shift in space. In contrast, larger individuals will have to shift to higher latitudes to increase feeding opportunities. Hence, we identify two warming-driven processes that have not previously been associated with recent body size declines: 1) selection for smaller phenotypes due to faster digestion and thus handling- or encounter-limitation at a smaller size (also found in **Paper II**), and 2) poleward shifts of larger individuals. Distribution shifts and body size declines are generally treated as two separate responses to climate change, but here we identify a mechanism that links these two responses.

In our analysis of mesopelagic fish, we found that the light summer nights above the polar circle prevent safe foraging and therefore led to low energy acquisition and high predation mortality, making polar waters population sinks for mesopelagic fish. This is likely to explain their low abundance in Arctic waters, as discussed in detail in Langbehn et al. (*in prep*). Warmer temperature and the subsequent increase in metabolic demand forced individuals to feed more frequently and therefore take more risk, resulting in higher mortality rates within the current predicted range. Importantly, warmer winters also led to a faster depletion of energy reserves, making long winters problematic. The same was found in our analysis of an epipelagic planktivore when we focused only on the winter season. Consequently, and in contrast to the common prediction, both our models predict equatorward shifts to be optimal under ocean warming: of the current leading range edge of diel vertically migrating fish that occupy high latitudes, and of epipelagic fish at higher latitudes in winter.

Implications for forecasting responses to climate change

What is the relevance of our findings for predicting responses of planktivorous fish to climate change? As case studies on organismal responses are rapidly accumulating, what stands out is not only consistent patterns, but also exceptions to these (Poloczanska *et al.*, 2013, 2016; Pinsky *et al.*, 2020). Understanding these exceptions is key for producing reliable anticipatory predictions that can be used for management and conservation purposes. Based on our analyses, can we identify any mechanisms that may explain exceptions in planktivorous fish? And, how can our findings help improve prediction?

Phenology

Phenological shifts in response to climate change are ubiquitous (Parmesan & Yohe, 2003; Poloczanska *et al.*, 2013) but the magnitude of these shifts have been difficult to explain since they vary among species in the same location, and among populations of the same species experiencing similar changes in their seasonal temperature regimes (e.g. Edwards & Richardson 2004, Both et al. 2009, Poloczanska et al. 2013). This constrains our ability to make anticipatory predictions. Breeding time is a complex trait, and particularly in in migratory organisms; it is the outcome of selection on both parental and offspring timing, and is an adaptation to conditions at several locations, which may experience different patterns and rates of environmental change (e.g. Visser *et al.*, 2004). This makes prediction complicated since a change in one component of the annual routine likely affects optimal decisions at other times of the year (Varpe, 2017).

Our state-dependent life-history model predicts optimal reproductive decisions (timing and effort) by considering selection pressures that act on the annual routines of parents, while taking seasonality in offspring fitness into account. Thus, these decisions represent adaptive endpoints under different environmental conditions (Houston & McNamara, 1999; Clark & Mangel, 2000) and can therefore be used to assess whether current responses are adaptive, and what response would be adaptive under future scenarios of environmental change. Moreover, by allowing for incorporation of conditions at spatially separated locations, our model framework is also suitable for investigating how reproductive schedules are affected by changes far away from breeding sites. This is rarely considered in studies on marine organisms, but commonly included in studies on phenological shifts in migratory bird populations (e.g. Both et al. 2005, Bauer et al. 2008, Saino & Ambrosini 2008). To better understand and predict changes in phenology and their consequences in marine systems, I therefore advocate for incorporation of both the parental and offspring perspective, for modelling optimal annual routines, and for considering changes at different locations.

Body size

Ocean warming is commonly predicted to lead to a shift from larger- to smaller-bodied plankton (Finkel *et al.*, 2010; Morán *et al.*, 2010) and recent changes in zooplankton community composition have been associated with warmer waters and altered water flows (Richardson & Schoeman, 2004; Beaugrand, 2009). By leading to more trophic links, and thus less efficient energy transfer through pelagic food-webs, this could negatively impact higher trophic levels (Boyce *et al.*, 2015). Some compensatory processes have been suggested to reduce this impact. For example, faster growth of smaller zooplankton, yielding higher overall lipid production and thus an increased energy flow (Renaud *et al.*, 2018), and conserved overall zooplankton biomass (Pinsky *et al.*, 2020). Moreover, ocean waring has been linked to recent reductions in predator performance through declining prey quality. In the eastern Bering Sea, poor growth of walleye pollock *Gadus chalcogrammus* was associated with a warming-driven shift toward less energy rich prey (Siddon *et al.*, 2013).

Our findings in **Paper II** suggest that these prey characteristics: abundance, biomass, and energy density, have a small effect on optimal body size and surplus energy in planktivorous fish, in comparison to that of prey size. Likewise, the influence of temperature was relatively small. Thus, inferences based on these proxies are likely to have limited predictive ability, and future work should prioritize other research questions to improve predictions of body size shifts in visually foraging planktivores. Firstly, we show that solid predictions require that the size-structure of the zooplankton community is known, and research into zooplankton responses to climate change should therefore be prioritized. Secondly, we show that visual encounters are key for energy acquisition, and better understanding the factors that influence this variable, such as light (seasonality, water clarity, attenuation…) and vision (eye sensitivity, zooplankton contrast, spectral resolution…) is crucial for making progress. Moreover, to improve model predictions well-estimated species-specific parameters of factors that restrict feeding success are urgently needed, such as values for handling time and capture success for different predators and prey, and under varying environmental conditions.

Distribution

Predictions of climate change-related distribution shifts in marine species primarily come from species distribution models (SDMs; also known as bioclimate envelope, niche, and habitat suitability models) (e.g. Cheung *et al.*, 2009; Jones and Cheung, 2015; García Molinos *et al.*, 2016). These models use correlations between current species' distributions and their physical environments to map their probability of occurrence in the future, thus assuming that species will track their physical tolerance limits (Robinson *et al.*, 2017). SDMs have been used to predict warming-driven shifts of more than 1,000 commercially exploited species (Cheung *et al.*, 2009) to over 10,000 species in general (García Molinos *et al.*, 2015), as well as subsequent changes in fisheries catch potentials (Cheung *et al.*, 2010, 2011). According to their predictions, the Arctic and Sothern Ocean will experience the greatest species turnover rates (over 60% of present biodiversity; Cheung et al. 2009) and increases in catch potential of 30-70% (Jones & Cheung, 2015). Marine SDMs have been increasingly used for management advice. Considering their simple and correlative nature, and therefore great likelihood of failing to identify the true limiting factors of a species' range (Elith & Leathwick, 2009; Kearney & Porter, 2009; Sorte, 2013), this is quite concerning. Our findings in **Paper III** support this point and highlight several details that should be considered when forecasting warming-driven redistributions of visual foragers at or into seasonal latitudes. The overall message: failure to account for the effect of the interaction between increasing light seasonality with latitude and temperature on energy budgeting and safe foraging will lead to predictions that are simplified and incomplete. This issue has raised before, but has not been explicitly tested (Kaartvedt, 2008; Saikkonen *et al.*, 2012; Poloczanska *et al.*, 2016; Sundby *et al.*, 2016; Langbehn & Varpe, 2017).

More specifically, we identify several population characteristics that may affect responses, such as size-structure and current location. In short, whether a population is dominated by smaller or larger individuals may affect its likelihood to shift, and large individuals in lower latitude populations would have to shift further poleward to maintain their current level of performance than those in higher latitude populations. Moreover, the migration capacity of a population may affect its response. Our findings suggest that warming will make the dark and long winters at higher latitudes increasingly problematic for populations at those latitudes, and could act as an obstacle for fish that are tracking their preferred thermal conditions poleward. This could make seasonal feeding migrations in and out of higher latitudes become more common in the future than today. However, horizontal migrations are costly (Jobling, 1994; Alerstam *et al.*, 2003) and may thus only be feasible for larger individuals that have a high migratory capacity (Schmidt-Nielsen, 1984; Roff, 1988), and if food is sufficient. SDMs have been criticized for not considering how interactions between species shape their ranges (e.g. Pearson & Dawson, 2003; Dormann et al. 2012; Thuiller et al. 2013; Urban et al. 2016). In **Paper III** we identify a mechanism through which the interaction between warming and predation pressure could push the leading range edge of a visual forager equatorward, by leading to increased risk taking. Our analysis in **Paper II** also indicates the importance of the composition of the prey community for feeding rates and hence energy acquisition in planktivorous fish. As such, our findings highlight the importance of understanding mechanistic links between interacting species in order to predict their future ranges.

Our modelling approaches: Advantages and shortcomings

The models used in this PhD research are obviously simplifications of the complexity found in nature. Nevertheless, the good fit between our predictions and empirical data suggests that they capture mechanisms that are important for the ecology of planktivorous fish. In the studies presented in this PhD thesis I search for optimal strategies by focusing on fitness maximization at the individual level. Hence, I search for the trait value, or combination of trait values and behaviours, that maximize the fitness of an individual in a certain environment, without taking potential feedbacks with the environment or population into account. By doing so, I implicitly assume that the population is at evolutionary stability and at a density-dependent equilibrium, and thus that optimal individual strategies are not affected by the number (density-dependence) or strategies (frequency-dependence) of other individuals (Houston & McNamara, 1999). It could be argued that this approach is insufficient to describe patterns in natural populations and methods have been developed to deal with this. For example, *evolutionary game theory* puts evolution in a frequency-dependent context (Maynard Smith, 1982), *adaptive dynamics* also incorporates population dynamics and hence density-dependence (Metz *et al.*, 992; Dieckmann & Law, 1996), and *eco-genetic models* combine adaptive dynamics with quantitative genetics to predict population-specific rates of evolutionary change (Dunlop *et al.*, 2009). Furthermore, McNamara (1991) presents a technique based on dynamic programming to find optimal strategies under density- and frequency-dependence. Although these methods allow for greater complexity, they also have their disadvantages: they include much detail, evolutionary stable strategies can be hard to find due to the feedbacks, and their predictions are often difficult to interpret and test (Stearns, 2000; McNamara & Houston, 2008). Thus, the suitability of an approach depends on the question it aims to answer, and making simplifications and omitting feedbacks may therefore sometimes be warranted (Houston & McNamara, 1999; Mouquet *et al.*, 2015).

In **Paper I**, the life-history problem of when to reproduce and how much to invest in reproduction is dictated by seasonal variation in food abundance and predation risk, and by an individual's state. Population level patterns emerge as a consequence of different histories of environmental exposure among individuals, which affects their energy reserves and thus leads to different optimal decisions (Houston & McNamara, 1999; Clark & Mangel, 2000). One shortcoming of our approach is that we only consider individuals of one size (the typical size of adult Pacific herring). Since the potential for energy acquisition and storage both differ with body size, the size-structure of a population could also influence population level patterns. In the system that we model, herring in Puget Sound, WA, USA, food is seasonal and successful reproduction relies on individuals synchronizing their spawning with that of other individuals. This suggests that effects of frequency-dependent selection on optimal spawning and feeding time are not very likely. We do not explicitly model potential feedbacks with the environment due to population density. However, since we predict optimal decisions at different food levels, the consequences of variation in food availability for optimal spawning decisions can still be explored.

In **Papers II** and **III**, we assume that trait values and behaviours for which annual surplus energy is maximized are optimal, and we define annual surplus energy as the energy available after subtraction of maintenance costs (digestion, standard and active metabolism) from maximum potential consumption over the annual cycle. This represents the trait value or behaviour for which an individual has the highest capacity of converting energy from the environment into reproductive output or other fitness-related tasks. Evolutionarily this implies that individuals are expected to display the predicted trait value and/or behaviour, unless a different solution has a considerable survival advantage.

In **Paper II** we use this approach to infer optimal body size in Norwegian spring-spawning herring (NSSH) and North Sea herring. How do we assess that a different solution does not have a survival advantage? For example, with strongly declining mortality with size, it can pay to grow bigger than the optimal body size in the absence of predation. In contrast, with increasing mortality with size or high mortality in general, it can pay to stop growing and begin reproducing earlier. For adult herring natural mortality is likely not particularly high or very size-dependent (M=0.15; ICES, 2018). Fishing mortality has reached high values historically for these stocks, particularly for NSS herring during the period of stock collapse (Dragesund & Ulltang 1978, Toresen & Jakobsson 2002; and the North Sea herring fishery was closed 1977-1983, Corten 2000), but no evidence of fisheries-induced evolution in life-history traits has been found (Engelhard & Heino, 2004). This suggests that energetic constraints are likely to have a major influence on optimal body size in these systems, which is common in environments where resources are seasonal (Boyce, 1979; Roff, 1992; Stearns, 1992). As a consequence, frequency-dependent effects on optimal body size are also likely to be low.

In addition to energetics and predation, several factors could lead to selection on fish body size. These include size-dependent effects on competition (Karplus *et al.*, 2000), fecundity (Trippel *et al.*, 1997), sexual-selection (Kitano, 1996), overwinter survival (Calder, 1984; Lindstedt & Boyce, 1985), and swimming efficiency (Schmidt-Nielsen, 1984). Out of these factors, the two latter could possibly explain why NSSH are larger than North Sea herring. Long-distance migration favours large body size since the weight-specific cost of swimming decreases with increasing body length (Schmidt-Nielsen, 1984; Roff, 1988), and larger body size could benefit overwinter survival by allowing for greater energy stores (Calder, 1984; Lindstedt & Boyce, 1985). The close match between our predictions and observations however suggest that these selection pressures are not responsible for the difference in size between NSSH and North Sea herring. Furthermore, our findings in **Paper III** indicate that cold waters and long day lengths in summer are a requirement for large body size to be beneficial. This suggests that NSSH are large due to their large prey, that they need to undertake feeding migrations to high latitudes to maintain this size, and that they can do so efficiently because they are large, which also allows them to store enough energy for overwinter survival.

In **Paper III** we use the same approach to predict how warmer temperature affects energy budgeting in our epipelagic planktivore. Our modelling approach has several advantages compared to conventional SDMs, which do not consider how seasonality may affect organisms that are tracking thermal conditions into higher latitudes, or how the interaction between warming and seasonality may affect organisms that currently occupy higher latitudes. Furthermore, SDMs treat a species as an entity and project statistical correlations between current presences and abiotic factors in time and space (reviewed in Robinson et al. 2017). This is a very coarse approach that does not consider the processes that underlie range extension- and contraction-dynamics caused by climate change, which are ultimately driven by changes in individual and population performance (Bates *et al.*, 2014; Lenoir & Svenning, 2015; Donelson *et al.*, 2019). Our approach allows for quantification of warming-driven changes in performance across latitudes based on an important fitness proxy, surplus energy. As such, it can be used to identify areas where changes in predicted population performance are indicative of range shift dynamics, and how specific populations within a species' range are likely to respond, which is important for management and conservation planning. Moreover, by explicitly considering size-specific effects we identify latitudes of opportunities and constraints for individuals of different sizes. Thus, the size structure of a population may have implications for how it responds and this is something that should be considered.

In the analyses in **Paper III** we only consider effects of an increase in temperature, keeping predator and prey dynamics constant. Since forecasts of shifts in phenology, distribution and abundance of populations and species are still uncertain, our analysis could be extended by systematically checking for effects of general patterns of change, such as an advancement or delay of spring and autumn phenology for prey, a reduction or increase in prey size, and higher versus lower predation pressure, as well as interactions between these factors. Although this would yield many hypothetical predictions, it could elucidate mechanisms and processes underlying different responses and thereby improve understanding and predictive ability.

Even though the models in this PhD work are simple, they highlight several features that are likely to be important for predicting how planktivorous fish will respond to climate change, and to environmental change in general. They also point to research that should be prioritized to improve future models, by indicating important drivers and sensitive parameters for which accuracy, and hence data collection, and reliable prediction is key. In the following section I conclude this synthesis by highlighting some perspectives and questions that emerged during this PhD work, which could advance our understanding of current and future responses of planktivorous fish to environmental change.

Future perspectives and open questions

Q1) Can constrained energy budgets or increased foraging-related predation explain recent shifts to lower latitudes observed in a number of species?

Despite the general pattern of poleward shifts, there is great variation in the direction of recent species redistributions, and equatorward shifts have also been reported (Poloczanska *et al.*, 2013, 2016; Pinsky *et al.*, 2020). Some of these movements have been associated with climate velocities at local scales (Pinsky *et al.*, 2013) but could more constrained energy budgets or increased foraging-related predation due to warmer temperatures provide a mechanistic explanation? To validate our predictions in **Paper III**, higher latitude populations for which equatorward shifts have been observed could be identified. Our modelling frameworks are suited for visual planktivores in general but could be extended to piscivores. Hence, the hypotheses could possibly be tested for any population fitting within these categories. Observations of distribution shifts are rapidly accumulating (Bonebrake *et al.*, 2018), hence if the relevant data for this type of analysis is not currently available, it may be so in the near future.

Q2) A closer collaboration between modellers and empiricists is urgently needed to make more reliable predictions

We are all in this boat together and we need to cooperate! Model predictions are not reliable without appropriate parameterization. This is a true problem for modellers since the literature is both full and void of species-specific parameters. For example, the size- and temperature-dependency of standard metabolic rate (SMR) has been estimated for a large variety of species and the methods for doing so are fairly standardized. In contrast, there is no standardized method for how to estimate and report digestion rates, which inevitably affects the reliability of energy budget calculations. By working together with empiricists, modellers could guide empirical work to provide required parameters in a suitable format. Format is also an issue; parameters are often reported with different and non-interchangeable units, or units that are not meaningful in a modelling framework. Moreover, the implications of intraspecific differences in important parameters should be assessed to better understand and predict effects of environmental change on marine organisms. It is well known that many temperature-dependent physiological rates vary among populations of the same species (Conover *et al.*, 2009; Burton *et al.*, 2011) and such differences will inevitably affect the rate, magnitude, and nature of population-specific responses. Collective efforts are therefore needed to provide more population-specific, rather than species-specific parameters.

Q3) Could evolution allow for conserved energy budgets under ocean warming?

Another factor that complicates appropriate parameterization is evolution. By using parameters estimated in the present to predict the future, we implicitly assume that no adaptation will take place. This is more plausible for some parameters than others. For example, in **Paper II** we find that energy intake is sensitive to variation in traits that could be characterized as feeding adaptations to prey characteristics, such as shape, evasiveness, anti-predator behaviours, and mobility. Since eons of natural selection has optimized the feeding machinery in trade-offs with other traits, the potential for evolution toward higher efficiency is presumably low. Considering the strong link between surplus energy and fitness, what about evolution of lower metabolic rate and greater energy storage capacity? The widespread intraspecific variation in resting metabolic rate (Burton *et al.*, 2011) suggests that this is possible, and rapid evolution of SMR in response to altered predation pressure has been shown in Trinidadian guppies *Poecilia reticulata* (Auer *et al.*, 2018). However, the link between SMR and fitness appears to be context-dependent (Burton *et al.*, 2011; Norin & Metcalfe, 2019), and whether higher SMR under warmer temperature will be selected against is therefore not clear. At warmer temperature digestion will also be faster, meaning that energy acquisition will increase as long as there is enough food. This may lead to other selection pressures becoming more important, such as higher mortality rates and more density dependence due to increased foraging. An evolutionary change in energy storage capacity is less likely. Since energy reserves and predation mortality are positively correlated (Ejsmond *et al.*, 2015), the “space” for reserves represents the optimal balance between the cost of having much space that can only be utilized occasionally, and too little space to survive periods of food shortage.

Consequently, whether and how evolution will modulate warming-effects on energy budgeting is an open but important question.

Q4) Why would evolution not eliminate digestion limitation in smaller individuals?

Our analyses in **papers II** and **III** suggest that digestion plays a major role in limiting energy intake in smaller individuals. Once again, considering the strong link between surplus energy and fitness, one could expect faster digestion to evolve. Although it is unlikely that our model accurately represents the true digestion rate in herring, it offers a number of potential non-exclusive reasons for why this may not occur. According to our model, a faster digestion rate would increase surplus energy but lead to a smaller optimal size. If this is true, it has several implications. Firstly, size-dependent mortality (Peterson & Wroblewski, 1984; Gislason *et al.*, 2010) could outweigh any positive effects of faster digestion. Secondly, in migratory populations there may be stronger selection for being large, since relative cost of swimming decreases with body length (Schmidt-Nielsen, 1984; Roff, 1988). Furthermore, by constraining the volume of the body cavity where oocytes are contained, a smaller body size could also limit the reproductive potential at each spawning event and therefore be selected against (Lambert, 2008). Lastly, digesting food is costly oxygen wise, and faster digestion would thus lead to less oxygen available for other important activities, such as avoiding predators (Priede, 1985; Holt & Jørgensen, 2015).

Q5) Will using changes in primary production as a proxy for changes in food availability for visually foraging fish lead to erroneous conclusions?

In both empirical and theoretical models, primary productivity is often used as a proxy for food availability for fish, i.e. high primary productivity is assumed to lead to high zooplankton production, which is assumed to lead to high food availability for fish. In **Paper II** we show that water clarity has a large effect on prey encounter rates and therefore energy intake, by affecting the distance at which prey can be detected. In comparison, the effect of variation in prey abundance is negligible. Hence, for planktivores that forage through vision, high primary productivity (leading to low water clarity) negatively affects energy intake even when prey are abundant. In contrast, successful attack in piscivores is determined by how close they can get to their prey without being detected. They therefore profit from high primary productivity and thus less clear waters. Since the relationship between primary and zooplankton production, and the energy intake of planktivore and piscivore fishes is not linear, this means that disregarding feeding limitations will lead to erroneous predictions of energy availability.

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PAPER I

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Parent-offspring conflict over reproductive timing: ecological dynamics far away and at other times may explain spawning variability in Pacific herring

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Parent-offspring conflict over reproductive timing: Ecological dynamics far away and at other times may explain spawning variability in Pacific herring

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Abstract

Timing of reproduction may be of crucial importance for fitness, particularly in environments that vary seasonally in food availability or predation risk. However, for animals with spatially separated feeding and breeding habitats, optimal reproductive timing may differ between parents and their offspring, leading to parent-offspring conflict. We assume that offspring have highest survival and fitness if they are spawned around a fixed date, and use state-dependent life-history theory to explore whether variation in conditions affecting only parents (food availability and survival) may influence optimal timing of reproduction. We apply the model to Pacific herring (*Clupea palasii*) in Puget Sound, USA, where 20 subpopulations spawn at different times of the year. Our model suggests that relatively small differences in adult food availability can lead to altered prioritization in the trade-off between maternal fecundity and what from the offspring's perspective is the best time to be spawned. Our model also shows that observed among-population variability in reproductive timing may result from adults using different feeding grounds with divergent food dynamics, or from individual variation in condition caused by stochasticity at a single feeding ground. Identifying drivers of reproductive timing may improve predictions of recruitment, population dynamics, and responses to environmental change.

Keywords: spawning phenology, match-mismatch, spatial ecology, stochastic dynamic programming, climate change, *Clupea harengus*

Introduction

Many fish species do not provide care for offspring after birth, but parents can still play a major role for the success of their offspring by deciding where and when to spawn. Although populations often return to the same areas year after year for reproduction, there may be substantial variation in when spawning takes place, both between years and among subpopulations. To understand this variation and furthermore how timing of reproduction may respond to climate change and other stressors, there is a need for evolutionary interpretations of local variation in reproductive timing as the outcome of adaptive behaviour.

Consider this baffling example from Puget Sound, WA, USA (Fig. 1a), where 20 different Pacific herring (*Clupea palasii*) subpopulations (stocks) spawn consistently but at different times of the year (between late January and June (Stick et al. 2014); Fig. 1b), even though all but two stocks show no discernible genetic variation (Small *et al.*, 2005). No known evidence exists that this variability in spawn timing is related to environmental conditions; though, at broader spatial scales, it is thought that annual temperature regimes regulate maturation and spawning time (Hay, 1985). This raises the question of why these stocks display so much variation in reproductive timing. In addition, peak spawn date has been shifting for many of the Puget Sound herring stocks in recent years, but in different directions and magnitudes (Fig. 1b). Local drivers of these changes have not yet been identified and similar shifts have been observed but not yet explained for Pacific herring elsewhere along the west coast of North America (R. Bartling, pers. comm., S. Dressel and K. Hebert, pers. comm.). Hence, it seems clear that some underlying process is affecting the spawning time of each stock, while allowing large among-stock variation.

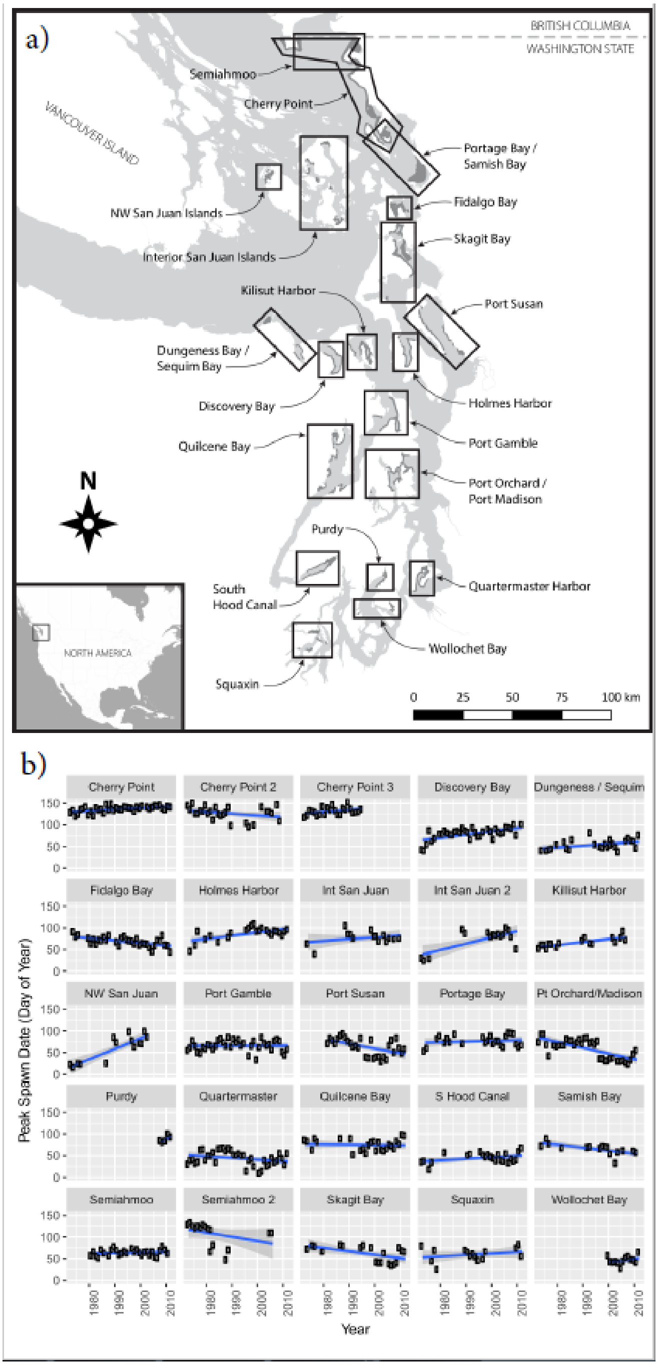

Figure 1. a) Puget Sound herring are managed by the Washington State Department of Fish and Wildlife (WDFW) as 20 separate spawning populations (inset shows location in

the northeast Pacific, WA, USA). b) Time series of peak spawn dates (with linear smoother and 95% confidence interval) for Pacific herring spawning sites in Puget Sound. Peak spawn date is defined as the survey date on which the cumulative observed egg abundance (based on WDFW rake surveys) exceeded 80% of the total egg abundance observed for that year. Note that some of the stocks recognized by WDFW (Fig. 1a, 20 in total) spawn in adjacent bays and have somewhat different peak spawn times, and have therefore been separated in the graphs showing spawning times (Fig. 1b, 25 in total). Int San Juan 2 = Lopez Island; Cherry Point 2 = Birch Point; Semiahmoo 2 = Point Roberts; Cherry Point 3 = Hale Passage.

In fisheries science reproductive timing has been a hot topic for over 100 years, ever since Johan Hjort presented his famous "critical period" hypothesis (Hjort, 1914) to explain recruitment variability. Hjort (1914) hypothesized that recruitment was determined as early as the time of first feeding, since starvation during this early larval phase could substantially reduce offspring survival. Cushing later expanded on this idea, and proposed the "match-mismatch" hypothesis (Cushing, 1973, 1990). He acknowledged that starvation of first-feeding larvae could contribute to variability in larval mortality, but built his argument on the observation that mortality declines with size (McGurk, 1986; Gislason *et al.*, 2010; Brodziak *et al.*, 2011). In Cushing's view, poorly fed larvae grow slowly and are therefore more susceptible to predation. Accordingly, the central assumption of the "match-mismatch" hypothesis is that timing of spawning is adapted to seasonal plankton production blooms in the larval distributional area. In its original formulation, the hypothesis also assumed that fish populations in temperate waters spawn at fixed times and thus that mismatches arise due to variable plankton phenology (Cushing, 1969, 1973). However, many temperate fish populations demonstrate large inter-annual variability in spawning time (e.g. see Wright & Trippel, 2009). For example, significant inter-annual variation over three decades (ranging 65-100 days) was reported for three Northwest Atlantic cod (*Gadus morhua*) populations (Hutchings & Myers, 1994). There is also large variation in timing of spawning among populations of the same species (e.g. Atlantic herring (*Clupea harengus*), Sinclair &

Tremblay, 1984; haddock (*Melanogrammus aeglefinus*), Page & Frank, 1989; cod, Brander & Hurley, 1992; Myers *et al.*, 1993; sardine (*Sardina pilchardus*), Stratoudakis *et al.*, 2007). While Atlantic herring populations spawn over the entire year, Pacific herring spawning can span over several months, and some populations spawn at different times of the year on the same spawning grounds (Sinclair & Tremblay, 1984).

Since the introduction of the "critical period" (Hjort, 1914) and "match-mismatch" (Cushing, 1973, 1990) hypotheses, much research has been devoted to explaining recruitment variation in fish populations (e.g. see Houde, 2008, and Wright & Trippel, 2009). Most of this research relies on the assumption that spawning times in fish have evolved so offspring encounter conditions that promote their survival, while any effects on the reproductive success of individual parents have been ignored (Wright & Trippel, 2009). However, environmental variability influences more than the early life stages; it also impacts the success and survival of adults. A key insight is that when resources and predation risk vary over the annual cycle, an adult may not be able to reproduce at the optimal time for its offspring if this conflicts with other priorities for adult survival or reproduction (Daan *et al.*, 1990; Rowe *et al.*, 1994; McNamara *et al.*, 2004; Varpe *et al.*, 2007). In short, what is good for the offspring may not be good for the parent, and evolutionary thinking allows us to study this trade-off. For example, a parent may increase lifetime reproductive success by breeding later than optimal for its offspring, so that the parent can have more time to acquire energy in preparation for spawning, and thus eventually produce more offspring (e.g. Drent and Daan, 1980; Daan *et al.*, 1990; Rowe *et al.*, 1994). In other cases, it can be better to reproduce earlier than optimal for the offspring, so that the parent can have returned to the feeding grounds in time for peak food availability. In addition to foraging considerations, variable predation risk can similarly influence adult reproductive decisions (Lima, 2009). Thus, it seems fair to say that our current understanding of the selective factors operating on timing of spawning is incomplete, which in turn implies that we lack a mechanistic understanding of the underlying drivers of recruitment variation (Munch *et al.*, 2005a, 2005b).

A better understanding of spawning phenology is also of interest for climate change research, since climate warming is generally expected to shift reproductive activities earlier in spring or later in autumn (Stenseth & Mysterud, 2002; Parmesan & Yohe, 2003; Visser & Both, 2005; Both *et al.*, 2009). For over a decade, Cushing's "match-mismatch" hypothesis has formed a main basis for studies on the effects of climate change on trophic interactions and their implications for population dynamics (Durant *et al.*, 2007; Parmesan, 2007; Thackeray *et al.*, 2010). Some of these studies show declines in population fitness as a consequence of asynchrony between offspring food demand and supply (e.g. Both *et al.*, 2006; Visser *et al.*, 2006).

In this study we incorporate these considerations by using the theory of parent-offspring conflict to model spawning time as a compromise between the mother's expected survival and fecundity on the one hand, and accumulated reproductive success through the survival of her offspring on the other (Reznick *et al.*, 2006; Varpe *et al.*, 2007). This follows the logic of Trivers (1974), who showed that sexual reproduction can cause a conflict between parents and their offspring when the current reproductive investment of the parent has a negative effect on its future fitness. The prerequisites for such a conflict are that the optimal levels of parental investment differ between a parent and its young, and that investing more in the offspring can benefit the offspring but at a cost to the parent (Roitberg & Mangel, 1993). This leads to joint evolution of parental and offspring traits, and the outcome can either be evolutionarily stable or result in a continuing arms race (see Kilner & Hinde, 2012, and references therein). A spawning time that diverges from the optimal timing from an offspring's perspective may thus result from stronger selection on related traits in parents, which may constrain offspring fitness although it maximizes parental fitness.

Since timing of reproduction emerges from the overall selection on parental timing and offspring survival (Trivers, 1974; Varpe *et al.*, 2007; McNamara & Houston, 2008), explaining variation in this trait requires consideration of a full life cycle perspective (i.e. both offspring and parents). In this study we include the parental view, and adopt a simplified annual routines approach to capture trade-offs resulting from life in a seasonal environment (McNamara & Houston, 2008; Barta, 2016). To explore how variation in conditions (food availability and mortality rate) that only affect parents influences optimal reproductive timing, while accounting for seasonality in offspring recruitment probability, we use a state-dependent life-history model. We focus on migratory Pacific herring spawning in Puget Sound as it exemplifies a system in which the conditions that affect adults for most of the year are separated by migration from those that determine survival of early life stages. Although our focus is on migratory pelagic fish populations, the mechanisms and relationships are general and could be applied to explore reproductive decisions of other migratory organisms as well.

Our aims are: 1) point to possible drivers of evolved patterns in spawning time in migratory fish populations and assess the potential magnitude of their effects on spawning time variability; and 2) expand "match-mismatch" thinking by parent-offspring conflict as basis for a richer explanation of reproductive phenology.

Method

Overview of the model

We will now provide verbal summaries of the model; the relevant equations are given in appropriate detail in Supplementary material 1.

To explore how variation in food availability and mortality rate at the feeding grounds of adults affects their optimal reproductive timing, while taking seasonality in offspring recruitment probability into account, we used state-dependent life-history theory in which optimal life-histories are found by stochastic dynamic programming (Houston & McNamara, 1999; Clark & Mangel, 2000). The central assumption of our model is that there are three seasonally fluctuating relationships that influence reproductive success: i) food availability and ii) predation risk at the feeding grounds, affecting only adults, and iii) probability of recruitment for offspring hatched on a certain day of the year (referred to as offspring fitness). We used the model to predict when it was optimal for parents to reproduce and how much energy they invest in current reproduction; both these decisions were conditional on the energy reserves of the parent, its location, and the day of the year. The model maximized expected lifetime reproductive output, accounting for current and future reproductive events. Thus, in this study decisions represent strategies and behaviours that have evolved by natural selection, and not decisions due to cognitive choice. We parameterized the model for Pacific herring in Puget Sound. After determining the optimal decisions for each state and time as they were constrained by physiology (bioenergetics) and ecology (food availability and mortality of adults and offspring), we used forward Monte Carlo simulation to predict individual lifetime trajectories. Differences across individuals thus arose from stochastic energy gain, and by summing across many individuals we obtained population-level distributions of key traits and behaviours. We have strived to present results as quantities that can be measured in the field.

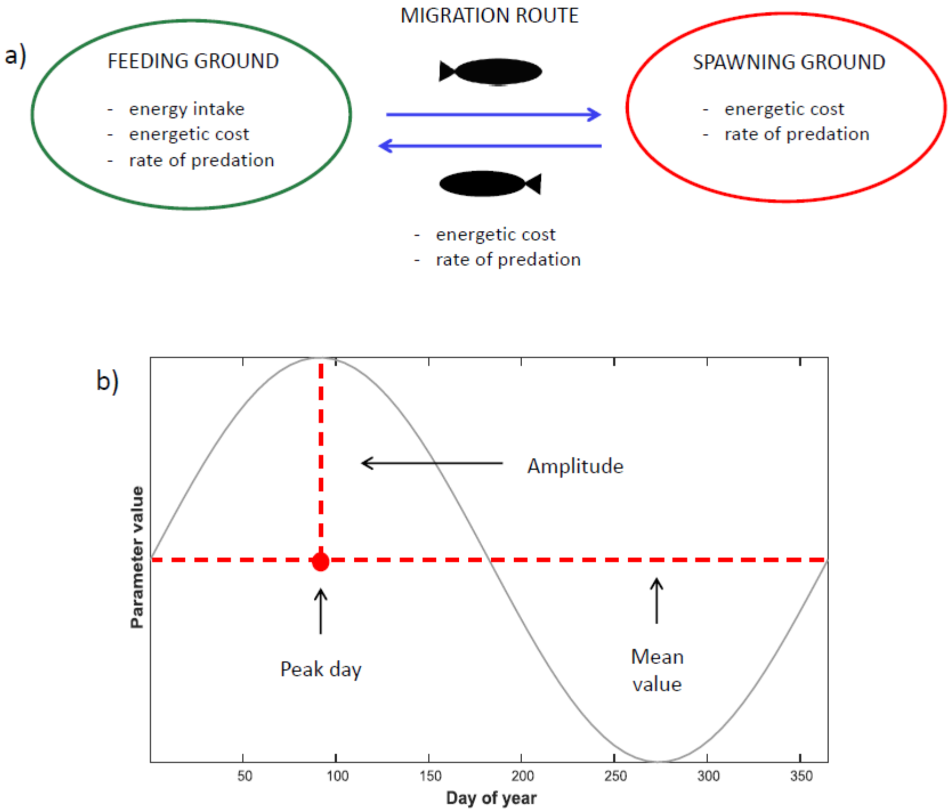

Figure 2. a) Schematic illustration of the model. Individuals can either be at the feeding ground foraging and building reserves for spawning, at the spawning ground to reproduce,

or migrating in between. Key variables are given in lowercase letters. b) Seasonal variability of parameter values. When the environment varies seasonally, the annual sine curves are characterized by their peak day, mean value, and amplitude.

Optimal decisions, state variables, the environment, and reproductive success

We consider three locations: a feeding ground; a migration route; and a spawning ground (see Fig. 2a for a schematic illustration of the model).

We only consider females, assuming that males are sufficiently abundant that all eggs are fertilized. When a female is on the feeding ground, her possible behaviours are 'stay' or 'migrate'; when on the spawning ground, they are 'wait', 'spawn a proportion of available reserves and migrate back to feeding grounds', or 'spawn all available reserves and die'. The latter option is not necessarily semelparity because it may be preceded by spawning events in which not all resources were used. It is thus better described as terminal spawning, and can occur at any time if conditions dictate so (Duffield *et al.*, 2017). The reproductive output of an individual that spawns on a particular day of the year is obtained by multiplying the energy allocated to reproduction by a recruitment probability for offspring spawned on that day. We thus assume a seasonal curve for offspring fitness, and use the identical curve across all simulations so all variation in spawning time predicted in this study stems from environmental effects on adults. We assume that natural selection has acted on these behaviours to maximize accumulated reproductive output (expected number of recruited offspring a parent produces, i.e. offspring that survive to join the adult population).

The model characterizes the female by the physiological state variable energy reserves, which on day t has the value x, measured in joules (J). The feeding ground is characterized by three environmental parameters: food availability (energy intake, i.e. consumed energy minus losses due to digestion and waste; J day^{-1}); energetic cost (temperature-dependent standard metabolism; J day^{-1}); and rate of mortality (day^{-1}). Depending on the specific analysis (see Analyses section), we treat these either as constant or following seasonal patterns, given by sinusoidal functions with an annual period. The annual sine curves are characterized by a mean value, peak day, and amplitude (see Fig. 2

b), Table 1). We model energy intake as stochastic and autocorrelated between days, and let the environmental state variable $Y(t)$ (J day^{-1}) represent the actual energetic intake on day t of the year. We assume that no feeding takes place during migration, or at the spawning ground, thus, these two locations are only characterized by an energetic cost and a rate of mortality. Hence, the state-dependent life-history model explicitly accounts for the trade-off between current and future reproductive output, within the constraint of the energy budget. See Supp. mat. 1 for equations and other details of numerical solution.

Analyses

Sources of environmental variability that could alter the cost/benefit ratio and thus timing of spawning are seasonal variation in resource availability and predation risk, because these potentially lead to feeding and survival opportunities lost to adults while they are away spawning. To systematically explore the effects of annual fluctuations in food availability and mortality rate at the adult feeding ground on optimal spawning time, we used three different analyses that vary these environmental variables within reasonable limits. First, we investigated the relative roles of energy intake ('Food availability analysis') and mortality rate ('Mortality analysis') in driving variation in reproductive timing, then we explored dynamics with the model parameterized to Puget Sound ('Puget Sound analysis'). See Table 1 for parameters investigated in these analyses.

Food availability analysis

In this analysis, we used three mean levels of the annual sine curve in energy intake over three different amplitudes, and with three constant levels of feeding ground mortality to investigate the effects of variation in food availability on optimal spawning time. To isolate the effects of variation in energy intake, we kept the energetic costs constant. Keeping all other parameters constant, we ran forward Monte Carlo simulations over three levels of energy intake (low, medium, high), for several different peak days of this variable), to represent feeding grounds of different quality and timing. To reduce the number of combinations of parameters to explore, we kept mortality rates constant and equal at all three locations.

Mortality analysis

In this analysis, we investigated the effects of variation in mortality rate on optimal spawning time. We simulated three mean levels of the annual sine curve in feeding ground mortality rate over three amplitudes, and three constant levels of energy intake. To isolate the effects of variation in mortality rate, we kept the energetic costs constant. Keeping all other parameters constant, we ran forward Monte Carlo simulations for several different peak days in mortality rate.

Puget Sound analysis

In this analysis, we explored the seasonal dynamics of herring spawning in Puget Sound. Food availability and energetic costs were characterized by annual sine curves, with parameter values representative of Puget Sound herring. Although the model is conceptual and parameters are coarse, it shows the potential range of spawning times that could be brought about by environmental fluctuations that affect only parents at the feeding grounds. Keeping all other parameters constant, we ran forward Monte Carlo simulations for several different peak days in energy intake.

Optimization and simulations

We used state-dependent life-history theory by stochastic dynamic programming (Houston & McNamara, 1999; Clark & Mangel, 2000) to find optimal life-history strategies by iterating backwards from a final point in time, constantly assuming that an individual acts optimally at every future decision point. Our model runs by daily time steps and finds the optimal strategy for when to move between feeding grounds and spawning grounds for each combination of the state variable and time. The optimization criterion is accumulated lifetime reproductive output, i.e. the sum of the energy spawned at each reproductive event discounted by survival probability to that event, and multiplied with offspring fitness (recruitment to the population) for that day of year. Thus, the predicted strategies are evolutionary optima for the specific parameter set used to describe the ecology of the system. To allow for investigation and visualization of individual and population level patterns emerging from the interaction between the optimal strategy and the environment, we simulated 10 000 individuals that followed the optimal strategy in a stochastic food environment.

Parameterization

The parameter values used in the model were chosen to represent Pacific herring spawning in Puget Sound (Table S1 in the Supplementary material). The majority of the parameter estimates were obtained from a model study on Pacific herring in an adjacent area, the west coast of Vancouver Island, British Columbia, Canada (Megrey *et al.*, 2007).

We used the Wisconsin bioenergetics framework (Hewett & Johnson, 1992) to model energy intake (see Supp. mat. 2.1 for equations, and Supp. mat. 2.2 for parameter values and references). Briefly, we estimated the daily energy intake [consumption – (specific dynamic action + excretion + egestion)]; J day^{-1}) and energetic cost due to respiration (J day^{-1}), for the highest (14°C, day 212) and lowest seasonal (7°C, only used for respiration cost) water temperature in the Puget Sound region (Megrey *et al.*, 2007). Depending on the analysis, particularly whether the environment was modelled as seasonal or constant, we used the estimated values to set the limits for the corresponding annual sine curve, or their mean value. Parameters for daily consumption rates are commonly derived from lab experiments conducted at the optimum temperature under *ad lib* feeding conditions. Thus, the estimated value for energy intake at the highest seasonal water temperature is the theoretical upper limit for this parameter, and we assumed a lower value to reflect realized intake. Puget Sound herring weigh approximately 100 g at the start of their feeding season and gain typically 30 g, sometimes up to 40 g, over the season (Schweigert *et al.*, 2002). We assumed that all this weight gain is fat, so that length and non-reproductive mass are constant over the feeding season, and parameterized the bioenergetics for an adult herring of average size (115 g).

The annual sine curve for offspring recruitment probability (offspring fitness) was set to depend on prey availability for newly hatched larvae, assuming that its combined effect on starvation (Hjort, 1926; McGurk, 1984; Huwer *et al.*, 2011) and predation mortality (McGurk, 1986; Bailey & Houde, 1989; Litvak & Leggett, 1992; Takasuka *et* *al.*, 2003; Jørgensen *et al.*, 2014) dictates the likelihood that offspring survive until recruitment. Hence, our offspring fitness curve represents the probability that individuals spawned on different days of the year survive from that day until recruitment, considering all factors acting on their survival during that time. The peak day in offspring fitness was set in early April, because this is the typical period of max abundance of nauplii larvae, which are prime food for herring larvae and produced by adult copepods during the spring phytoplankton bloom. The exact dates of peak food abundance for larvae versus adults in Puget Sound are of less importance in this study, since we do not aim to precisely fit the model to data, but rather to use the Puget Sound case for motivation and a general sense of what needs to be explained. Depending on the analysis, adult mortality rates were set to different levels within an ecologically appropriate range. Natural mortality rates for adult herring of 0.2-0.4 yr^{-1} are considered typical for herring worldwide, and similar values were reported for Puget Sound herring up until the late 1970s (Stick *et al.*, 2014). Since then, mortality has increased. A mortality rate of 0.8 yr^{-1} was reported for the years 1973-1990 (Siple *et al.*, 2017) and the current rate is thought to be around 1.2 yr^{-1} (Stick *et al.*, 2014; Siple *et al.*, 2017). In the 'Puget Sound analysis', we used an intermediate mortality rate of 0.5 yr^{-1}, assuming that herring life-histories in this area are undergoing adaptation to the new and higher natural mortality, but have not yet fully adapted to this new selection regime. Results for a mortality rate of 0.8 yr^{-1} are qualitatively similar and shown in Fig. S7.

Table 1. Parameters and variables (italics) used in the three analyses.

Location	Parameter	Puget Sound			Food availability analysis	Mortality analysis	Units
Feeding ground (f)	Energy intake $\bar{Y}(t)$						
	Mean	10	11	12	10, 11, 12	10, 11, 12	kJ/day
	Amplitude	10	11	12	1.375, 2.75, 4.125	0	kJ/day
	Peak day	Every 50 days (30, 80, 130, 180, 230, 280, 330)			Every 50 days (30, 80, 130, 180, 230, 280, 330)	[constant]	Day of year
	Energetic cost $a_{\mathrm{f}}(t)$						
	Mean	6.7			6.7	6.7	kJ/day
	Amplitude	1.8			0	0	kJ/day
	Peak day	212			[constant]	[constant]	Day of year
	Rate of mortality $m_{\mathrm{f}}(t)$						
	Mean	0.5			0.1, 0.3, 0.5	0.2, 0.4, 0.6	Year^{-1}
	Amplitude	0			0	0.05, 0.1, 0.15	Year^{-1}
	Peak day	[constant]			[constant]	Every 50 days (30, 80, 130, 180, 230, 280, 330)	Day of year

Migration route (m)	Energetic cost $a_{\mathrm{m}}(t)$				
	Mean	9.13	9.15	9.15	kJ/day
	Amplitude	1.8	0	0	kJ/day
	Peak day	212	[constant]	[constant]	Day of year
	$m_{\mathrm{m}}(t)$	$= m_{\mathrm{f}}(t)$	$= m_{\mathrm{f}}(t)$	$= m_{\mathrm{f}}(t)$	Year^{-1}
Spawning ground (s)	$a_{\mathrm{s}}(t)$	$= a_{\mathrm{f}}(t)$	$= a_{\mathrm{f}}(t)$	$= a_{\mathrm{f}}(t)$	kJ/day
	$m_{\mathrm{s}}(t)$	$= m_{\mathrm{f}}(t)$	0.2	0.2	Year^{-1}
	Offspring fitness $F_{\mathrm{offspring}}(t)$				
	Mean	0.4	0.4	0.4	
	Amplitude	0.4	0.4	0.4	
	Peak day	91	91	91	Day of year

Results

A common feature of our results is that food dynamics at the feeding grounds of adults influenced optimal timing of spawning (both mean and variance), and that lower food availability lead to a wider spread in spawning time.

Food availability analysis

Food availability was a major driver of optimal spawning time, and spawning dates were more variable when there was little food (Fig. 3). From Figure 3, the isolated effect of different food levels can be read by comparing the location and size of the predictions of spawning day (‘Spawning day’), for the same peak day in energy intake (‘Peak day for Energy intake’), across the three levels of energy intake (horizontal panels). Similarly, the effects of different amplitudes in energy intake, and for the three levels of mortality, can be read by comparing with figures S1, S2, and S3 in the Supplementary material. Of particular interest is comparisons between simulations that differ in the strength of the parent-offspring conflict. Where the red dotted and solid green lines cross on figures 3 and 5, food availability peaks at the date of maximum offspring fitness, thus implying maximum conflict between parental feeding and the fitness return from each egg spawned. This conflict is minimal where the red dotted and solid green lines are half a year apart, i.e. around October in figures 3 and 5. In addition to at low food levels, spawning dates were more variable when this conflict was large. This was associated with a greater degree of mismatch (approximated by the distance between predicted spawning days and the peak day in offspring fitness) and lower relative fitness.

In Figure 4, we show individual trajectories in detail, assuming a peak day in zooplankton abundance ~ 1st July (see boxes in Fig. 3). Spawning times were more variable at low food levels. Further, individuals spawned earlier if they had acquired little energy for reproduction, so that they were away for spawning closer to the trough of the annual food curve. This strategy allowed them more time to forage for the subsequent spawning event, and more of that time was around the food peak. As a consequence of the stochastic food environment, which yielded a particularly low rate of energy accumulation in some years, individuals sometimes skipped spawning at this food level. At medium and high food levels, individuals spawned more consistently around the peak of the offspring fitness curve, indicating that the trade-off between this and next year's fecundity was less severe. More figures related to this analysis are available in Supp. mat. 3.1.

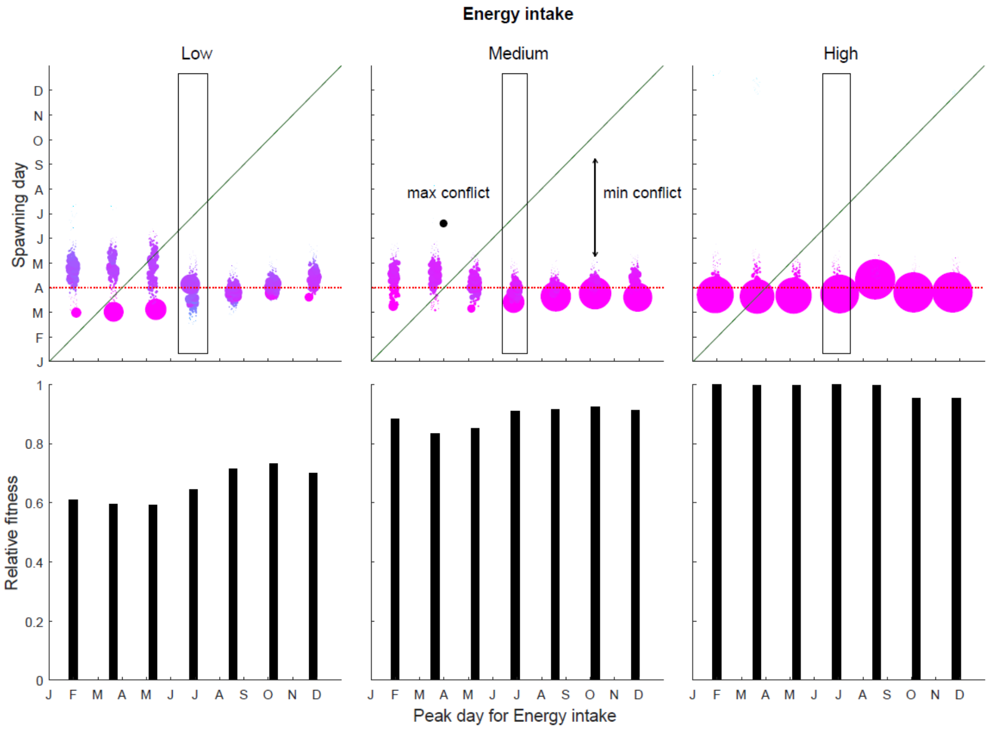

Figure 3. The top panel shows the predicted spawning days for 10 000 individuals following the optimal strategies for the reference case in the 'Food availability analysis', showing the effects of variation in food availability. Dots represent predicted spawning days for different peak days and three mean levels of energy intake under a medium feeding ground mortality rate. The size of the dot indicates the frequency of spawning events predicted for that day and the color the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The dotted red horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in energy intake. Rectangle indicates the case explored in Fig. 3. The bottom panel shows the relative fitness value of each peak day in food availability (energy spawned on each predicted spawning day multiplied with offspring fitness for that day, summed across all individuals simulated and for all days, and divided by the number of individual-years simulated).

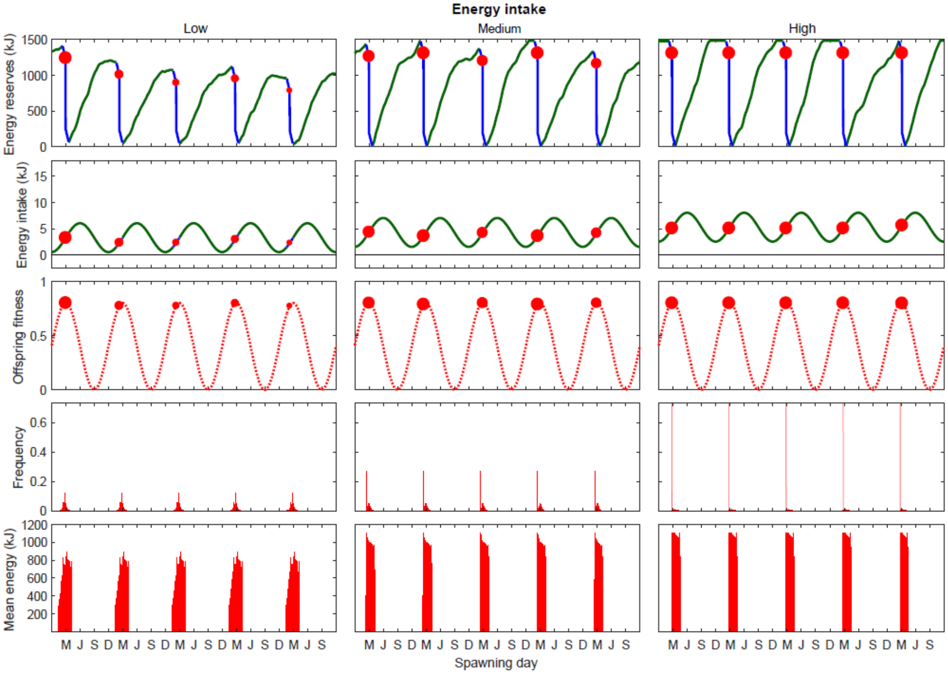

Figure 4. Detailed results for an individual following the optimal strategies, assuming a peak day in zooplankton abundance ~1st July and the three levels of food availability in the 'Food availability analysis' over five years. First row: the energy reserves of the individual, green line indicates that the individual is on the feeding ground and blue line that it is migrating. The red dot represents a spawning event and its size the amount of energy spawned (proportion of maximum amount of energy spawned). Second row: the energy that an individual can acquire if on the feeding ground. Third row: offspring fitness. Fourth and fifth rows: frequency of spawning and mean energy allocated to reproduction, respectively, for each day of the year for 10 000 individuals. Note that individuals may spawn considerable energy at spawning dates when very few fish spawn.

Mortality analysis

Varying mean level, peak day, and amplitude of mortality rate at the feeding ground had only negligible effects on spawning time (Figs. S5-S7). In agreement with the results of the 'Food availability analysis', the spread in predicted spawning days was higher at low levels of food availability and decreased with higher food levels, regardless of the seasonality in feeding ground mortality.

Puget Sound analysis

When using parameters representative of Puget Sound, the model predicted variable spawning dates, generally within the broad range observed from February to June (Fig. 5). A major reason there is more variation in spawning time within the 'Puget Sound analysis' is the long period of negative food intake, typically in winter in the wild but in the simulations we vary its timing. This means that, even with fixed environmental effects on early life stages, certain adult feeding conditions can bring about variation in spawning times comparable to that observed in Puget Sound. Further, at the meta-population level, different sub-stocks of herring may utilize food resources that differ in their abundance or timing, so that spawning in Puget Sound as a whole may be assembled by different spawning components sampled across the three panels in Figure 5. In this analysis mismatches were, unexpectedly, more pronounced at higher food levels, and there was no association between degree of mismatch and level of relative fitness.

For a peak day in adult energy intake that corresponds to the approximate current peak in zooplankton abundance in the Puget Sound region (~ 1st July, Moore *et al.*, 2016; see boxes in Fig. 5), we predicted a range in spawning time of approximately four months across the three food levels (early February to late May). Skipped spawning was observed at all three food levels, but was rare at the highest level. We consider a peak day in adult zooplankton abundance between November and February unlikely for Puget Sound and hence do not include these results in our interpretation and discussion. They could however be relevant for other systems, so the results are reported on the figures for theoretical completeness.

Figure 6 shows individual trajectories for the current case (peak day in energy intake ~1st July; see boxes in Fig. 5) for three levels of food availability. These results suggest that the diverse spawning times displayed in Figure 5 can be driven by different prioritization in the trade-off between feeding to ensure high fecundity versus hitting the peak in offspring fitness. At low food levels, spawning often took place slightly before the optimal spawning time, since there was not enough food in spring for adults to substantially increase fecundity. In some cases individuals stayed behind at the feeding grounds and spawned later than the optimum, this happened when current feeding conditions were particularly good. At intermediate and high food levels, adults fed more consistently in spring, thus increasing fecundity, but they also spawned slightly after the fitness peak. These differences in prioritization are illustrated in the individual as well as the frequency plots in Figure 6. For example, at the low food level, the frequency of spawning events peaked before the peak offspring fitness, whereas at the medium and high food levels the frequency was distributed around and after the peak. More figures related to this analysis are available in Supp. mat. 3.3.

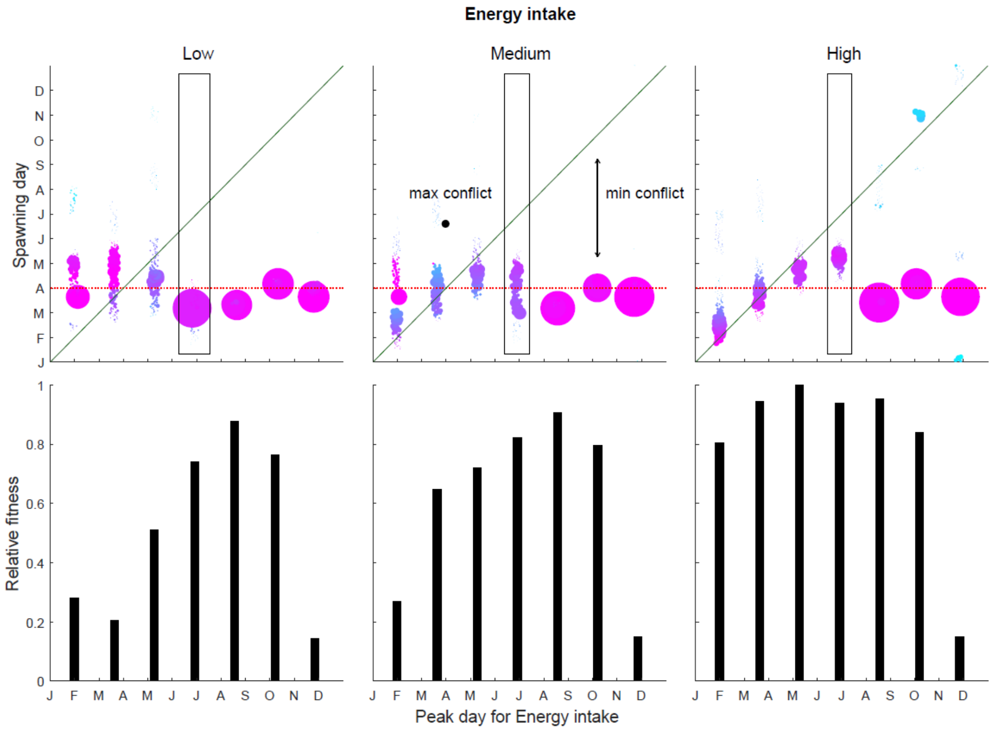

Figure 5. The top panel shows predicted spawning days for 10 000 individuals following the optimal strategies with parameters representative of Pacific herring in Puget Sound ('Puget Sound analysis'). Dots represent predicted spawning days for different peak days

and three levels of energy intake. The size of the dot indicates the frequency of spawning events predicted for that day and the color of the dot indicates the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The dotted red horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in energy intake. Rectangle indicates the case explored in Fig. 6, representing the approximate current peak day in zooplankton abundance in Puget Sound (~1st July). The bottom panel shows the relative fitness value of each peak day in food availability (energy spawned on each predicted spawning day multiplied with offspring fitness for that day, summed across all individuals simulated and for all days, and divided by the number of individual-years simulated).

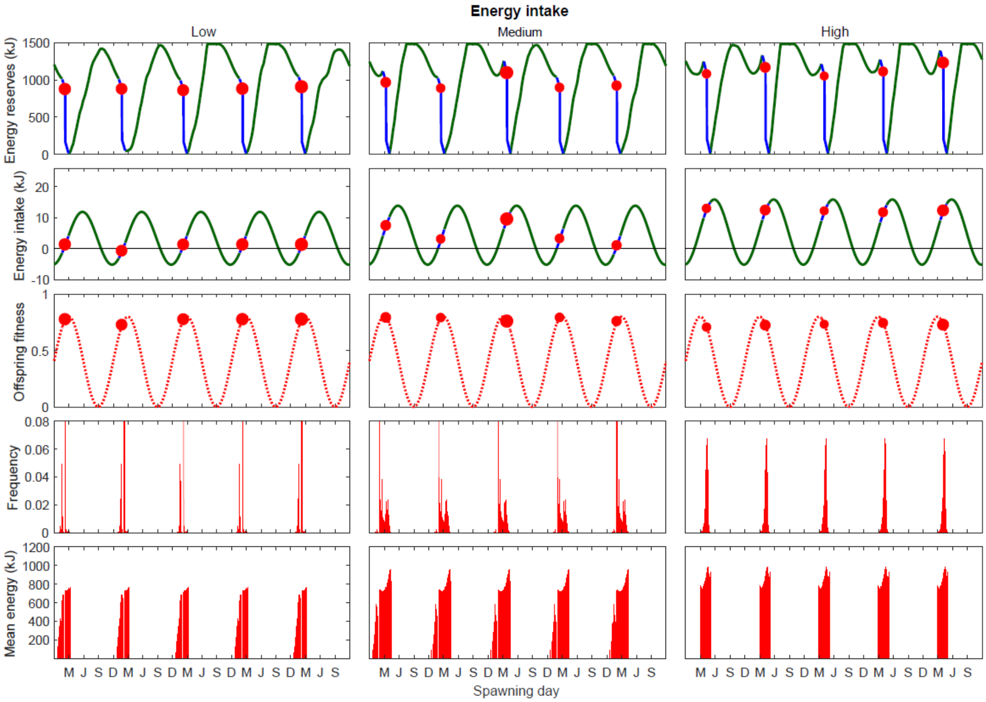

Figure 6. Detailed results for an individual following the optimal strategies for the approximate current peak day in zooplankton abundance in the Puget Sound region (~1st July) and the three levels of food availability in the 'Puget Sound analysis' over five years. See legend for Fig. 3. for description of plot specifications.

Model sensitivity

Most key parameters have been subject to analysis in the sections above, with additional results reported in the Supplementary material. Another parameter of potentially influential role is the duration of migration, which when approaching zero would imply that breeding takes place in the feeding habitat and not a separate location. Results for each analysis of using migration durations of 10, 30, and 40 days (instead of the default value of 20 days) are reported in the Supplementary material 4. Changing the parameter did not qualitatively alter model predictions, except for the Puget Sound scenario where reproduction became more frequent and almost continuous at the shortest migration duration (see Supp. mat. 4.2).

Discussion

To date, most research on reproductive phenology and recent shifts associated with climate change has focused on offspring (e.g. see reviews by Visser and Both, 2005; Durant *et al.*, 2007; Wright and Trippel, 2009). This is natural, since timing of birth is of crucial importance for offspring fitness in many species, and particularly in seasonal environments (Price *et al.*, 1988; Olsson & Shine, 1997; Reznick *et al.*, 2006; Varpe *et al.*, 2007; Plard *et al.*, 2015). In this study we explored how conditions that only affect parents influence optimal reproductive timing, by modelling the annual routine of a pelagic fish that migrates between spatially separated feeding and spawning grounds. Even though we kept environmental conditions for the offspring constant, we found that resource dynamics at the feeding grounds of adults influenced optimal timing of reproduction. Variation in both the mean level and timing of peak food availability for adults affected when it was optimal to reproduce, how much variance there was in reproductive timing, and the degree of mismatch between time of reproduction and optimal time of birth from an offspring's perspective.

Drivers of variability in reproductive timing

In all oceans, primary production varies both spatially and temporally over the season due to a range of factors, including variation in light, temperature, and circulation patterns. If populations use different feeding grounds, it is thus likely that they experience divergent resource dynamics or predator regimes. How large do these differences have to be to produce alternative life-history strategies? The results of our model suggest that relatively small differences in resource availability can affect optimal strategies, and lead to altered prioritization in the trade-off between optimal timing of reproduction (from an offspring's perspective) and fecundity (maternal resources invested into reproduction).

Ever since the "critical period" (Hjort, 1914) and "match-mismatch" (Cushing, 1973, 1990) hypotheses were introduced, much effort has been devoted to identifying a "match-mismatch" effect on recruitment. However, this mechanism alone fails to explain recruitment patterns in most fish populations (e.g. see Houde, 2008, Wright & Trippel, 2009, and references therein). In our model, mismatches were evident even when adults had a high food supply. This is best explained by focusing on a resource-poor environment: when the cost of investing into offspring is high (in terms of energy and starvation risk), it is important to get the maximum possible return for the investment and hence to time it right. However, when investing into young is not as costly, timing becomes less important and parental priorities may have stronger effects on reproductive timing. This was most pronounced in the Puget Sound scenario, where net intake was negative for substantial parts of the year and energetic trade-offs therefore more dominant. Hence, our model illustrates that a mismatch could be the optimal outcome of selection on both parents and their offspring, and that this may be associated with high adult fecundity. In some cases, high adult fecundity may thus benefit recruitment, despite a suboptimal match between offspring food demand and supply. Moreover, our results suggest that low resource levels can lead to large annual and inter-annual variation in the duration and timing of spawning even within a single feeding ground. This is due to stochasticity in the food source, where individuals may experience different histories of environmental exposure, which in turn affect their energy reserves and lead to different behaviours (Houston & McNamara, 1999; Clark & Mangel, 2000).

Spawning time in Puget Sound herring – proximate and ultimate causes

In Puget Sound, herring spawn between January and June, with the bulk of the subpopulations spawning between February and April (Stick *et al.*, 2014). There is no known evidence that this variation is associated with environmental gradients. In this study we use our model to generate new hypotheses about potential ultimate causes of this pattern. Ultimate causes explain why strategies and behaviours have evolved under a set of environmental conditions, while proximate explanations describe how these strategies and behaviours can be modulated in response to the immediate environment. The model suggests that a wide span in timing among populations that breed in the same location, such as Puget Sound herring, could result from the use of different feeding grounds with divergent food dynamics, or act through individual variation in condition caused by high stochasticity at a single feeding ground.

Herring in this region have been observed to spend variable times in prespawning aggregations before maturation and spawning, and variation in spawn timing has been associated with maturation rate as estimated by the gonadosomatic index (GSI; Ware & Tanasichuk, 1989), a measure of reproductive condition and allocation. Furthermore, both body weight and temperature has been linked to the GSI of herring in this region (Ware & Tanasichuk, 1989), indicating that maturation rate may be a proximate cause of their spawning time behaviour. As such, in addition to the ultimate explanations for spawning time variability explored in this study, variation in GSI due to the immediate environment could contribute to explaining both the duration of spawning within a stock at a given spawning site, and the variability across stocks in a broader geographic region.

Puget Sound herring are thought to consist of a mix of migratory and resident stocks (Penttila, 2007; Stick *et al.*, 2014), with the migratory stocks moving between spawning grounds inside the estuary and feeding grounds on the continental shelf outside Vancouver Island (see Fig. 1a). Migratory and resident individuals within single stocks have also been proposed (Penttila, 1986). In our model, particularly poor food environments led to females prioritizing fecundity over timing by regularly skipping spawning events. At a population level, this pattern of skipped spawning (generally referred to as 'skipped breeding partial migration'; Chapman *et al.*, 2011, 2012; Shaw and

Levin, 2011) means that some individuals forgo migration and breeding within a given season while the rest migrate to breed. Although not predicted by our model, strong trade-offs may possibly also lead to partial migration with regards to feeding migrations, which could explain the apparent mix of migratory and resident individuals within single herring stocks in Puget Sound.

Whether migratory stocks and individuals of Puget Sound herring use the same or different feeding grounds, migration timings and routes, is currently largely unknown. In addition, the stocks associated with spawning sites in the central Puget Sound are well mixed (Small *et al.*, 2005; West *et al.*, 2008), indicating diffuse migration strategies. Our results show that locating where and when different stocks feed, by tagging studies or molecular markers to determine stock structure, may potentially add new insights into why herring stocks spawn at such variable times in this area. Until this effort is made, current evidence may allow the spatio-temporal structure of the environment to be qualitatively compared with the quantitative output from this model to generate new hypotheses for more targeted field studies.

Here, we considered variation in spawn timing around the peak spawn date. Other potential metrics of spawn timing include onset of spawning activities, i.e. the date of first observed spawn, and duration of spawning activities, i.e. the time between first and last observed spawn. Future work could consider how behavioural trade-offs and other factors influence these features of spawn timing. Peak spawn was selected for the present analysis in part because the existing herring spawn monitoring program in Puget Sound is not guaranteed to capture the exact first or last day of spawning; each spawn site is surveyed at most once per week. Thus, there is potential for error in estimating start/end day by 7+ days. In addition, because herring spawning activities occur at individual sites over a period of days to weeks, peak spawn measures a point in time by which the majority of spawn has occurred, or the point in time by which the majority of individuals returning to that site have done so. Also, it has been hypothesized and there is traditional knowledge that older individuals spawn before younger individuals at a given site (MacCall *et al.*, 2018). Because our model is not age-structured, using peak spawn avoids age-based bias that would not be accounted for in our model.

A meta-population perspective

In this study we assume local adaptation and thus predict optimal life-history strategies under conditions at set feeding and spawning grounds. However, there could also be other mechanisms that are relevant for the dynamics seen in Puget Sound herring. One consequence of the wide variability in spawning times among stocks is that it provides a portfolio effect (Siple & Francis, 2016), by which subpopulation diversity can confer a stabilizing effect on the overall spawning population (Gillespie, 1974, 1977; Schindler *et al.*, 2010, 2015). In a strict sense, the portfolio effect cannot be the evolutionary mechanism acting on individuals to create diversity in spawning times, as that would presuppose a group selection type of argument. However, dispersal bet-hedging, through which risk is spread across space by decoupling the fates of individuals of the same genotype or lineage, could provide an evolutionary explanation for such an effect (Starrfelt & Kokko, 2012; Schindler *et al.*, 2015). This could happen if females produce offspring that can take on a range of spawning strategies, which drift into different locations, and acquire the strategy of the individuals at that location. There is some evidence in Atlantic herring that younger fish learn migration patterns from older fish, whom they follow to spawning sites (the 'adopted-migrant hypothesis'; McQuinn, 1997; Corten, 2002; Huse *et al.*, 2002, 2010; MacCall *et al.* in prep). As such, bet-hedging could be an adaptation to unpredictable environmental variation that could play out as a stabilizing effect at the population level.

In recent years, spawn timing has shifted significantly in half of the 25 Puget Sound spawning stocks, with equal numbers spawning on average earlier and later (Fig. 1b). These changes are occurring against a backdrop of wide variability, but no consistent trend, in the timing of the spring bloom (Moore *et al.*, 2016). There is little understanding about what factors are associated with these changes, though there is some evidence that local shifts may be associated with population age structure, with Puget Sound stocks having more old fish spawning earlier and fewer old fish spawning later (T. Francis, unpublished data). There are several possible explanations for this pattern. An age structure dominated by younger individuals may, for example, influence spawn site selection according to the 'adopted-migrant hypothesis' (McQuinn, 1997; Corten, 2002;

Huse *et al.*, 2002, 2010; MacCall *et al.*, 2018). This mechanism could lead to delayed spawning for subpopulations dominated by younger fish, not familiar with migration routes, or waiting for social cues to begin spawning. Since fecundity increases with age in many fishes (e.g. Hay, 1985; Lambert, 1987; Trippel *et al.*, 1997; Slotte & Fiksen, 2000; Wright & Gibb, 2005), age could also affect the trade-off between fecundity and reproductive timing. Another potential explanation for the inconsistent changes in spawning time is replacement of extirpated local populations by individuals from other subpopulations. This mechanism has, for example, been suggested to be responsible for marked demographic and phenotypic changes in a North Sea cod population (Hutchinson *et al.*, 2003). In addition to these explanations, our results suggest that changes in adult feeding conditions could be a contributing factor.

Implications for research on reproductive phenology

Puget Sound is not the only system in which migratory herring spawn at highly variable times. In the Pacific, there are both winter-spring and spring-summer spawning herring subpopulations (Haegele & Schweigert, 1985), and different Atlantic herring stocks spawn in all months of the year (Sinclair & Tremblay, 1984). Other species show similar dynamics. For example, in the northeast Atlantic, sardine (*Sardina pilchardus*) spawn all throughout the year (Stratoudakis *et al.*, 2007). Hence, our findings suggest that research on spawning time and recruitment variability in several fish stocks and species could benefit from incorporating the parental perspective. The possibility that specific characteristics of seasonal food cycles in adult feeding areas can influence spawning time was already suggested by Iles in 1964 (Iles, 1964), in an attempt to explain spawning variability among several Atlantic and North Sea herring populations. He, however, abandoned this hypothesis since it could not account for the full range of spawning times observed in these populations. This can be expected because timing of reproduction is a life-history trait that is shaped by selection on both parents and their offspring (Trivers, 1974; Varpe *et al.*, 2007; McNamara & Houston, 2008). Hence, identifying the underlying mechanisms that form the annual routines of adults, while accounting for seasonality in offspring fitness, is a prerequisite for understanding the causes and consequences of reproductive variability.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the article.

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Supplementary material

1. Model overview and dynamic optimization

We assume three locations where an individual can be: a feeding ground, a migration route and a spawning ground. Optimal behavioural decisions at the feeding ground are ***stay*** or ***migrate***; at the spawning ground they are ***wait to spawn***, ***spawn a proportion of available reserves and migrate back to feeding ground***, or ***spawn all available reserves and die***. We let a single physiological state variable $x(t)$ characterize the energy reserves of an individual at time t. We assume that there is an upper limit to the amount of energy that an individual can accumulate x_{max}, and if $x \leq 0$ at any time the individual dies from starvation. The feeding ground is characterized by three parameters: food availability $Y(t)$ (energy intake, i.e. consumed energy minus losses due to digestion and waste), energetic cost $a_{\text{f}}(t)$, and rate of mortality $m_{\text{f}}(t)$.

The spawning ground is characterized by two parameters, an energetic cost and a rate of mortality $a_{\text{s}}(t)$ and $m_{\text{s}}(t)$, respectively. For the migration route, the energetic cost is given by

$$a_{\text{m}}\,(t) = \ a_{\text{f}}(t) + 0.5min_{\alpha\text{f}} \tag{1}$$

where $min_{\alpha\text{f}}$ is the energetic cost for the lowest seasonal water temperature in the Puget Sound region (7°C; Megrey et al., 2007). The rate of mortality for the migration route $m_{\text{m}}(t)$ equals the mortality rate at the feeding ground. The migration duration τ_{m} = 20 days and the total cost of migration is

$$a_{\text{mtot}} = \sum_{t=t_{\text{start}}}^{t_{\text{start}}+\tau_{\text{m}}} a_{\text{m}}\,(t) \tag{2}$$

Depending on the analysis, we treated these parameters either as a constant or as a seasonal function of the day of the year *t*. We used a sinusoidal function with an annual period ($1 \leq t \leq 365$; referred to as annual sine curve) for the time varying case, represented by

$$Z(t) = mean + amplitude \cdot z(t) \tag{3}$$

where

$$z(t) = \cos((t - t_{\mathrm{peak}})\frac{2\pi}{365} \tag{4}$$

and t_{peak} is the peak day of the function (Fig. 2; see Table 1 and Supp. Mat. 3 for details on how the annual sine curves were parameterized).

Food availability – autocorrelated and stochastic

We modelled food availability on the feeding ground as stochastic and auto-correlated between days and let the environmental state variable *S* represent the stochastic influence on experienced food environment with a mean of 1. By drawing random values *N*(*t*) from a normal distribution with zero mean and variance of 1, the stochastic influence is given by the autocorrelation coefficient C_1 = 0.95 and a factor C_2 = 1.5 that scales the variance (Ripa & Lundberg, 1996):

$$S(t) = 1 + C_1(S(t-1) - 1) + C_2 N(t)\sqrt{1 - C_1^2} \tag{5}$$

Energy intake at time *t* is then

$$Y(t) = S(t)\bar{Y}(t) \tag{6}$$

Reproduction

If a female spawns an amount of energy $c(t)$ (measured in the same units as her current reserves *x*), then if $c(t) \leq x - \alpha_{\mathrm{mtot}}$ she reproduces and returns to the feeding ground, and if $c(t) = x$ she uses all of her reserves and dies. The probability that an offspring spawned on day *t* survives to recruit to the population (hereafter referred to as offspring fitness) is given by the annual sine curve $F_{\text{offspring}}(t)$. This function is fixed in all scenarios with the peak day set 10 days prior to the peak day in zooplankton abundance (day = 172). The increment in lifetime accumulated reproduction from spawning energy reserves $c(t)$ on day *t* is then $c(t)F_{\text{offspring}}(t)$. We do not consider intra-clutch competition among offspring as we assume that there is no parental care or cannibalism.

Adult fitness function

We envision a reproductive lifespan of $t_{\max}$ days and define a fitness function $F_{loc}(x, E, t)$ to be the expected accumulated reproduction between t and $t_{\max}$, given that the female is at the feeding ground (*loc* = f) or the spawning ground (*loc* = s) on day *t* with reserves $x(t)$ and food in the environment E (which is 0 on the spawning ground). Since no reproduction occurs after $t_{\max}$, $F_{loc}(x, E, t_{\max}) = 0$. For times prior to $t_{\max}$, we let $V_{\text{feed}}(x, E, t)$ and $V_{\text{migrate}}(x, t)$ denote the fitness values of remaining on the feeding ground or moving to the spawning ground when the reserves are x and the food in the environment is E. Then

$$F_{\mathrm{f}}(x, E, t) = max\left[V_{feed}(x, E, t),\ V_{migrate}(x, t)\right] \tag{7}$$

The fitness value of remaining to feed is

$$V_{\text{feed}}(x, E, t) = \mathrm{e}^{-m\mathrm{f}(t)} < F_{\mathrm{f}}(x - \alpha_{\mathrm{f}}(t) + Y(t, E), E', t+1) > \tag{8}$$

where $< \ >$ denotes the expectation taken over all the possible states that an individual can end up in due to the stochastic feeding environment which takes the value *E*' in the next time step, conditional on survival $\mathrm{e}^{-m\mathrm{f}(t)}$ at the start of the next time step $t + 1$. The value of migrating to the spawning ground when reserves at time *t* are *x* is

$$V_{\text{migrate}}(x,t) = \ \mathrm{e}^{-m_{\text{mtot}}}[F_{\text{s}}(x-\alpha_{\text{mtot}}, t+\tau_{\text{m}})] \quad (9)$$

where

$$m_{\text{mtot}} = \sum_{t=t_{\text{start}}}^{t_{\text{start}}+\tau_{\text{m}}} m_{\text{m}}\,(t) \quad (10)$$

If we let $V_{\text{wait}}(x,t), V_{\text{spawn}}(x,t)$, and $V_{\text{spawn\_all}}(x,t)$ denote the fitness values of waiting on the spawning ground, spawning a proportion of available reserves and migrate back to feeding ground, and spawning all available reserves, respectively, then

$$F_{\text{s}}(x,t) = \max\left[V_{\text{wait}}(x,t),\ V_{\text{spawn}}(x,t), V_{\text{spawn\_all}}(x,t)\ \right] \quad (11)$$

The fitness value of waiting is

$$V_{\text{wait}}(x,t) = \ \mathrm{e}^{-mf(t)}[F_{\text{f}}(x-\alpha_{\text{s}}(t), t+1)] \quad (12)$$

and the value of spawning a proportion of available reserves and migrate back to the feeding ground is

$$V_{\text{spawn}}(x,t) = \max_{c(t)}\left[c(t)F_{\text{offspring}}(t) + \mathrm{e}^{-m_{\text{mtot}}} < F_{\text{f}}(x-c(t)-\alpha_{\text{mtot}}, E', t+\tau_{\text{m}}) >\right] \quad (13)$$

where $c(t) \leq x - \alpha_{\text{mtot}}$ since she cannot spawn more than her current reserves, and $<\ >$ denotes the expectation taken over all the possible states that an individual can end up in due to the stochastic feeding environment which takes the value *E*' when back at the feeding grounds, conditional on survival $\mathrm{e}^{-m_{\text{mtot}}}$ at the start of period $t+\tau_{\text{m}}$. $\max_{c(t)}$ means that the c(t) that maximizes the expression within the brackets is chosen. The value of spawning all available reserves when reserves at time *t* are *x* is

$$V_{\text{spawn\_all}}(x,t) = xF_{\text{offspring}}(t) \tag{14}$$

The solutions of these equations generate rules for remaining on the feeding ground or moving to the spawning ground and, if at the spawning ground, for waiting or spawning and how much to spawn (as a function of time and physiological state). To avoid the effect of the terminal time on the backward iterations, we ran them until decisions were stationary across years (Mangel & Clark, 1988) and the optimal strategies were picked from year 1.

Forward Monte Carlo simulations

Using the optimal stationary decisions for each scenario in a stochastic food environment, we simulated 10 000 individuals forwards in time. We ran the forward simulations for 20 years (much longer than the maximum lifespan of a herring). To avoid confounding effects of initial conditions, we first let the bioenergetics stabilize over 10 years and only used data for the last 10 years in our analyses. In these simulations individuals were not subjected to predation but could die from starvation. For each scenario and individual, we recorded i) the timing of spawning, ii) how much energy was allocated to reproduction, iii) the state of the individual.

2. Bioenergetics

2.1 Equations

We followed the Wisconsin bioenergetics framework to model energy acquisition and expenditure (Hewett & Johnson, 1992). We estimated the daily energy intake N and loss due to respiration R for an adult Pacific herring of average body size (115 g) at the highest and lowest seasonal water temperature T (7 and 14°C) in the Puget Sound region (Megrey *et al.*, 2007). Depending on the specific analysis, these values were either used to define the maximum and minimum value of the annual sine curve in energy intake, or their mean value was used as a constant. See (Megrey *et al.*, 2007). In Table S1, we show the values and references for the parameters in the functions given below.

Energy intake

Energy intake is

$$N = C_{\text{max}} - F - U - S \tag{15}$$

where C_{max} is maximum daily consumption rate, and *F*, *U* and *S* are the amount of energy lost to egestion, excretion, and specific dynamic action, respectively.

The maximum daily consumption rate (g(prey) g(herring)$^{-1}$ day^{-1}) at water temperature *T* (°C) is

$$\text{C}_{\text{max}}(T) = a_{\text{C}} W^{b\text{C}} f_{\text{C}}(T) \tag{16}$$

where $a_{\text{C}} W^{b\text{C}}$ is an allometric function relating body weight *W* to maximum consumption, and a_{C} and b_{C} are the intercept and slope of this function. We took values for a_{C} and b_{C} from Rudstam (1988) who use values derived by De Silva and Balbontin (1974) for adult Atlantic herring *C. harengus*. The temperature dependence of maximum consumption $f_{\text{C}}(T)$ for ectotherms is a dome-shaped function and we parameterized it following Rudstam (1988) (see Megrey *et al.*, 2007, for a more detailed description). The parameters for C_{max} are commonly estimated from lab experiments conducted at the optimum temperature under *ad lib* feeding conditions. Hence, C_{max} represents maximum daily consumption rate and realized consumption can be assumed to be lower than this value.

We modelled egestion *F* as a constant proportion of consumption

$$F = a_{\text{F}} C_{\text{max}} \tag{17}$$

and excretion *U* and specific dynamic action *S* as constant proportions of assimilation

$$U = a_{\mathrm{U}}(C_{max} - F) \qquad 18)$$

$$S = a_{\mathrm{S}}(C_{max} - F) \qquad (19)$$

We converted C_{max} to J day^{-1} by multiplication with body weight and the average energy density of prey.

Respiration

We assumed that total energy lost to respiration *R* (J day^{-1}) depends on body weight, temperature, and swimming speed

$$R(T) = a_{\mathrm{R}} W^{-b\mathrm{R}} f_{\mathrm{R}}(T) A \qquad (20)$$

where a_{R} (J g(fish)$^{-1}$ day^{-1}) is the intercept and b_{R} the slope of the allometric function relating body weight *W* to standard metabolism, $f_{\mathrm{R}}(T)$ is the temperature dependence of respiration, and A accounts for metabolism due to swimming activity. We parameterized the function for standard metabolism following Rudstam (1998).

We modeled the temperature dependence of respiration $f_{\mathrm{R}}(T)$ by

$$f_{\mathrm{R}}(T) = e^{c\mathrm{R}T} \qquad (21)$$

where the coefficient c_{R} relates temperature to metabolism.

The swimming activity factor A is represented by

$$A = e^{d\mathrm{R}U} \qquad (22)$$

where *U* (cm/s) is swimming speed and d_{R} the coefficient relating swimming speed to metabolism.

We followed Rudstam (1988) and assumed that swimming speed scaled allometrically with body weight and exponentially with temperature up to a certain threshold temperature

$$U = a_{\mathrm{A}} W^{b\mathrm{A}} e^{c\mathrm{A}T} \tag{23}$$

Since swimming speed is likely to be higher during migration, we assumed that the energetic cost during migration is

$$R_{\mathrm{M}}(T) = R(T) + 0.5R(T_{\mathrm{min}}) \tag{24}$$

where T_{min} is the minimum seasonal water temperature in the Puget Sound region.

2.2 Parameter values and sources

Table S1. Values and references for the parameters of the bioenergetic functions used to parameterize the model (variables are given in italics).

Explanation	Function	Parameter	Value	Units	Reference
Weight		W	115	g	Schweigert *et al.*, 2002
Water temperature		T	7-14	°C	Megrey *et al.*, 2007
Consumption	$\boldsymbol{C_{\mathrm{max}}(T) = a_{\mathrm{C}} W^{b\mathrm{C}} f_{\mathrm{C}}(T)}$			g(prey) g(fish)$^{-1}$ day^{-1}	
		a_{C}	0.642	g(O_2) g(fish)$^{-1}$ day^{-1}	
		b_{C}	0.256		
	$\boldsymbol{f_{\mathrm{C}}(T)}$	See Megrey et al., 2007			Rudstam, 1988
Egestion	$\boldsymbol{F = a_{\mathrm{F}} C_{\mathrm{max}}}$			g(prey) g(fish)$^{-1}$ day^{-1}	Rudstam, 1988
		a_{F}	0.16		

Excretion	$\boldsymbol{U = a_{\mathrm{U}}(C_{\mathrm{max}} - F)}$			g(prey) g(fish)$^{-1}$ day^{-1}	Rudstam, 1988
		a_{U}	0.10		
Specific dynamic action	$\boldsymbol{S = a_{\mathrm{S}}(C_{\mathrm{max}} - F)}$			g(prey) g(fish)$^{-1}$ day^{-1}	Rudstam, 1988
		a_{S}	0.175		
Respiration	$\boldsymbol{R(T) = a_{\mathrm{R}} W^{-b\mathrm{R}} f_{\mathrm{R}}(T) A}$			J g(fish)$^{-1}$ day^{-1}	
		a_{R}	44.748	J g(fish)$^{-1}$ day^{-1}	Rudstam, 1988
		b_{R}	0.227		Rudstam, 1988
	$\boldsymbol{f_R(T) = \mathrm{e}^{cRT}}$	c_{R}	0.0548	°C^{-1}	Rudstam, 1988
	$\boldsymbol{A = \mathrm{e}^{dRU}}$	d_{R}	0.03		Rudstam, 1988
	$\boldsymbol{U = a_{\mathrm{A}} W^{bA} \mathrm{e}^{cAT}}$				
	$T < 9$°C	a_{A}	3.9	cm s^{-1}	Rudstam, 1988
		b_{A}	0.13		Rudstam, 1988
		c_{A}	0.149		Rudstam, 1988

	$T \geq 9$°C	a_{A}	15.0	cm s^{-1}	Rudstam, 1988
		b_{A}	0.13		Rudstam, 1988
		c_{A}	0.0		Rudstam, 1988

3. Results

3.1 Figures Food availability analysis

Low feeding ground mortality rate

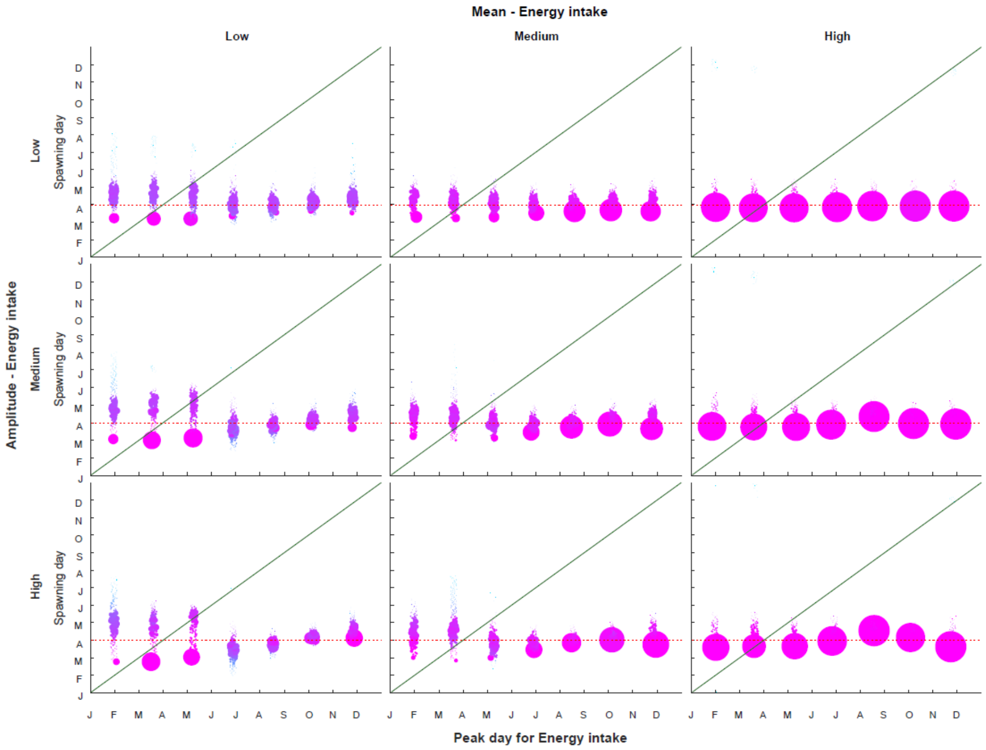

Figure S1. Subplots show predicted spawning days for 10 000 individuals following the optimal strategies for the 'Food availability analysis' under a low feeding ground mortality rate. Dots represent predicted spawning days for different peak days and three mean levels of energy intake. The size of the dot indicates the frequency of spawning events predicted for that day and the colour the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The red dotted horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in energy intake.

Medium feeding ground mortality rate

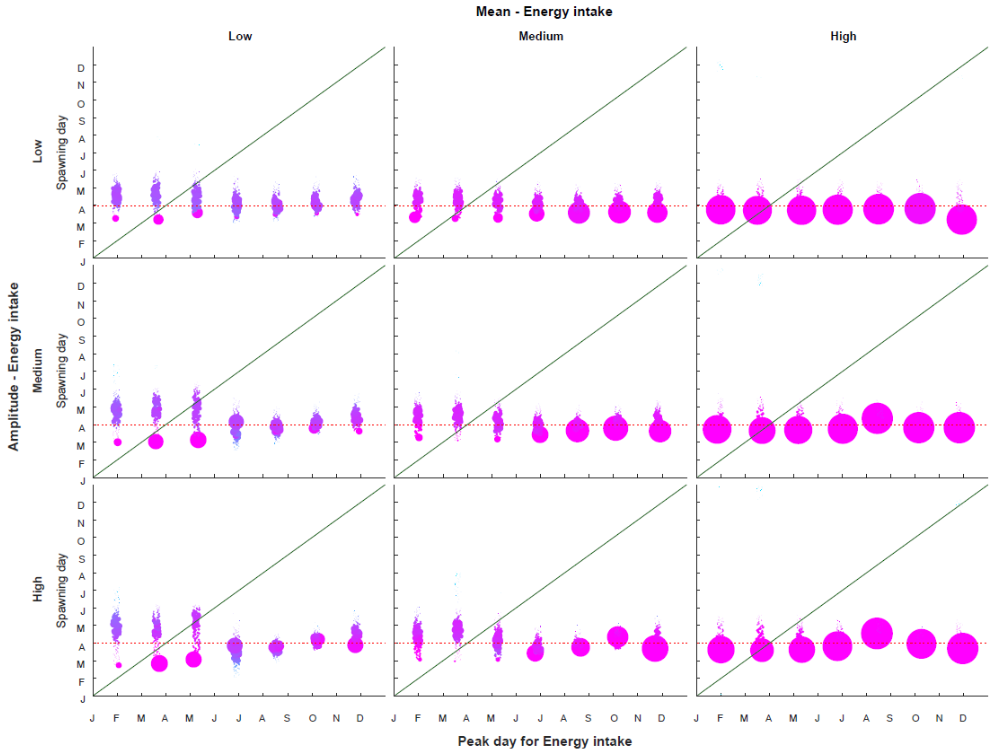

Figure S2. See figure legend for Fig. S1. This figure shows predicted spawning days under a medium feeding ground mortality rate.

High feeding ground mortality rate

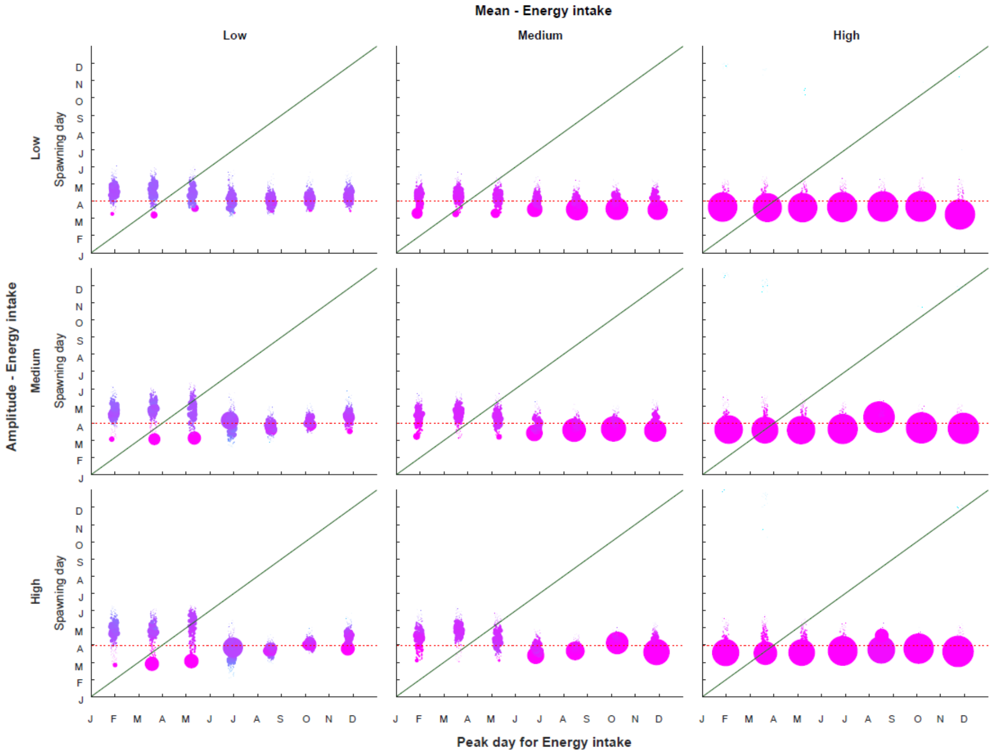

Figure S3. See figure legend for Fig.S1. This figure shows predicted spawning days under a medium feeding ground mortality rate.

3.2 Figures Mortality analysis

Low feeding ground mortality rate

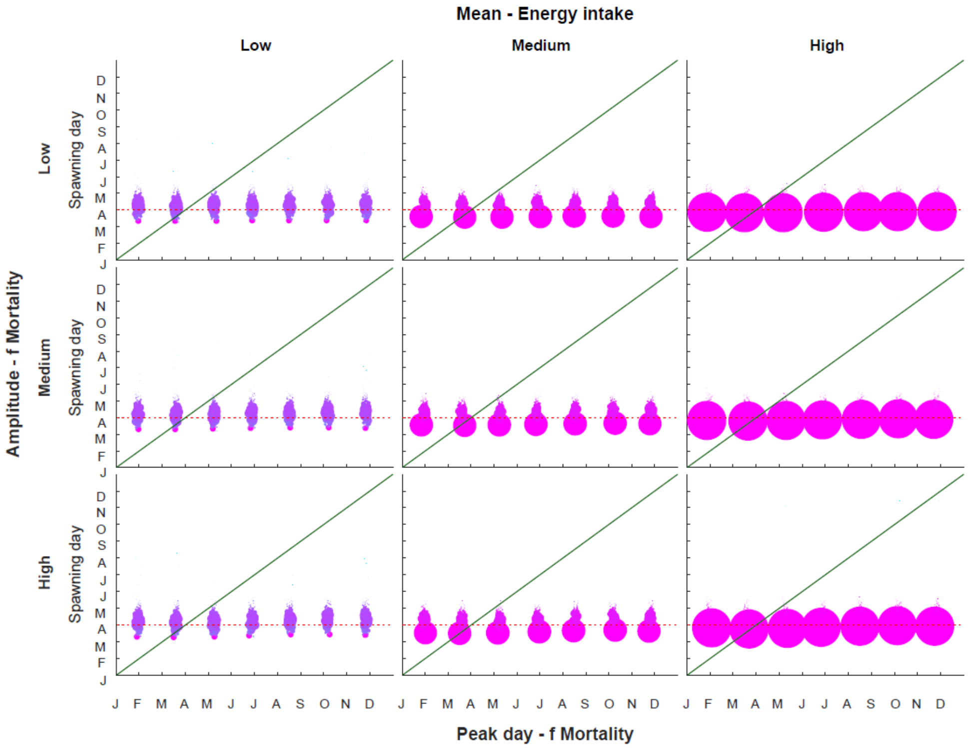

Figure S4. Subplots show predicted spawning days for 10 000 individuals following the optimal strategies for the ‘Mortality analysis’ under a low feeding ground mortality rate (f Mortality). Dots represent predicted spawning days for different peak days and three mean levels of energy intake. The size of the dot indicates the frequency of spawning events predicted for that day and the colour the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The red dotted horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in f Mortality.

Medium feeding ground mortality rate

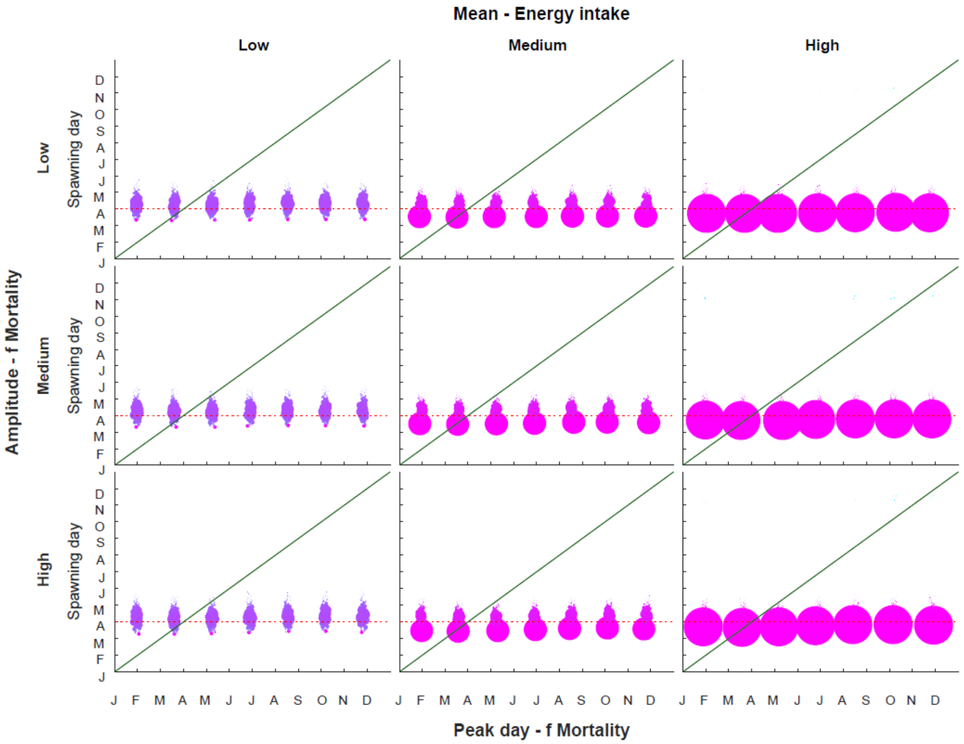

Figure S5. See figure legend for Fig. S5. This figure shows predicted spawning days under a medium feeding ground mortality rate.

High feeding ground mortality rate

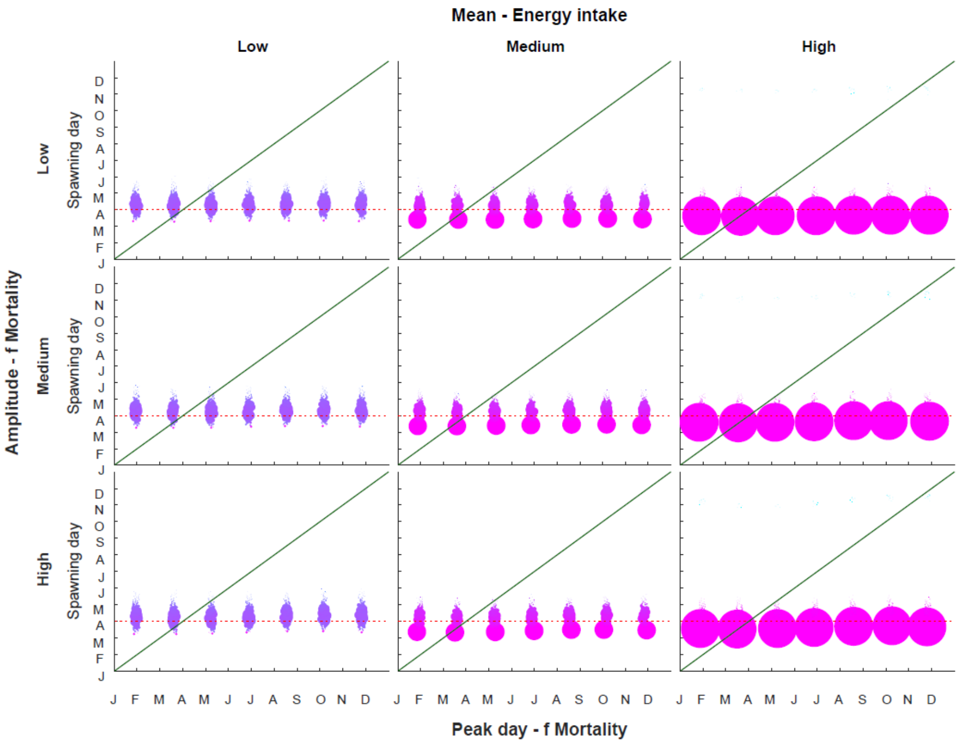

Figure S6. See figure legend for Fig. S5. This figure shows predicted spawning days under a high feeding ground mortality rate**.**

3.3Figures Puget Sound analysis

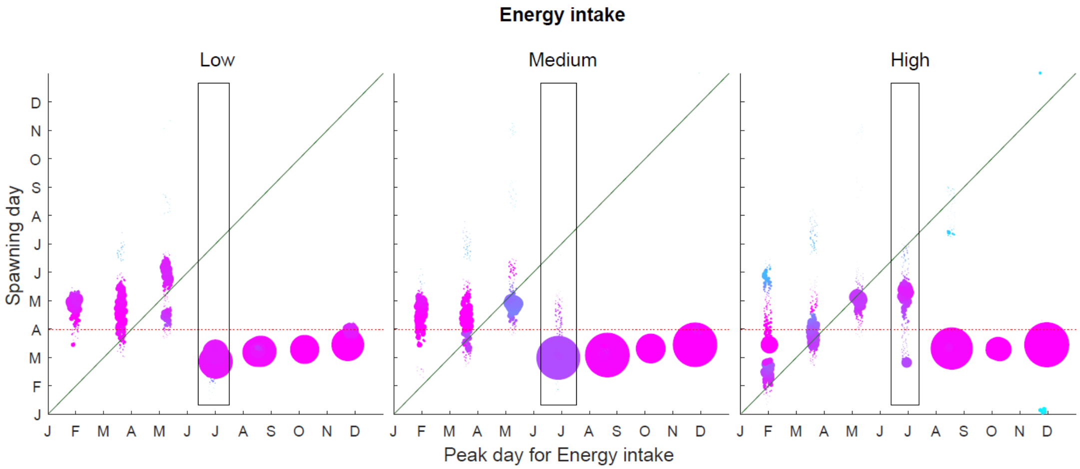

Figure S7. Predicted spawning days for 10 000 individuals following the optimal strategies for the 'Puget Sound analysis', results for a mortality rate of 0.8 yr^{-1}. Dots represent predicted spawning days for different peak days and three levels of energy intake. The size of the dot indicates the frequency of spawning events predicted for that day and the colour of the dot indicates the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The red dotted horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in energy intake. Rectangle indicates the case explored in Fig. 6, representing the approximate current peak day in zooplankton abundance in Puget Sound.

4. Model sensitivity

4.1 Food availability analysis

Migration duration = 10 days

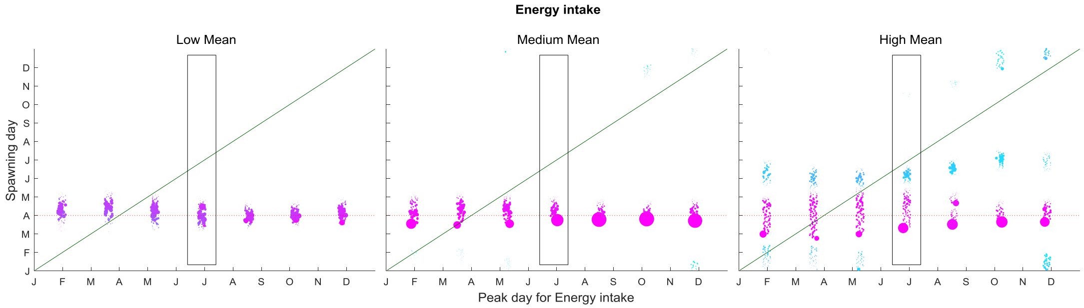

Figure S8. Predicted spawning days for 10 000 individuals following the optimal strategies for the reference case in the 'Food availability analysis', for a migration duration of 10 days.

Migration duration = 30 days

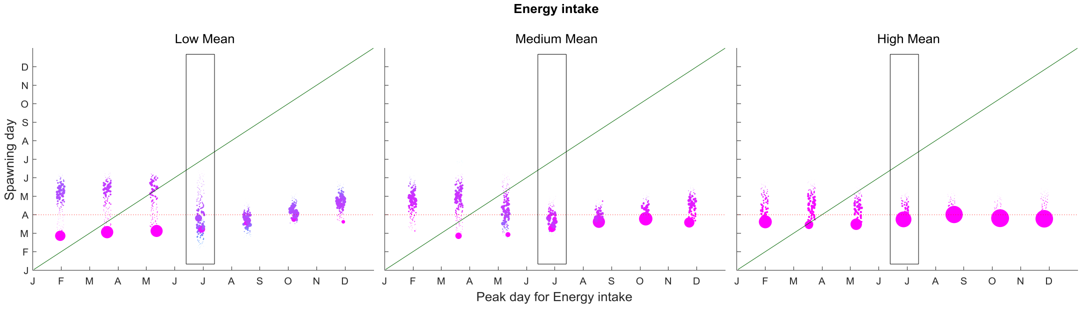

Figure S9. Predicted spawning days for 10 000 individuals following the optimal strategies for the reference case in the 'Food availability analysis', for a migration duration of 30 days.

Migration duration = 40 days

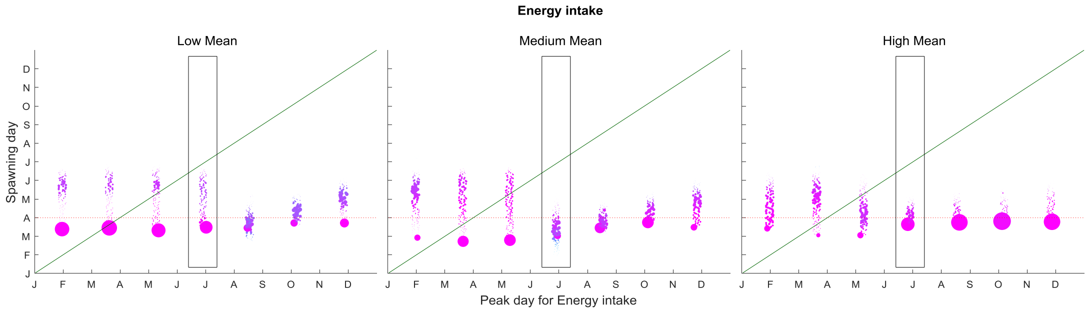

Figure S10. Predicted spawning days for 10 000 individuals following the optimal strategies for the reference case in the 'Food availability analysis', for a migration duration of 40 days.

4.2 Puget Sound analysis

Migration duration = 10 days

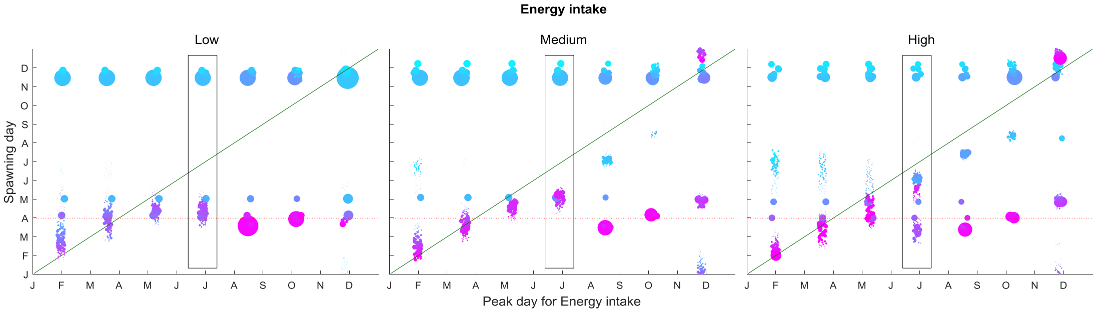

Figure S11. Predicted spawning days for 10 000 individuals following the optimal strategies with parameters representative of Pacific herring in Puget Sound ('Puget Sound analysis'), for a migration duration of 10 days.

Migration duration = 30 days

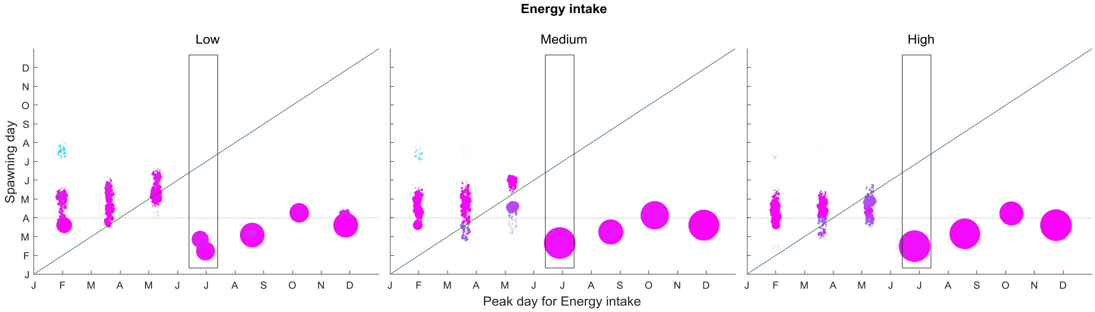

Figure S12. Predicted spawning days for 10 000 individuals following the optimal strategies with parameters representative of Pacific herring in Puget Sound ('Puget Sound analysis'), for a migration duration of 30 days.

Migration duration = 40 days

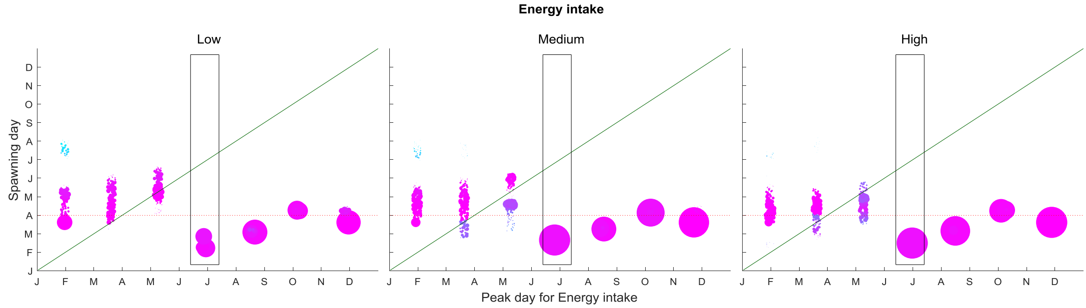

Figure S13. Predicted spawning days for 10 000 individuals following the optimal strategies with parameters representative of Pacific herring in Puget Sound ('Puget Sound analysis'), for a migration duration of 40 days.

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PAPER II

Ljungström G, Claireaux, M, Fiksen Ø, Jørgensen C

Local adaptations in body size under global change: zooplankton community more important than temperature or food abundance in model of a zooplanktivorous fish

In review *Marine Ecology Progress Series*

Local adaptations in body size under global change: zooplankton community more important than temperature or food abundance in model of a zooplanktivorous fish

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ABSTRACT

One of the most well-studied biogeographic patterns is the increase in body size with latitude, and recent body size declines in marine and terrestrial organisms have received growing attention. Spatial and temporal variation in temperature is the generally invoked driver but food abundance and quality are also emphasized. However, the mechanisms underlying the latitudinal gradient in body size and recent declines are not clear and the actual cause is likely to differ both within and among species. Here we focus our attention on drivers of body size in planktivorous fish that forage through vision. This group of organisms plays a central role in marine ecosystems by linking the flow of energy from lower to higher trophic levels. Using a model that incorporates explicit mechanisms for vision-based feeding and physiology, we investigate the influence on optimal body size from several biotic (prey size, prey energy content, and prey biomass concentration) and abiotic factors (temperature, latitude, and water clarity) known to affect foraging rates and bioenergetics. We found prey accessibility to be the most influential factor for body size, determined primarily by prey size but also by water clarity, imposing visual constraints on prey encounters and thereby limiting feeding rates. Hence, for planktivores that forage through vision, an altered composition of the prey field could have important implications for body size, and for the energy available for reproduction and other fitness-related tasks. Understanding the complicated effects of global change on zooplankton communities is thus crucial for predicting impacts on planktivorous fish, as well as consequences for energy flows and body sizes in marine systems.

Keywords: optimal body size, planktivore, visual foraging, wasp-waist, zooplankton community

1. INTRODUCTION

Why are there organisms of different body size? What causes size-variation among organisms that otherwise occupy similar ecological niches? Size variation has received abundant attention because it is so readily observable, and sweeping theories that squeeze all species into one explanation abound. In this paper, we argue that variation in body size also can serve as a lens through which a more nuanced picture may emerge. By acknowledging that observed size differences can reflect local adaptation, scrutinizing environmental differences can uncover the potential ecological drivers that constrain energetics, growth, and life histories. But before we can delve into one species in detail, we need to establish the null expectations from established theories for biogeographic clines in body size.

The tendency of organisms to be smaller at higher temperatures and lower latitudes is one of the most well-studied biogeographic patterns, and biologists have long been trying to explain the underlying mechanisms (discussed in Blackburn *et al.*, 1999; Angilletta *et al.*, 2004; Millien *et al.*, 2006; Teplitsky and Millien, 2014). Two common hypotheses link size differences directly to temperature, through Bergmann's rule (Bergmann, 1847) and the temperature-size rule (Atkinson, 1994, Angilletta and Dunham, 2003; Kingsolver and Huey, 2008). The former relates body size to thermoregulatory capacity in endotherms (Bergmann, 1847), whereas the latter describes the effect of temperature on growth and maturation in ectotherms (Atkinson, 1994). Apart from temperature, latitudinal and seasonal variation in food availability and quality is often invoked to explain why body size varies in time and space (see references in McNab, 2010; Watt *et al.*, 2010; Teplitsky and Millien, 2014; Vinarski, 2014). For example, larger body size at higher latitudes could be an adaptation to reduce the risk of overwinter starvation (Cushman *et al.*, 1993), or a consequence of less competition for resources due to higher density-independent mortality and fewer species associated with strongly seasonal environments (Blackburn *et al.*, 1999).

Reductions in body size is evident in a growing number of species, comprising endotherms and ectotherms in terrestrial and aquatic environments (Gardner et al. 2011, Sheridan & Bickford 2011). The scale and geographic pattern of this trend make body size declines the third universal response to climate change, after shifting spatial distributions and altered phenologies (Daufresne et al. 2009, Gardner et al. 2011, Sheridan & Bickford 2011, Cheung et al. 2013). This trend is particularly strong in aquatic environments (Forster *et al.*, 2012; Horne *et al.*, 2015), and although harvesting is likely partly responsible, current rates of decline are faster than expected from fishing alone (Baudron *et al.*, 2011; Audzijonyte *et al.*, 2013). In addition to Bergmann's rule and the temperature-size rule, warming-related constraints on aerobic respiration have been invoked to cause size reductions in aquatic species that breathe with gills or similar structures (Pauly, 1981; Atkinson *et al.*, 2006; Cheung *et al.*, 2011; Verberk *et al.*, 2011; Forster *et al.*, 2012), but this hypothesis has received criticism (e.g. Brander et al. 2013, Lefevre et al. 2017, summarized in Audzijonyte et al. 2019).

Contrary to the directional effect of temperature, climate change-induced alterations in food resources can lead to both smaller and larger size (Millien *et al.*, 2006; Gardner *et al.*, 2011; Teplitsky & Millien, 2014). For example, a decrease in food availability or quality can restrict energy acquisition and lead to smaller size, whereas a longer growing season may extend foraging opportunities and thus increase growth potential. Moreover, in ectotherms, both digestion and metabolic rate are influenced by temperature, meaning that the net effect of warming on energy surplus depends on the relative magnitude of these two factors, as well as on food availability.

Identifying the underlying drivers of spatial and temporal variation in body size is crucial for understanding its origins, and for predicting how this trait will respond to environmental change. However, since many environmental factors are correlated and some are changing in parallel over time, without a causal link between them, disentangling their relative effects on body size variation is inherently difficult (Blackburn *et al.*, 1999; Millien *et al.*, 2006; Gardner *et al.*, 2011; Teplitsky & Millien, 2014; Audzijonyte *et al.*, 2019). A useful tool for assessing causality is mechanistic modelling, whereby functional relationships are used to predict a system's behaviour. Undoubtedly, intra- and interspecific body size clines are not determined by one, but several different mechanisms (Blackburn *et al.*, 1999; Angilletta & Dunham, 2003; Angilletta *et al.*, 2004; Millien *et al.*, 2006). Therefore, to compare general explanations with the details relating to particular ecological lifestyles, we focus this study on drivers of body size in one group of aquatic ectotherms: zooplanktivorous fish that forage through vision.

Planktivorous fish, often collectively referred to as forage fish, play a central role in aquatic ecosystems since nearly all energy from lower to higher trophic levels flows through them (Alder *et al.*, 2008). They are highly specialized for feeding on small zooplankton and are themselves key prey for larger fish, sea birds, and marine mammals. Using a model that incorporates explicit mechanisms for vision-based feeding and physiology, we investigate the influence on optimal body size from several biotic and abiotic factors known to affect foraging rates and bioenergetics. We model proximate effects on the energy budget of different sized individuals and interpret our findings in light of the consequence for optimal body size. We define optimal body size as the length at which annual surplus energy is maximized, representing the size at which the invidual has the highest capacity of converting energy from the environment into reproductive output or other fitness-related tasks. Evolutionarily, this implies that individuals are expected to stop growing at this size, unless being larger or smaller has a considerable fitness advantage due to intra- and inter-specific interactions. For example, being larger could be optimal if this leads to an advantage in competitions for food (Karplus *et al.*, 2000) or mates (Kitano, 1996), or if mortality declines strongly with size (Roff, 1992; Charlesworth, 1994). Conversely, maturation at a smaller size could be optimal if the prospects for survival and hence future reproduction are low (Michod, 1979; Roff, 1981). In this study we focus on how bottom-up processes and abiotic factors affect optimal body size, and therefore omit potential adaptations to predation risk and intra-specific interactions.

The Atlantic herring *Clupea harengus* is an appropriate study species for exploring the effects of bottom-up processes and abiotic factors on optimal body size; it is aquatic and long-lived. Aquatic organisms have an advantage over their terrestrial counterparts: they do not have to carry their body weight as tissue density is not very different from that of water (Schmidt-Nielsen, 1997b). Thus, environmental factors and selection pressures linked to bioenergetics are likely to cause larger variation in body size and thus leave a more visible fingerprint. For example, although a bird in an abundant resource environment could potentially grow larger, the physics of flight efficiency sets an upper limit to its body size, while foraging, reproduction, and predation risk may constrain the lower limit (Schmidt-Nielsen, 1984). Further, organisms with long life-spans presumably experience low predation, suggesting that energetic trade-offs are the main constraint on reproduction and therefore have strong bearing on the evolution of body size. The wide distribution of Atlantic herring makes it highly suitable for studying environmental influences on geographic trait patterns; it is found across the North Atlantic from Spitsbergen in the north (ca. 80°N) to the northern Bay of Biscay in the south (ca. 50°N), and from the Baltic Sea in the east to southwestern Greenland, Labrador, and southward to South Carolina (ca. 30-70°N) in the west (Whitehead, 1985).

The present paper consists of two parts. First, a case study of herring in the Norwegian Sea and North Sea, aimed at identifying the underlying mechanisms responsible for the striking body size difference observed between herring in these two neighbouring systems. The Norwegian Sea and the North Sea provide a good comparison since they vary in several characteristics proposed to influence body size, including water temperature, seasonality in production, prey community composition, and latitude. The second part is a detailed analysis to investigate the sensitivity of herring body size to variation in the abiotic (water temperature and light) and biotic environment (prey size, prey energy content, and prey biomass concentration). Our findings are therefore relevant for explaining geographic patterns and shifts in body size in visually foraging planktivores.

2. MATERIALS & METHODS

To investigate how intrinsic and extrinsic factors come together to influence optimal body size we combined two models: (1) a mechanistic model of prey encounter and foraging including light and vision; and (2) a bioenergetics model for internal prey processing and energy budget.

This coupled model captures feeding and the energy budget over the annual cycle as a function of body size and environmental settings. Feeding rate is influenced by prey properties (Fig. 1a, c), the diel cycle of irradiance (season and latitude, Fig. 1b), and optical properties of the water (Fig. 1d). More hours of light allow for more time feeding (Fig. 1b) and prey are easier to detect in clearer water, leading to higher encounter rates (Fig. 1d).

Herring detect larger prey at a longer distance R, and because the volume searched scales with R^2 (eq. 2, Table 1), prey encounter rate is more sensitive to variation in prey size than prey biomass concentration. The visual acuity of fish tends to increase proportionally with eye size (Caves *et al.*, 2017), and this is included in our model (eq. 7, Table 1). Since swimming speed scales with body length (eq. 2, Table 1), the volume searched for prey scales with herring body length L^3. Body mass also scales with L^3, but because beam attenuation blurs images exponentially with detection distance (eqs. 4 and 5, Table 1), there is a diminishing return of volume searched for large herring. This implies that the number of prey detected increases less than proportionally with herring body mass, which contributes to constraining the energy budget of larger fish. Finally, handling prey takes time and at some point this limits the rate at which prey can be ingested (Fig. 1a, c).

Internal constraints set by gut filling and digestion rate determine how much food can be digested and this capacity also increases with size and with temperature (Fig. 1e). One of these processes, i.e. encounter rate, handling time, or digestion rate, always limit the acquisition rate. A further critical factor is that the rate of metabolism increases with temperature, so net energy surplus only goes up when temperature has a higher effect on acquisition through digestion than on metabolic loss (Fig. 1e). Whether it is feeding or digestive processes that eventually limit the body size of fish depends on a range of physiological traits and environmental factors, and we have captured some of the most important in our model.

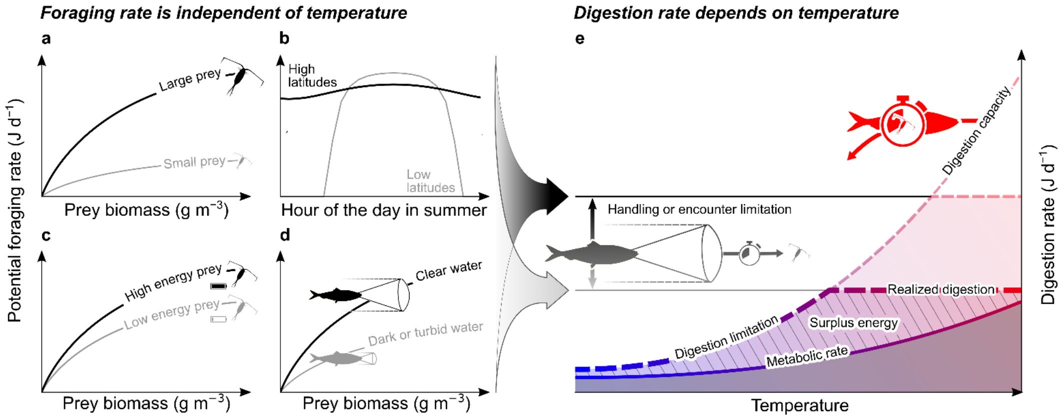

Figure 1. Effect of prey properties (Fig. 1a, c), the diel cycle of irradiance (season and latitude, Fig. 1b), and optical properties of the water (Fig. 1d) on the potential foraging rate of herring, which is determined by prey encounter or handling time limitation (Fig. 1e). Foraging rate is independent of temperature. Internal constraints set by gut filling and digestion rate determine how much food can be digested and this capacity increases temperature (Fig. 1e). One of these processes, i.e. encounter rate, handling time, or digestion rate, always limit the acquisition rate (realized digestion; Fig. 1e). A critical factor for the energy budget is that metabolic rate increases with temperature, so net energy surplus only goes up when temperature has a higher effect on acquisition through digestion than on metabolic loss (Fig. 1e).

Table 1. Equations of the model (see Table 2 for variables and parameters; NWG= Norwegian Sea, NTH = North Sea). Functions are general to planktivores but parameters are species-specific for herring.

Eq.	Explanation [units]	Equation	Source
(1)	Feeding rate for multiple prey items for hour on day [J s^{-1}]	$i_{t,d} = \sum_{p=1}^{n} \frac{e_p P_{c,p} \beta_{p,t,d} N_{p,d}}{1 + \sum_{j=1}^{n} h_j \beta_{j,t,d} N_{j,d}}$	Case, 2000
(2)	Search or clearance rate [m^3 s^{-1}]	$\beta_{p,t,d} = \frac{1}{2} \pi R_{p,t,d}^2 v(L)$	
(3)	Length-dependent swimming speed [m s^{-1}]	$v(L) = 1.5L$	Gibson & Ezzi, 1985; Pitcher et al. 1985
(4)	Prey detection distance R [m]. The equation is solved for R by iteration.	$R_{p,t,d}^2 \mathrm{e}^{c_{loc} R_{\mathrm{t,d}}} = \mathrm{C}_p A_p E(L) \frac{I_{t,d}}{\mathrm{k_R} + I_{t,d}}$	Aksnes & Utne, 1997
(5)	Beam attenuation coefficient [m^{-1}]	$c_{\mathrm{NWG}} = 0.0579 + 0.363 chla^{0.57}$ $c_{\mathrm{NTH}} = 0.066 + 0.3627 chla^{0.57}$	Morel, 1991 Mobley, 1994
(6)	Prey image area [m^3]	$A_p = 0.75 l_p d_p$	
(7)	Visual eye sensitivity. This assumes *R* is one fish body length for 4.0 mm long prey when light is not limiting (in clear water, $c_{loc} = 0$)	$E(L) = \frac{L^2}{\mathrm{A}_E \, \mathrm{C}_p}$	Varpe & Fiksen, 2010
(8)	Ambient irradiance at foraging depth [W m^{-2}]	$I_{t,d} = I_0(t,d) \mathrm{e}^{-a_{loc} z}$	

(9)	Diffuse attenuation coefficient [m^{-1}]	$a_{\mathrm{NWG}} = 0.064 + 0.0223 chla^{0.65}$ $a_{\mathrm{NTH}} = 0.125 + chla(0.0506\, e^{-0.606 chla} + 0.0285)$	Voss, 1992 Mobley, 1994
(10)	Prey biomass concentration [g m^{-3}]	$N_{loc,d,p} = s_d N_{\max,p}$	See figures S1 and S2 in Supplement 1
(11)	Net energy uptake [J]	$U(d) = D_\mathrm{d} - [(\alpha_\mathrm{F} D_\mathrm{d}) + \alpha_\mathrm{U}\big(D_\mathrm{d} - (\alpha_\mathrm{F} D_\mathrm{d})\big) + \alpha_\mathrm{S}\big(D_\mathrm{d} - (\alpha_\mathrm{F} D_\mathrm{d})\big)]$	
(12)	Digested food [J]	$D_d = \sum_{t=1}^{24} \min\left[D_{\mathrm{rate}} t, S_t + i_{t,d}\right]$	
(13)	Digestion rate [or stomach evacuation rate; J h^{-1}]	$D_{\mathrm{rate}}(t) = \frac{\mathrm{k_D} 44.748 W^{0.7730} \mathrm{e}^{0.0548T(d)}}{24}$	Adapted from Rudstam, 1988
(14)	Water temperature [°C]	$T(d) = T_\mathrm{M} + T_\mathrm{A}\, z(d)$ $z(d) = \cos((d - d_{\mathrm{peak}})\frac{2\pi}{365}$	
(15)	Stomach fullness [J]	$S_{t+1} = \min\left[S_t + i_{t,d}, S_{\max}\right] - D_{\mathrm{rate}}(t)$	
(16)	Metabolic cost [J]	$M(d) = 44.748 W^{0.7730} \mathrm{e}^{0.0548T(d)} + S(W)$	Adapted from Rudstam, 1988
(17)	Weight-dependent swimming cost [J]	$S(W) = p_\mathrm{S} 44.748 W^{0.7730}$	

2.1 Model of foraging and bioenergetics

The output of the coupled foraging and bioenergetics model is an estimate of the annual surplus energy (kJ year^{-1}). This is the total annual energy intake minus all costs, computed for a range of adult body sizes (10-45 cm), which represents the energy available for growth and reproduction each year. We modelled the surplus energy for each day *d* and summed over all *d* to find the annual surplus. The procedure was repeated for each body length *L*:

$$\varepsilon = \sum_{d=1}^{365} [U(d, L) - M(d, L)]$$

where $U(d, L)$ is net energy uptake from feeding (kJ d^{-1}), and $M(d, L)$ is the metabolic cost (kJ d^{-1}). All equations leading to *U* and M are summarized in Table 1. We did sensitivity analyses of the following parameters: fish length, prey prosome length, prey energy content, prey biomass concentration, handling time, capture success, latitude, water temperature, and chlorophyll *a* concentration.

The foraging model is a multiple prey Holling type II functional response where feeding rate satiates at high prey concentration (prey m^{-3}) due to handling time limitation. The model estimates feeding rate as a function of prey characteristics, diel (*t*, hourly) and seasonal (daily) variation in solar irradiance, optical properties of the water, the visual acuity of the predator, and the capture success and handling time for prey (eq. (1) in Table 1; Huse & Fiksen, 2010; Varpe & Fiksen, 2010). The metabolic cost M is modelled as a function of body weight and temperature with parameters estimated for Atlantic herring (weight-dependence) and other clupeids (temperature-dependence) (eq. (16) in Table 1; Rudstam 1988). We set the cost of swimming equal to the weight-dependent metabolic rate (Ware, 1978) and assumed that herring swim at this rate 75% of the time in summer and 10% in winter (eq. (17) in Table 1). Digestion and gut evacuation are complex processes that may depend on a number of factors, such as gut fullness, meal frequency, and prey characteristics. Since we could not find a relevant empirical relationship in the literature to describe these processes, we let one rate represent their aggregated effect (digestion rate; eq. (13) in Table 1). We used the same parameters for size- and temperature-dependency as for metabolic rate and calibrated the rate of digestion to annual surplus energy approximated from data (see section 1 in Supplement 1).

Over a wider temperature range, digestion, like many other physiological functions, is a dome-shaped function: it increases up to an optimal temperature and then decreases as a result of one or several factors, such as enzyme malfunctioning or reduced oxygen availability (Pörtner, 2010). Considering the current range of temperatures at which viable herring populations are found, e.g. in the Baltic Sea where summer temperatures reach about 25°C, we assume that digestion in NSS and North Sea herring at the temperatures that we model (4-14°C ± 2°C) can be represented by the positive exponential part of a dome-shaped function.

A full list of all model equations with references is given in Table 1, and the corresponding parameters and variables are given in Table 2.

Table 2. Parameters and variables used in the coupled foraging and bioenergetics model (see Table 1 for equations).

Symbol	Description	Value	Units	Source
$\mathbf{A}_{E}$	Eye-sensitivity coefficient	$4.0 \cdot 10^{-6}$	m	Varpe & Fiksen, 2010
$\boldsymbol{\alpha}_{\mathbf{F}}$	Egestion coefficient	0.16	–	Rudstam, 1988
$\boldsymbol{\alpha}_{\mathbf{S}}$	Specific dynamic action coefficient	0.175	–	Rudstam, 1988
$\boldsymbol{\alpha}_{\mathbf{U}}$	Excretion coefficient	0.10	–	Rudstam, 1988
$\boldsymbol{chla}$	Chlorophyll *a* concentration	See Table 3	mg m^{-3}	
$\mathbf{C}_{p}$	Prey contrast	0.3	–	Utne-Palm, 1999

$\boldsymbol{d}$	Day of year		–	
$\boldsymbol{d_p}$	Prey width		m	
$\boldsymbol{d_{\mathrm{peak}}}$	Peak day for water temperature	212 (31 July)	Julian day	van Deurs et al. 2010
$\boldsymbol{e_p}$	Prey energy content	See Table 3	J g^{-1}	
$\boldsymbol{h_p}$	Prey handling time	See Table 3	s $prey^{-1}$	
$\boldsymbol{I_0}$	Ambient irradiance at surface		W m^{-2}	Bleck 2002
$\boldsymbol{k_{\mathrm{D}}}$	Factor calibrating digestion rate to annual surplus energy approximated from data	10	–	Slotte, 1999; See section 1 in Supplement 1
$\boldsymbol{k_{\mathrm{R}}}$	Light saturation of R	1	μE m^{-2} s^{-1}	Varpe & Fiksen, 2010
$\boldsymbol{L}$	Fish length	Varied from 10 to 40 cm	cm	
$\boldsymbol{l_{\mathrm{p}}}$	Prey prosome length	See Table 3	m	
$\boldsymbol{N_{\mathrm{max},p}}$	Maximum prey abundance	See Table 3	Prey m^{-3}	
$\boldsymbol{P_{\mathrm{c},p}}$	Prey capture success scaling factor	See Table 3	–	
$\boldsymbol{p_{\mathrm{S}}}$	Proportion of time devoted to swimming	0.75 (summer); 0.1 (winter)	–	

$\boldsymbol{s_d}$	Seasonal prey abundance scaler	See Supplementary 1 3.2	–	
$\boldsymbol{S_{\mathbf{max}}}$	Maximum gut capacity	3% of fish weight	Joules	Bernreuther et al. 2008
$\boldsymbol{t}$	Hour of day		–	
$\boldsymbol{T_{\mathbf{A}}}$	Temperature amplitude	See Table 3	°C	
$\boldsymbol{T_{\mathbf{M}}}$	Mean temperature	See Table 3	°C	
$\boldsymbol{W}$	Fish weight	$W(L) = 0.00603L^{3.0904}$	g	ICES, 2007
$\boldsymbol{z}$	Foraging depth	See Table 3	m	

2.2 Study systems: comparing two herring populations

The Norwegian spring-spawning (NSS) herring is a stock of Atlantic herring that feeds in the Norwegian Sea (Fig. 2a) during spring and summer (April-September), overwinters in fjords or off the coast of northern Norway (September-January), and then spawns at banks along the Norwegian coast in February and March (Dragesund *et al.*, 1997; Helmuth *et al.*, 2005; Huse *et al.*, 2010). The oldest observed adults reach a body size of about 38.5 cm (Fig. 2b), which is the largest for this species. The diet of NSS herring consists primarily of *C. finmarchicus* (ca. 60% of diet wet weight), euphausiids, and amphipods (Dalpadado *et al.*, 2000; Gislason & Astthorsson, 2002; Dommasnes *et al.*, 2004; Bachiller *et al.*, 2016). Stomach data indicates that NSS herring stop feeding from the onset of wintering until the termination of spawning activities (Slotte, 1999).

In the North Sea, there are three herring populations: the northern, central, and southern North Sea herring (Corten, 2000, 2001). All three populations share the same feeding ground in the northern North Sea where foraging takes place between April and

August (Fig. 2a; Corten, 2000, 2001). The central and northern populations spawn in the western North Sea in August and September and overwinter in the region of the Norwegian Trench, whereas the southern population spawns in December to January in the eastern English Channel, and then overwinter in the southern North Sea. North Sea herring are smaller than NSS herring, with a length of the oldest observed adults of about 33 cm (Fig. 2b). During the summer season North Sea herring feed primarily on the calanoid copepods C. *finmarchicus* and C. *helgolandicus*, and post-larval stages of fish (Last, 1989). Some feeding appears to also take place outside of the main foraging season, with stomach samples from February containing mainly *Calanus*, hyperiid amphipods, euphausiids, and fish eggs (Last, 1989; Segers *et al.*, 2007). However, few individuals have food in their stomachs, and low stomach contents suggest that feeding during this period is limited (Daan *et al.*, 1985; Last, 1989).

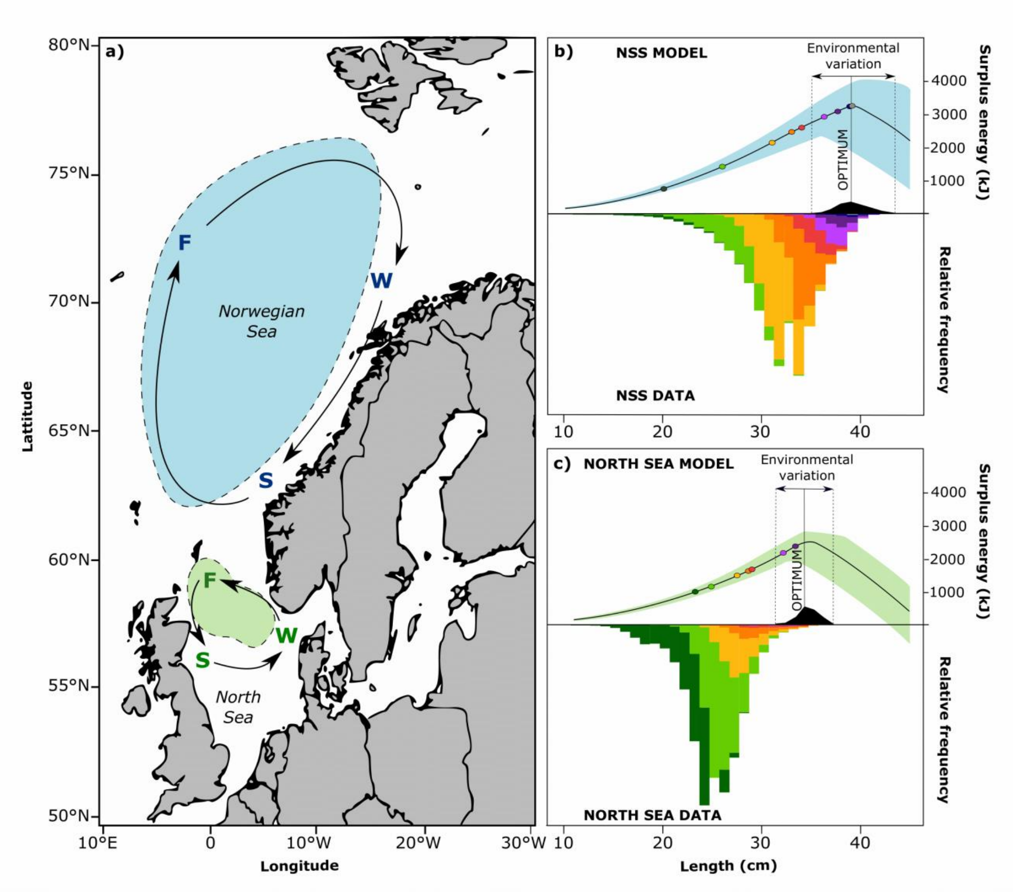

Figure 2. a) Annual migration patterns of Norwegian spring spawning herring (NSS; top) and North Sea herring (bottom). F, W, and S indicate feeding, overwintering and spawning locations. The feeding areas of Norwegian spring spawning herring and North Sea herring are highlighted in blue and green, respectively. For the North Sea, the northern and central components are shown, the southern stock spawns and overwinters further south. Distribution of real body lengths (DATA) and predicted optimal lengths (MODEL) under environmental variation (annual water temperature, default ±2°C; prey abundance, default ±20%; chlorophyll *a* concentration, default ±20%) for b) NSS herring, and c) North Sea herring. Colours from dark green to grey refer to cohorts aged 3-4, 5-6, 7-8, 9-10, 11-12,13-14, 15-16, and 17+. The data plots show the frequency of each cohort

relative to the total number of individuals and the coloured circles represent the mode of each cohort group.

The Norwegian Sea and the North Sea differ in several aspects known to influence foraging rates and bioenergetics of planktivores: 1) Located at a higher latitude the Norwegian Sea has more daylight hours in spring and summer, 2) In summer, the North Sea is considerably warmer than the Norwegian Sea while winter temperatures are similar, 3) The North Sea has a lower water clarity and hence less light can penetrate the water column, 4) The zooplankton communities in the two seas are quite different: the total biomass is higher in the Norwegian Sea (9.2 vs. 5.7 g dry weight m^{-2}; Norwegian Sea: 1995-2015, Broms, 2016; North Sea: 2005-2014, Falkenhaug, 2016), and the deeper Norwegian Sea mainly contains zooplankton of larger size, while the shallower North Sea is characterized by smaller-sized zooplankton (Melle *et al.*, 2004; Pitois *et al.*, 2009). In spring, however, *C. finmarchicus* are advected into the northern North Sea where they mix with *C. helgolandicus* (Fransz *et al.*, 1991). There is no discernible difference in size or energy content between *C. finmarchicus* and *C. helgolandicus* in the North Sea (Wilson *et al.*, 2015), but *C. finmarchicus* is typically larger at higher latitudes (Boxshall & Schminke, 1988; Skjoldal, 2004; Jónasdóttir *et al.*, 2005; Jonasdottir & Koski, 2011).

We collected environmental drivers for the Norwegian and North Sea systems from the literature: seasonal water temperatures (Slotte & Fiksen, 2000; van Deurs *et al.*, 2010); seasonal and diurnal cycles in surface solar irradiance as a function of latitude (Bleck, 2002); water clarity (based on chlorophyll *a* concentrations; Norwegain Sea, Huse & Fiksen, 2010; North Sea, van Deurs *et al.*, 2015); seasonal prey biomass distributions (North Sea, Colebrook, 1979; Norwegain Sea, Varpe & Fiksen, 2010); and zooplankton biomass and size fractions (Broms, 2016; Falkenhaug, 2016). Length- and weight-at-age data for NSS and North Sea herring were obtained from scientific surveys conducted by the Institute of Marine Research, Bergen, Norway. Samples from 60°N upwards are categorized as NSS herring, while data below this latitude is North Sea herring. We used data for the years 1995 to 2005 as this represents a period of relatively stable stock dynamics for both stocks. Especially for the younger age-classes, fish of the same age can have very different lengths depending on the time of the year they have been sampled. To reduce this bias, we used individuals sampled between January and June, as it is also the period where most of the data was sampled. In total, we used 253,105 individuals for NSS herring, and 141,624 individuals for North Sea herring.

2.3 Analyses

2.3.1 Predicting optimal body size in two herring populations

The Norwegian Sea and the North Sea differ in several aspects known to influence foraging rates and bioenergetics. Can these environmental factors explain the difference in body size observed between herring in these two seas? To answer this question, we ran the model with environmental drivers representative for each system (default scenarios; see Table 3, 'Case study') and with interannual variation in annual water temperature (default ±2°C), prey biomass concentration (default ±20%), and chlorophyll *a* concentration (default ±20%) typical in these systems. We assumed the diet of NSS herring to consist of 60% *C. finmarchicus* and 40% euphausiids and amphipods, as this is the approximate wet weight ratio observed in stomach content data from summer samples (Dalpadado *et al.*, 2000; Gislason & Astthorsson, 2002; Dommasnes *et al.*, 2004; Bachiller *et al.*, 2016). To simplify interpretation of the results, and to account for some feeding outside of the main foraging season in North Sea herring, we assumed a wet weight ratio in the diet of North Sea herring of 60% *C. finmarchicus* and *C. helgolandicus*, and 40% larger prey (Last, 1989). See section 2 in Supplement 1 for details about the diets of the two herring populations, section 3 for values and references used to parameterize prey characteristics, and section 4.1.1 for assumptions and calculations relating to prey biomass fractions.

Table 3. Parameter values used in the case study and sensitivity analysis of Norwegian spring-spawning herring and North Sea herring and in the detailed analysis.

Parameter	**General analysis**	**Case study (Sensitivity analysis)**	
		North Sea	***Norwegian Sea***
Prey characteristics **(in case study specified for prey type : 1 (small) and 2 (large))**			
Prosome length (mm)	2, 3, 4	2.6, 14.4 (±20%)	3.0, 14.4 (±20%)
Energy content (J g^{-1})	$2.72 \cdot 10^3$, $3.26 \cdot 10^3$, $3.81 \cdot 10^3$	$3.48 \cdot 10^3$, $2.83 \cdot 10^3$ (±20%)	$3.26 \cdot 10^3$, $2.83 \cdot 10^3$ (±20%)
Max biomass concentration (g m^{-3})	0.35, 0.70, 1.05	0.39, 0.12 (±20%) (see Supplement 1, 4.1.1 for calculations)	0.70, 0.18 (±20%) (see Supplement 1, 4.1.1 for calculations)
Foraging depth (m)	30	20, 20	30, 60
Physical environment			
Latitude (°N)	58, 68, 78	58 (±10 deg)	68 (±10 deg)
Water temperature (°C)	T_M = 3.5, 5.5, 7.5 T_A = 1.5, 1.5, 1.5	*Annual warming:* T_M = 7, 9, 11 T_A = 5, 5, 5 *Summer warming:* T_M = 8, 9, 10 T_A = 4, 5, 6	*Annual warming:* T_M = 3.5, 5.5, 7.5 T_A = 1.5, 1.5, 1.5 *Summer warming:* T_M = 4.5, 5.5, 6.5 T_A = 0.5, 1.5, 2.5

		Winter warming: $T_M = 8, 9, 10$ $T_A = 6, 5, 4$	*Winter warming:* $T_M = 4.5, 5.5, 6.5$ $T_A = 2.5, 1.5, 0.5$
chlorophyll *a* concentration (mg m^{-3})	0, 1, 2	2 (±20%)	1 (±20%)
Other parameters			
Handling time (s prey^{-1})	1.5	1.5, 5 (±1 s)	1.5, 5 (±1 s)
Capture success scaling factor	0.3	0.5, 0.3 (±10%)	0.3, 0.1 (±10%)

2.3.2 Drivers of optimal body size in Norwegian spring-spawning and North Sea herring

Why does body size in the spatially adjacent NSS and North Sea herring populations differ? We explored this by running a sensitivity analysis of our results from the 'Case study' (default scenarios) by systematically changing prey characteristics (prosome length, energy content, and biomass concentration) and the physical environment (latitude, water clarity, water temperature: annual, summer, and winter) (see Table 3, 'Sensitivity analysis'). Importantly, to be able to assess the influence of prey size on optimal size, we assumed a constant prey biomass concentration (g m^{-3}) and scaled prey concentration (prey m^{-3}) according to prey size (see section 4.1.2 in Supplement 1 for calculations). We also checked the sensitivity of the model to two other parameters that could have potential large effects on feeding rate: prey handling time, and capture success (accounting for feeding constraints imposed by capture efficiency, overlapping search fields, schooling behaviour, different habitats of prey, etc.).

2.3.3 Drivers of optimal body size in planktivores

To investigate the effect of each of the environmental drivers on foraging rates and bioenergetics in more detail, we used parameter values typical for the Norwegian Sea and NSS herring as default scenario and specified general but realistic ranges for the parameters used to describe prey characteristics and the physical environment. We then checked the sensitivity of the predicted default optimal size to variation in each of these parameters, while keeping the other parameters constant (see 'General analysis' in Table 3 for parameter values tested and 4.1.3 in Supplement 1 for calculations of prey size-specific prey concentrations).

3. RESULTS

3.1 Optimal size in Norwegian spring-spawning and North Sea herring

We define optimal body size as the size at which surplus energy is maximized, and hence being smaller or larger would imply less energy available for reproduction and other fitness-related tasks. Since herring display indeterminate growth and are unlikely to live until they die of old age, the oldest individuals in these populations should thus be the ones that display body sizes close to our predicted value (represented by the dark purple, blue, and grey colours in Fig. 2b). The optimal lengths predicted by our model from typical values in water temperature, prey biomass concentration, and water clarity corresponds well with observations for NSS (39 vs. 38.5 cm; Fig. 2b) and North Sea herring (34 vs. 33 cm; Fig. 2b), suggesting that the model captures the main drivers of herring body size in these systems. Optimal length was predicted to be smaller for North Sea herring than NSS herring (34 vs. 39 cm), which is also in line with observations (Fig. 2b). For both stocks, energy intake in smaller and medium sized fish is primarily limited by digestion, while prey encounters is the main limiting factor for larger individuals (see Fig. 3). The deviation between the dotted line (showing the maximum amount of food that can be digested in a year), and the solid line, (showing actual digested food), visible in the top panel of Fig.

3 results from encounter limitation for some hours of some days of the feeding season (see eq. 12 in Table 1).

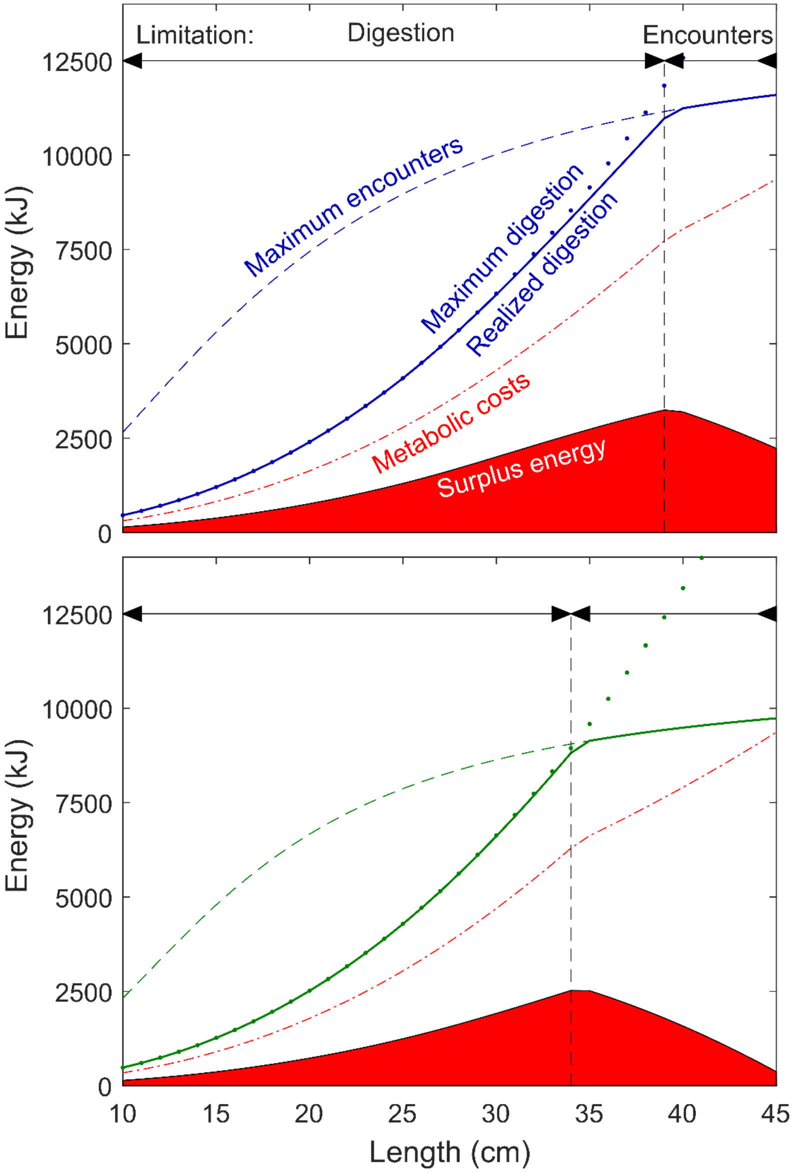

Figure 3. Predictions for the Norwegian (top) and North Sea (bottom) default scenarios. Solid lines show digested food (depends on stomach content; kJ year^{-1}) and dotted lines

the maximum amount of food that can be digested (independent of stomach content; kJ year^{-1}), dashed blue and green line show maximum potential food intake when there is no digestion limitation (sum of feeding rate; kJ year^{-1}), and red dotdash lines the metabolic cost (kJ year^{-1}). Red areas represent the difference between digested food and metabolic cost and thus represent annual surplus energy (kJ) of herring in the Norwegian Sea a) and the North Sea b). Dashed vertical lines show the predicted optimal size. 'Limitations' indicate the lengths at which digestion and prey encounters, respectively, limit energy acquisition.

3.2 What drives the difference in body size in NSS and North Sea herring?

Prey size was the most influential factor on the optimal size of both NSS and North Sea herring: larger prey increased optimal herring size and surplus energy, even if the total prey biomass concentration was held constant (Fig. 4). Prey energy content also had a large effect on optimal size, while that of prey biomass concentration was only minor. Likewise, applying the seasonal prey biomass curve of the North Sea to the Norwegian Sea scenario and vice versa had no effect on the optimal size of NSS herring, and gave a slightly smaller optimal size for North Sea herring (see Fig. S3 in Supplement 1). Since energy content and handling time was the same for both systems, this suggests that the smaller optimal size predicted for North Sea herring results from their slightly smaller and thus less visible prey.

Higher temperature reduced optimal size, whereas more light (higher latitude, clearer water) gave larger optimal size (Fig. 4). Is it possible that a higher metabolic cost in the warmer North Sea leads to less surplus energy and hence a smaller optimal size? Our results do not suggest so since the difference in annual metabolic cost between the two systems is marginal (Fig. 3). Furthermore, for both stocks optimal size was very sensitive to variation in capture success and handling time of the smaller prey item, with lower capture success and longer handling times leading to smaller optimal size (Fig. 4).

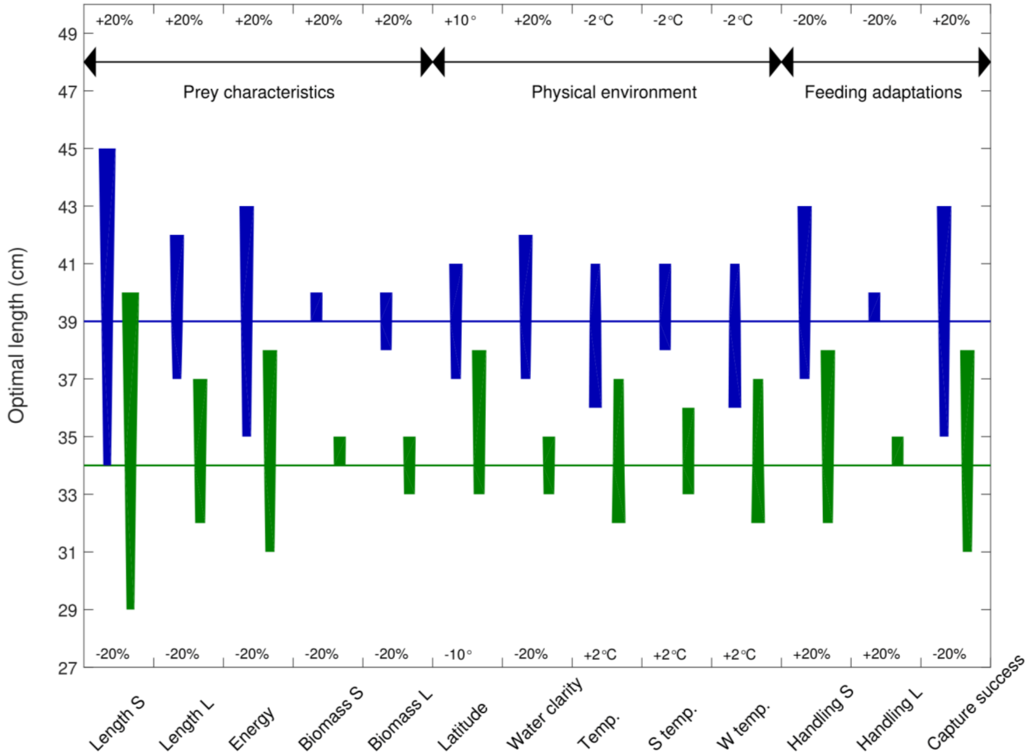

Figure 4. Sensitivity of optimal length and surplus energy at optimal length to variation in prey characteristics, the physical environment and feeding adaptations. The horizontal blue and green lines show predicted optimal lengths for NSS and North Sea herring, respectively, for parameter values representing their natural environment (default). The values along the x- and y-axis correspond to the end points of the bars, and the thickness of the bars represent amount of surplus energy in proportion to the default scenario. For parameters *length*, *biomass concentration*, and *handling time*, sensitivity to variation in the smaller (S) and larger (L) prey item is shown.

3.3 What drives optimal body size in planktivores?

All the environmental drivers included in our model except temperature affect feeding rates, which is illustrated by the difference in the asymptotes of the dashed lines in Fig. 5, showing maximum potential food intake when there is no digestion limitation. Under constant rates of digestion and metabolism (constant temperature), higher feeding rates thus lead to larger optimal size. Prey size had the most dominant effect on feeding rate, with a difference in prey length of 1 mm leading to an average difference in optimal length of more than 10 cm. The second most influential prey parameter was energy content, while the effect of variation in prey biomass concentration was negligible. More daylight hours at higher latitudes increased feeding opportunities, and variation in water clarity had a strong effect. Higher temperature was associated with smaller optimal size but with approximately the same amount of surplus energy. This was due to faster digestion, which alleviates digestion limitation at smaller sizes and thus allows for a greater energy uptake. This is in line with the temperature-size rule. However, contrary to the intuitive result of a more constrained energy budget with higher temperature, our model shows that such a relationship may arise even with a conserved energy budget.

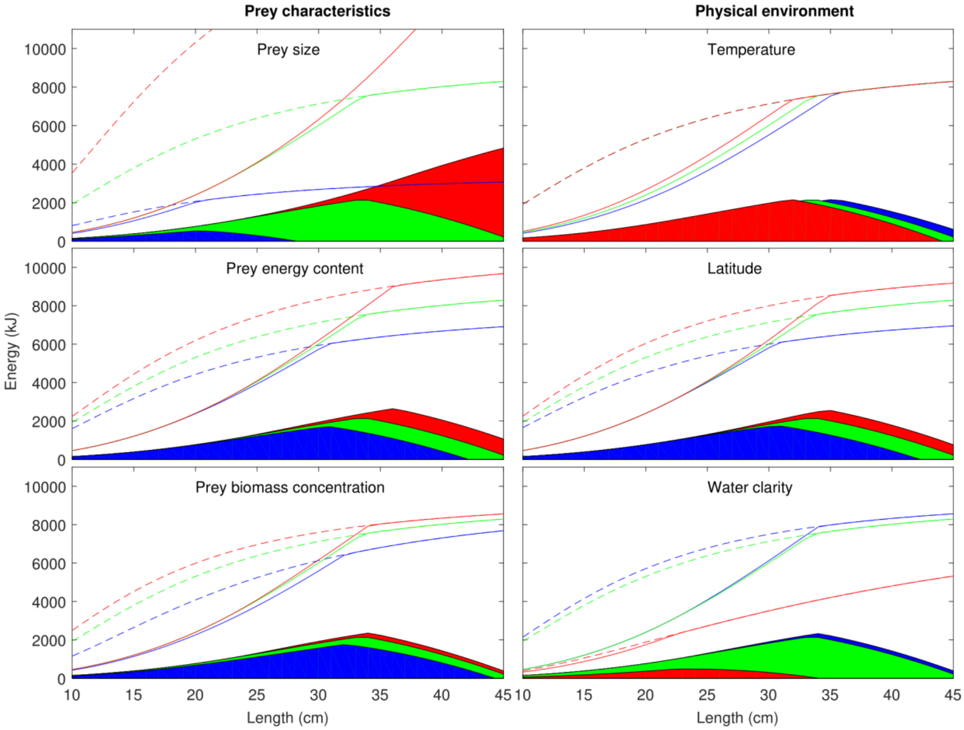

Figure 5. Sensitivity of optimal length to variation in prey characteristics and the physical environment. Solid lines show digested food (kJ year^{-1}), and dashed lines show maximum potential food intake when there is no digestion limitation (sum of feeding rate; kJ year^{-1}). Filled areas represent annual surplus energy (kJ; difference between digested food and metabolic cost) and optimal predicted length can be read from their maximum values. Green color represents the default scenario (middle value), and blue and red color lower and higher values of the parameter, respectively: prey size (2, 3, 4 mm), prey energy content ($2.72 \cdot 10^3$, $3.26 \cdot 10^3$, $3.81 \cdot 10^3$ J g^{-1}), prey biomass concentration (0.35, 0.70, 1.05 g/m^3), mean water temperature (3.5, 5.5, 7.5°C), latitude (58, 68, 78 deg. N), and water clarity (*chla*; 0, 1, 2 mg m^{-3}).

4. DISCUSSION

4.1 Environmental drivers of optimal body size in planktivores

4.1.1 Prey characteristics

Our main finding is that prey size appears to be a dominant driver of body size variation, by affecting prey detection distance and therefore encounter rates. Prey energy content also had a major influence through its effect on the relative profitability of different prey types. A similar model for lesser sandeel *Ammodytes marinus* in the North Sea shows corresponding results: the potential growth rate is roughly halved when large, energy-rich *Calanus* are replaced by smaller copepods (van Deurs *et al.*, 2015). The importance of resources for geographic variation in body size has been highlighted before (discussed in McNab, 2010; Watt et al. 2010; Teplitsky & Millien, 2014; Vinarski, 2014), but the focus has generally been on the effects of food abundance and spatio-temporal availability. Similarly, ecosystem models that include multiple predator-prey interactions commonly base consumption estimates solely on prey biomass concentration. In our model, biomass concentration was the least essential prey characteristic for feeding rates. We therefore suggest that models of consumption should consider all prey traits that are important for visual feeding rates, as well as factors that restrict feeding (see sections on 'Feeding adaptations' and 'Light' below). Prey biomass should not be ignored, but it may impact survival more than growth (Fiksen & Jørgensen, 2011), and hence the relationships between prey abundance, consumption rates, and predator biomass assumed in many ecosystem models are not necessarily linear.

4.1.2 Feeding adaptations: Prey handling time and capture success

In addition to prey size and energy content, our model predictions were sensitive to variation in prey handling time and capture success. Thus, if possible, individuals would benefit from being more efficient predators. In the model, these two parameters are assumed to encompass several factors that limit feeding rate, including prey shape, evasiveness, anti-predator behaviours and mobility. Handling time and capture success are outcomes of eons of natural selection, that has optimized the feeding machinery in trade-offs with other traits. The potential for evolution toward higher efficiency is thus presumably low. Our findings suggest that the accuracy with which handling time and capture success are parameterized is crucial for realistic estimates. Hence, research should be devoted to investigating the actual values of these parameters for different predators and prey, and under varying environmental conditions.

4.1.3 Light

Visual prey detection is not only affected by prey size, but also by light (Aksnes & Utne, 1997). More hours of light allow for more time feeding and prey are easier to detect in clearer water, yielding higher prey consumption and therefore larger optimal size. This suggests that longer days in spring and summer at higher latitudes contribute to a latitudinal size cline in visually foraging planktivores that acquire most of their energy during this period. Similarly, longer days in spring are a main driver of the rapid increase in body condition observed in NSS herring from spring to mid-summer, while prey phenology and abundance are less important (Varpe & Fiksen, 2010).

Our results also suggest that clearer water facilitates growth to a larger size in visual planktivores, and more so at low than high latitudes, as long as food uptake is not constrained by digestive capacity. Correspondingly, low water clarity has a negative impact on feeding rates in several planktivorous fish (e.g. bluegill *Lepomis macrochirus*, Vinyard & O'Brien, 1976; trout *Salvelinus fontinalis*, Confer et al. 1978; goby *Gobiusculus flavescens* Utne, 1997; three-spined stickleback *Gasterosteus aculeatus*, Helenius et al. 2013; damselfish Pomacentridae, Johansen & Jones, 2013). The general importance of light-related constraints for foraging is well known from both experimental (Vinyard & O'Brien, 1976; Utne, 1997; Sørnes & Aksnes, 2004) and modelling studies (Eggers, 1977; Aksnes & Utne, 1997; Langbehn & Varpe, 2017). Nonetheless, one may claim its broader ecological effects are underappreciated and reiterated emphasis thus needed (e.g. see Varpe et al. 2015, Langbehn & Varpe 2017, Langbehn et al. 2019).

4.1.4 Temperature

In agreement with the generally expected effect of temperature on body size, our model predicts smaller optimal sizes at higher water temperatures. The mechanism responsible for this pattern is, however, different from those previously proposed. In contrast to a consequence of temperature effects on growth and maturation (Atkinson, 1994; Angilletta & Dunham, 2003; Audzijonyte *et al.*, 2019), or on metabolic rate (Sheridan & Bickford, 2011), a smaller predicted optimal size at higher temperature was due to faster digestion, leading to prey encounter limitation at a smaller size. The level of surplus energy did not change with temperature. Thus, even though a decrease in size due to warmer temperatures may be disadvantageous from a size-based predation-risk perspective (size-dependent mortality; Peterson & Wroblewski, 1984), conserved energy reserves could imply unchanged foraging-related predation and reproductive potential. These findings are relevant for a 2°C warming, which is within the range of temperatures at which herring currently do well. However, since many physiological functions break down or are impeded above an optimum temperature, several degrees of warming would likely lead to different results.

4.2 Different optimal size in Norwegian spring-spawning and North Sea herring

Our model predictions of optimal body size for herring in the Norwegian Sea and the North Sea correspond well with field observations of the sizes of the oldest individuals of herring in these two seas (39 vs. 38.5 cm for NSS and 34 vs. 33 cm for North Sea herring). This indicates that our model captures the main drivers of body size and hence that the physical environments of the Norwegian Sea and the North Sea (water temperature, hours of daylight and water clarity) are not likely to be responsible for the observed difference in body size between NSS and North Sea herring. Rather, the likely cause is the smaller prey in the diet of North Sea herring, imposing visual constraints and thus prey encounter limitation at a smaller size. The close match between our predictions and observations also indicates that energetics rather than predation risk and intra-specific interactions determines body size in these systems. This assumption is not unrealistic since energetic constraints generally have a large influence on life-history strategies in environments where resources are seasonal (Boyce, 1979; Roff, 1992; Stearns, 1992; Varpe, 2017; Ljungström *et al.*, 2019).

In this study, we model optimal body size. Thus, the good fit between our predictions and observations also suggests that NSS and North Sea herring differ in size because of local adaptation or evolved phenotypic plasticity to the local prey field. The prey field of herring in the Norwegian Sea is more homogeneous and less variable than in the North Sea, where it contains many species that vary in relative abundance on a seasonal and inter-annual scale (Beaugrand *et al.*, 2002). Based on our predictions, this suggests that the large size of NSS herring is due to local adaptation, but that both populations may be expected to display variable body sizes through adaptive phenotypic plasticity with variable environmental conditions (Kawecki & Ebert, 2004; Ghalambor *et al.*, 2007).

4.3 Adaptive body size shifts under global change

Reductions in body size have recently been proposed as the third universal response to climate change (Daufresne et al., 2009; Gardner et al., 2011; Sheridan and Bickford, 2011) and have been linked to negative population level effects, including declines in biomass and fecundity, and increased mortality rates (Cheung *et al.*, 2011, 2013; Baudron *et al.*, 2014; Waples & Audzijonyte, 2016). In our analyses, smaller optimal sizes at warmer temperatures were not associated with lower levels of surplus energy, indicating that negative effects on productivity are not necessarily universal. Moreover, for planktivores that forage through vision, our findings suggest that an altered prey field composition could have a greater impact on body size, and on the energy available for reproduction and other fitness-related tasks, than warming-driven changes in digestion and metabolic rate. This is likely to be a plausible prediction for many species within this group, which are highly specialized for feeding on small zooplankton prey.

Primary production in the marine realm is forecasted to undergo large-scale changes in timing, distribution, and intensity (e.g. Sarmiento et al. 2004, Steinacher et al. 2010, Chavez et al. 2011, Chust et al. 2014), and recent shifts in zooplankton community composition have been associated with warmer waters and altered water flows

(Richardson & Schoeman, 2004; Behrenfeld *et al.*, 2006; Beaugrand *et al.*, 2009). A subsequent change in optimal body size, and hence the size at which fitness is maximized, could have several possible outcomes for a local population. A population that is adapted to a fairly homogeneous and stable prey environment, such as NSS herring, would only maintain its fitness by tracking a prey field that is of similar quality. In contrast, a population that is adapted to a more heterogeneous and temporally fluctuating prey field, such as North Sea herring, may have better prospects to stay and cope with the new conditions. As a consequence, the most pronounced body size shifts in response to changes in the local prey field may be expected in species that depend on specific physical characteristics of their habitat, thus making dispersal or range shifts difficult. As an example, the lesser sandeel in the North Sea is behaviourally attached to its sandy bottom habitat and the average body size in this population has been decreasing since the late 1980s, in parallel with a switch in the local prey field from their preferred prey C. *finmarchicus* to smaller prey items (van Deurs *et al.*, 2015).

Apart from changes in temperature and prey quality, our model predicts that altered water clarity influences body size in visually foraging planktivores. We modelled water clarity as a function of primary production (chlorophyll *a* concentration), but this variable is also affected by dissolved organic matter and particle load (Kirk, 2011). These two factors are mainly influenced by terrestrial runoff, and thus rainfall and wind patterns, which are also projected to be altered by climate change (Kirtman *et al.*, 2013). Thus, populations in regions with e.g. increased primary production or stronger winds, or in coastal regions with increased freshwater runoff, could also experience selection for smaller body size. The importance of accounting for changes in the light regime in analyses of marine ecosystem change has been highlighted before (Aksnes, 2007; Varpe & Fiksen, 2010; Varpe *et al.*, 2015; Langbehn & Varpe, 2017), but to our knowledge, not in relation to body-size shifts in visual planktivores under climate change.

Lastly, our findings also have implications for the prediction of range shifts under climate change. Range shifts in marine species have predominantly been predicted based on projections by bioclimate envelope models (e.g. Cheung et al. 2009; Jones & Cheung, 2015; García Molinos et al. 2016), which use statistical relationships between current species' distributions and their physical environments to project where a species should be present in the future. For marine species, the most commonly used predictor is temperature, but salinity, depth, and habitat type are also typically included to determine habitat suitability (e.g. Cheung et al. 2009; Hare et al. 2010; Cheung et al. 2011, also include oxygen content and acidity; García Molinos et al. 2016). The underlying assumption of these models is thus that species will track preferred physical conditions (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009) and they have been criticized for not considering how species interactions shape their distributions (see e.g. Pearson & Dawson, 2003; Dormann et al. 2012; Thuiller et al. 2013; Urban et al. 2016). By suggesting that prey accessibility (mediated by prey characteristics and light availability) is more important for the energy budget of visual aquatic foragers than temperature, the findings of this study highlight the importance of understanding mechanistsic links between interacting species in order to predict their future ranges.

5. CONCLUDING REMARKS

Spatial and temporal variation in temperature may be a primary global driver of latitudinal clines and recent reductions in body size. However, here we show that prey characteristics are the most influential determinant for optimal body size in a planktivorous fish, imposing visual constraints on prey encounters and thereby limiting feeding rates. In the oceans, planktivores determine the flux of energy from lower to higher trophic levels. Thus, to accurately predict the consequences of environmental change for energy flows and body sizes in marine systems, there is a need to consider all factors that affect energy budgeting in this group of organisms.

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SUPPLEMENT 1

Supplementary materials for manuscript “Body size and climate change: predator-prey interactions are more important than temperature for planktivore fish” by G. Ljungström, M. Claireaux, Ø. Fiksen, and C. Jørgensen.

1. ASSUMPTIONS FOR PARAMETER $\mathbf{k_D}$

The parameter $\mathbf{k_D}$ (scaling stomach evacuation rate) was used to calibrate the model to fit with adult surplus energy requirements inferred from data. In our modelling framework, surplus energy needs to cover costs associated with both growth and reproduction. Slotte, 1999, shows that for NSS herring a 28 cm and 38 cm fish spends about 15 g and 25 g fat, respectively, on their spawning migration. Using the energy value for fat commonly used in the literature of 39.75 kJ g^{-1}, this represents approximately 596.25 and 993.75 kJ. We also used the mean (for 1995 and 1996) from equations of length-specific ovary weights (1995: $W_o = 0.805e^{0.13L}$ for 1995; 1996: $W_o = 1.79e^{0.104L}$ for 1996; with the energy density of ovaries of 8 kJ g^{-1}) in Slotte, 1999, to estimate the energy of spawning products for a herring of 28 and 38 cm. To account for the energy required to build gonads, we assumed the total energy expenditure for gonad production to be twice the energy of gonads (i.e. 508.71 kJ for 28 cm, and 1645.30 kJ for 38 cm). From the data on NSS herring used in this study, growth for individuals above 33 cm (all individuals mature) is approximately 16 g yr^{-1}. We assume that a mixed diet gives 10 kJ g^{-1} and that the cost of growing equals the cost of the actual growth, i.e. 320 kJ. Altogether, this means that our estimate of the surplus energy for a herring of 28 cm should around 1425 kJ, and that for a 38 cm herring should be around 2959 kJ and we scaled $\mathbf{k_D}$ to match our predictions to these values. For herring of body lengths 28 and 38 cm our model predicts surplus energy values of 1708 and 3131 kJ, respectively.

2. DIETS OF NORWEGIAN-SPRING SPAWNING ANF NORTH SEA HERRING

We assumed the diet of NSS herring to consist of 60% *Calanus finmarchicus* and 40% euphausiids and amphipods, as this is the approximate wet weight ratio observed in stomach content data from summer samples (Dalpadado *et al.*, 2000; Gislason & Astthorsson, 2002; Dommasnes *et al.*, 2004; Bachiller *et al.*, 2016). Summer stomach content data for North Sea herring are scarce, but their diet appears to consist primarily of *C. finmarchicus* and *Calanus helgolandicus*, with the remainder being mainly post-larval stages of fish (Last, 1989). To simplify interpretation of the results and to account for some feeding outside of the main foraging season, we assumed a wet weight ratio in the diet of North Sea herring of 60% *C. finmarchicus* and *C. helgolandicus*, and 40% larger prey (Last, 1989). For the default scenarios these ratios were obtained by scaling the predicted stomach content so that it corresponds to stomach data, and the same scaling factors were used in the sensitivity analyses. According to observations, we characterized *C. finmarchicus* in the North Sea simulation by a slightly smaller prosome length than in the Norwegian Sea simulation (Boxshall & Schminke, 1988; Skjoldal, 2004; Jónasdóttir *et al.*, 2005; Jonasdottir & Koski, 2011). Furthermore, due to the lack of discernible size differences between *C. finmarchicus* and *helgolandicus* in the North Sea (Wilson *et al.*, 2015), these species were modelled as one prey type. For generality, the 'larger prey' fraction in the diet of North Sea herring was parameterized as for euphausiids and amphipods in the Norwegian Sea simulation. NSS herring mainly forage in the upper 50 m during the main feeding season (Nøttestad *et al.*, 2004). We defined one foraging depth for each prey type in the Norwegian Sea (30 m for the 'smaller prey' and 60 m for the 'larger prey'), and set the foraging depth to 20 m in the North Sea to account for shallower and less clear waters. Seasonal prey abundance distributions were modelled and parameterized to fit with observations (see section 4.2; North Sea, Colebrook, 1979; Norwegain Sea, Varpe & Fiksen, 2010). Section 4 contains values and references used to parameterize prey characteristics.

3. INPUT DATA

3.1 Prey size, energy density and concentration

Table S1. Parameter values and references for prey characteristics

Prey type	**Parameter**	**Value**	**Reference**
Norwegian Sea			
Calanus finmarchicus	Length	3.0 mm	Castellani & Edwards, 2017
	Weight	0.1523 mg dw	Using length-weight formula adapted from Uye (1982)[1].
	Energy density	6400 cal/g dw	Laurence, 1976
	Max concentration	600 prey/m^3	Varpe & Fiksen, 2010
Amphipods and euphasiids[2]	Length	14.4 mm	Lindley, 1978, 1982; Lindley et al. 1999; Kraft et al. 2012
	Weight	7.6896 mg dw	Using length-weight formula adapted from Uye (1982)[1].
	Energy density	5200 cal/g dw	Percy & Fife, 1981; Kulka & Corey, 1982
	Max concentration	3 prey/m^3	See 4.1.1

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[1] Prey weight (mg dry weight) = $10^{2.5\log(1000l_p)-6.51}10^{-3}$; Adapted from Uye (1982)

[2] Mean for *Themisto abyssorum* and *compressa*, *Meganyctiphanes norvegica*, and *Thysanoessa inermis* and *longicaudata*.

North Sea			
Calanus finmarchicus and *helgolandicus*	Length	2.6 mm	Jónasdóttir et al. 2005; Jonasdottir & Koski, 2011
	Weight	0.1065 mg dw	Using length-weight formula adapted from Uye (1982)[1].
	Energy density	6400 cal/g dw	Laurence, 1976; Kattner & Krause, 1989
	Max concentration	473 prey/m^3	See 4.1.1
Larger prey	Length	14.4 mm	Assume same value as for amphipods and euphausiids in the Norwegian Sea.
	Weight	7.6896 mg dw	Using length-weight formula adapted from Uye (1982)[1].
	Energy density	5200 cal/g dw	See text above.
	Max concentration	2 prey/m^3	See 4.1.1

3.2 Seasonal prey abundance distributions

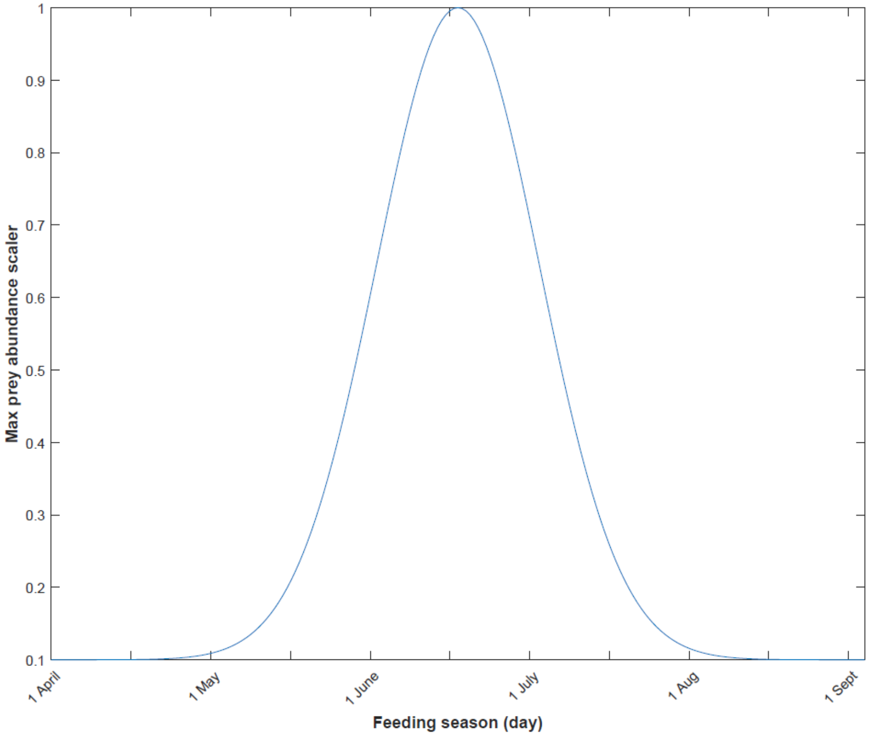

Figure S1. Seasonal prey biomass distribution s_d used to scale the maximum prey abundance $N_{\max,p}$ for the Norwegian Sea (see Equation 10 in Table 1)

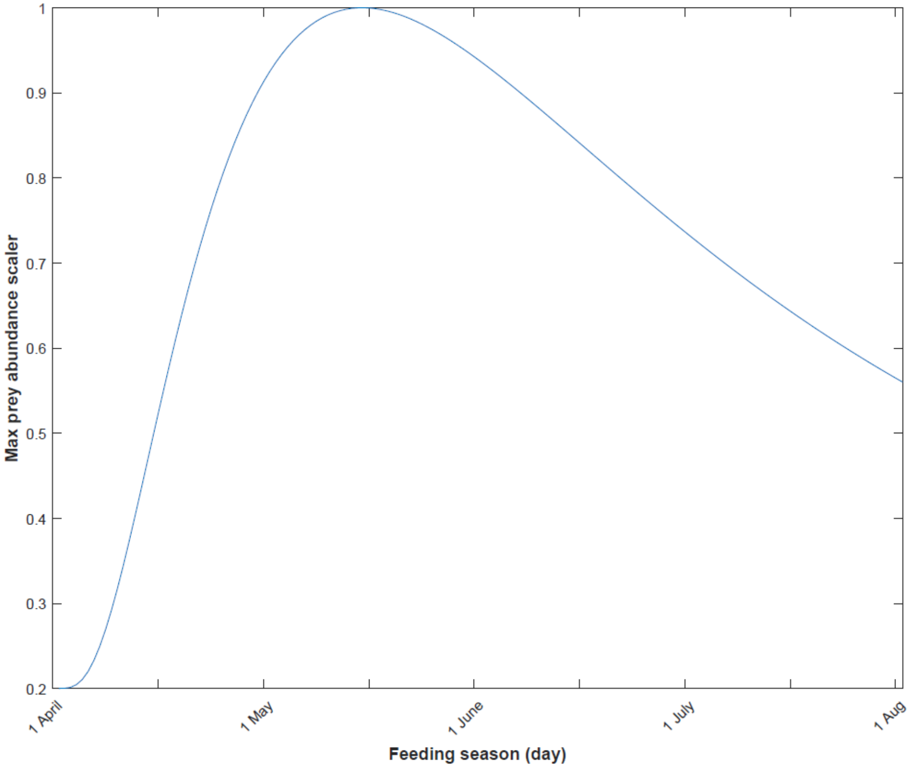

Figure S2. Seasonal prey biomass distribution s_d used to scale the maximum prey abundance $N_{\mathrm{max},p}$ for the North Sea (see Equation 10 in Table 1)

4. ASSUMPTIONS AND CALCULATIONS

4.1 Prey biomass fractions

4.1.1 Predicting optimal body size in two herring populations

NORWEGAIN SEA

Approximation of biomass fractions by mesh size (dry weight; data obtained from Cecilie Broms, IMR):

<1 mm = 43 %

1-2 mm = 45 %

>2 mm = 12 %

Assumptions:

- *Calanus finmarchicus* constitute 45 % of the prey field
- Peak *C. finmarchicus* biomass concentration is 0.70 g/m^3 (600 prey/m^3; Varpe & Fiksen 2010) using prey dry weight from Table S1 and a dry weight to wet weight ratio of 0.13 (Rudstam, 1988)
- Amphipods and euphausiids constitute 12 % of the prey field
- This yields a peak biomass concentration for amphipods and euphausiids of 0.18 g/m^3 (3 prey/m^3)

NORTH SEA

Approximation of biomass fractions by mesh size (dry weight; Falkenhaug, 2016):

<1 mm = 50 %

1-2 mm = 40 %

>2 mm = 10 %

Assumptions:

- Biomass ratio North Sea and Norwegain Sea = 5.7/9.2 (Broms, 2016; Falkenhaug, 2016), assume the same ratio between C. *finmarchicus* and *helgolandicus*
- C. *finmarchicus* and *helgolandicus* constitute 40 % of the prey field
- This yields a peak biomass concentration for C. *finmarchicus* and *helgolandicus* of 0.39 g/m^3 (473 prey/m^3)
- Larger prey constitute 10 % of the prey field
- This yields a peak biomass concentration for larger prey of 0.12 g/m^3 (2 prey/m^3)

4.1.2 Drivers of optimal body size in Norwegian spring-spawning and North Sea herring

NORWEGAIN SEA

- For this analysis default prey size (3 mm and 14.4 mm) is varied by ±20%
- Assuming a constant biomass concentration (see 4.1.1; Norwegian Sea) for all prey sizes yields peak prey concentrations for 3 mm ±20% prey of 750 prey/m^3 and 500 prey/m^3 for smaller and larger size, respectively
- Assuming constant biomass concentration (see 4.1.1; Norwegian Sea) for all prey sizes yields peak prey concentrations for 14.4 mm ±20% prey of 3.75 prey/m^3 2.5 prey/m^3 for smaller and larger size, respectively

NORTH SEA

- For this analysis default prey size (2.6 mm and 14.4 mm) is varied by ±20%
- Assuming constant biomass concentration (see 4.1.1; North Sea) for all prey sizes yields a peak concentration for 2.6 mm ±20% prey of 591 prey/m^3 and 394 prey/m^3 for smaller and larger size, respectively
- Assuming constant biomass concentration (see 4.1.1; North Sea) for all prey sizes yields a peak concentration for 14.4 mm ±20% prey of 2.5 prey/m^3 and 1.67 prey/m^3 for smaller and larger size, respectively

4.1.3 Drivers of optimal body size in planktivores

Assumptions:

- Peak C. *finmarchicus* (3 mm prey) biomass concentration is 0.70 g/m^3 (600 prey/m^3; Varpe & Fiksen 2010)
- Assuming constant biomass concentration for all prey sizes yields a peak prey concentration for 2 mm prey of 1652 prey/m^3, and for 4 mm prey of 292 prey/m^3 (using the length-weight formula adapted from Uye (1982) and a and a dry weight to wet weight ratio of 0.13 (Rudstam, 1988))

5. SENSITIVITY TO ALTERED SEASONAL PREY DISTRIBUTIONS

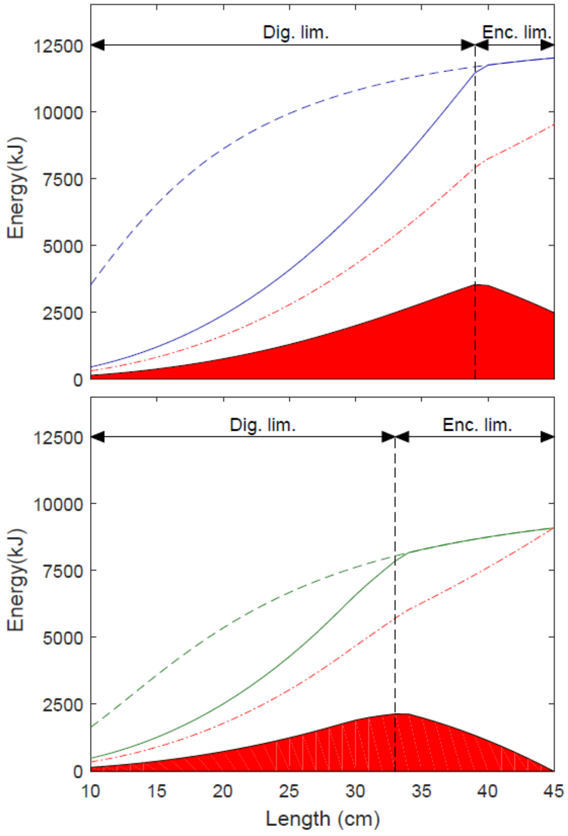

Figure S3. Predictions for the Norwegian Sea (top) using the seasonal prey abundance distribution for the North Sea (see Figure S2) and for the North Sea (bottom) using the seasonal prey abundance distribution for the Norwegian Sea (see Figure S3). Solid lines show digested food (kJ year^{-1}), dashed blue and green line show maximum potential food intake when there is no digestion limitation (sum of feeding rate; kJ year^{-1}), and red dotdash lines the metabolic cost (kJ year^{-1}). Red areas represent the difference between amount of digested food and the metabolic cost and thus represent annual surplus energy (kJ) of herring in the Norwegian Sea a) and the North Sea b). Dashed black lines show the predicted optimal size. 'Dig. lim.' and 'Enc. lim.' indicate the lengths at which digestion and prey encounters, respectively, limit energy acquisition.

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PAPER III

Ljungström G, Langbehn T, Jørgensen C

Increasing light seasonality with latitude: implications for forecasting of warming-driven redistributions in visual foragers

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