# Light and visual foraging in the pelagic: Opportunities and constraints along gradients of seasonality

Tom Langbehn

Thesis for the Degree of Philosophiae Doctor (PhD)
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# Scientific environment

The work presented in this thesis was carried out at the Department of Biological Sciences, Faculty of Mathematics and Natural Sciences, University of Bergen, within the Theoretical Ecology Group, from February 2016 to February 2019, including a three-month research secondment at the Centre for Ocean Life at DTU Aqua in Copenhagen, Denmark.

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*Faculty of Mathematics and Natural Sciences*

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Tom Langbehn

Tom Langbehn

# Summary

Light has a twofold fundamental impact on marine ecosystems; it allows photosynthesis that is at the source of most marine food chains, but it also governs top-down control through visual foraging. Here, I focus on the latter. *Seeing* and *doing* are intrinsically linked. A broad range of marine taxa, from invertebrates, to seabirds and fish rely on vision, and thus light, for varied and complex behaviours such as navigation, signalling, predator evasion, finding food and orientation. This makes light one, if not the most important environmental factor governing species interactions in the pelagic, with consequences for the biogeography, ecology and evolution of life in the oceans.

Unlike in terrestrial systems, light gives structure in the otherwise featureless pelagic habitat, creating a *lightscape* of opportunities and constraints. Visual and behavioural adaptions to light are testament to the importance of the light regime along gradients of depth and latitude. One common behavioural strategy in the oceans in response to light is diel vertical migration, where organism ascend towards the surface with nightfall and sink to depth before sunrise. This behaviour is generally considered to arise from the trade-off between foraging and mitigating the risk of exposure to visually hunting predators. Towards higher latitudes, seasonality increases and organisms that live here cannot do so without special adaptations to deal with the seasons, including energy stores, dormancy or seasonal migration to latitudes with less seasonality. Adaptations that are advantageous in aseasonal environments, e.g. diel vertical migration, might not provide the same benefit in seasonal environments, or even become disadvantageous to fitness. Therefore, we must account for constraints and dependencies that differ with latitude and season, when studying species distributions and climate-driven range shifts.

Studying vertical distributions arising from predator-prey games in response to light has a long history in marine science and lake ecosystems. Few studies, however, have applied the same thinking across latitudinal gradients and into systems where the light regime becomes increasingly seasonal, fundamentally changing the rules of the game and therefore, which behavioural and life-history strategies become optimal in terms of Darwinian fitness.

In this thesis, I explore how light, and in particular visual search, may affect distribution patterns and the evolution of behavioural strategies to cope with various light regimes. The thesis includes three chapters that address different, but interlinked problems pertaining how the light regime governs pelagic foraging interactions. My approach is mechanistic and dynamic modelling rooted in evolutionary ecology. I focus on high-latitude marine systems, where the seasonality in light is extreme and the environment changes rapidly in response to climate change.

Specifically, in the first chapter, I quantify the potential for increased visual search as sea-ice declines in response to a warming climate. I find, that the reduced seasonal shading of the waters below the ice will boost visual search and extend the favourable foraging season for horizontal migrants, potentially benefiting the large sub-Arctic stocks of planktivorous fish, such as herring, capelin and mackerel. I predict, however, that the polar night will persist to be a bottleneck for visual foragers. I discuss the implications of increased top-down control through visual foraging on potential eco-evolutionary dynamics in a climate change context.

For the following two chapters, I developed a state-dependent model of optimal migration behaviour in mesopelagic fish that I calibrate and confront with empirical data. I apply the model to the case of the Norwegian Sea to test if extreme photoperiod at high latitudes explains the lack of success of mesopelagic fish in polar waters. My model suggests the midnight sun prevents mesopelagic fishes from safely migrating to the surface to feed, causing starvation at daytime depth. I further predict, that above the Arctic Circle, only sink population exists, because mesopelagic fish at higher latitudes are unable to build up surplus energy needed for reproduction to sustain populations. First, because they are unwilling to take the high extra risk associated with foraging during the summer month and second, because copepods migrate out of the surface waters during winter to depths where it is too dark to forage efficiently. The effect of temperature on vertical distributions was small compared to light. Based on the model results, rising temperatures will not facilitate poleward range extension of mesopelagic biogeography, but further aggravate starvation because of increased metabolic demands.

In conclusion, I provide model evidence that photoperiodic constraints shape the pelagic biogeography of high-latitude oceans, with likely ecological and evolutionary knock-on effects. The light regime should, therefore, be considered in range shift studies and guide our future research linking the epi- and mesopelagic realm.

# List of publications

## Publications included in the thesis

### PAPER I

**Langbehn TJ** & Varpe Ø (2017). Sea-ice loss boosts visual search: fish foraging and changing pelagic interactions in polar oceans. *Global Change Biology* 23:5318-5330; doi: 10.1111/gcb.13797 (published)

### PAPER II

**Langbehn TJ**, Aksnes DL, Kaartvedt S, Fiksen Ø & Jørgensen C. Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient. *Marine Ecology Progress Series* (in review)

### PAPER III

**Langbehn TJ**, Aksnes DL, Kaartvedt S, Fiksen Ø & Jørgensen C. Poleward distribution of mesopelagic fish is constrained by seasonality in light.
(manuscript, prepared for *Nature Ecology & Evolution*)

## Contributions to other publications during the PhD period

Geoffroy M, Berge J, Majaneva S, Johnsen G, **Langbehn TJ**, Cottier F, Mogstad AA, Zolich A & Last K (2018). Increased occurrence of the jellyfish *Periphylla periphylla* in the European high Arctic. *Polar Biology* 41:2615-2619; doi: 10.1007/s00300-018-2368-4 (published)

Kaartvedt S, **Langbehn TJ** & Aksnes DL (2019). Enlightening the ocean's twilight zone. *ICES J. Mar. Sci.* doi: 10.1093/icesjms/fsz010 (published)

Sguotti C, Otto SA, Frelat R, **Langbehn TJ**, Ryberg MP, Lindegren M, Durant JM, Stenseth NC & Möllmann C. Catastrophic dynamics limit Atlantic cod recovery.
(in review at *Proc. R. Soc. B Biol*)

# Contents

# Synthesis chapter

## Introduction

### Latitudinal gradients in light as arenas for evolutionary adaptations

Light, and in particular sunlight, is central to most biological systems; plants, algae and corals depend on it to grow and many animals rely on vision, and therefore light, for signalling and communication, navigation, to find food and mates but also to evade predators (Cronin *et al.*, 2014).

Aside from organisms inhabiting the deep-sea, dwelling in caves, or living subterraneously for the entirety of their life, most organisms experience large cyclic variation in light. Light intensity and spectral composition varies over the diel (day vs. night) and annual (seasonal) cycle because the earth spins around itself while circling around the sun on a tilted axis. Seasonality in other abiotic factors, such as ice-cover, temperature, wind, clouds and precipitation then follow from the annual cycle in solar radiation.

The light environment at high latitudes is fundamentally different from that at low latitudes (Fig. 1). Close to the equator, the days (dawn to dusk) and nights (dusk to dawn) are equally long throughout the year. Towards higher latitudes, however, the day-night cycle starts to diverge seasonally, with longer and lighter days during summer, opposed by longer and darker nights during winter. Above the polar circle, north of 66.6° N and south of 66.6°S, the photoperiod seasonally extends beyond the 24 hours of a day: in summer during the midnight sun period, the sun does not set, and in winter during the polar night the sun does not rise. At the polar extremes, there is only one sunrise and one sunset each year (Fig. 1).

One additional and often neglected implication of the latitudinal change in light regime is the distribution of twilight or semi-darkness, i.e. light at times when the sun is just below the horizon. In the tropics, daily twilight periods are relatively brief and invariant

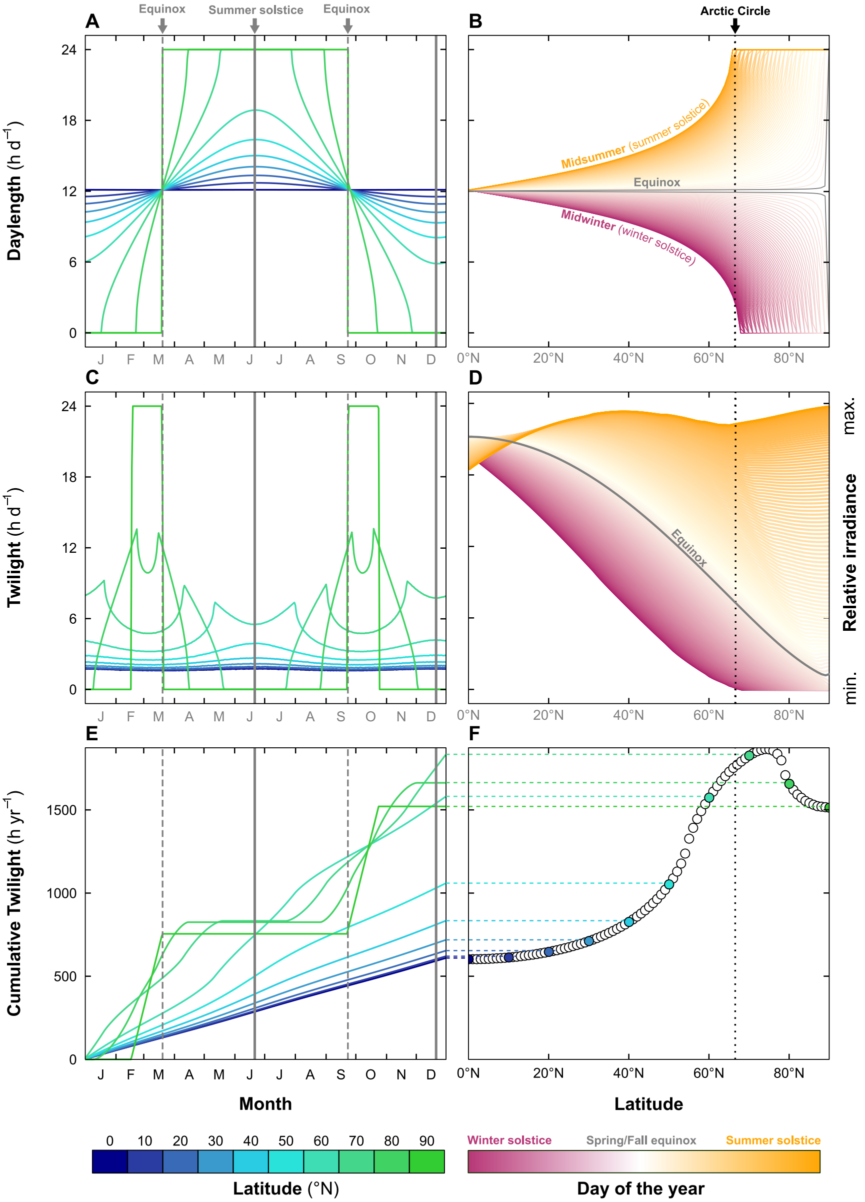

**Figure 1: Seasonal variation in light conditions across latitudes**. Towards the poles, the light regime becomes increasingly extreme. At high latitudes, above the polar circle, a clear day-night cycle does not exist during the polar night and during the midnight sun in summer **(A-B)**. Light intensities are generally higher in summer than during winter, with the largest seasonal differences at the poles **(D)**. Latitudes around the polar circle receive most twilight hours over the year **(E-F)**. There, twilight, however, is concentrated during a short period around the equinoxes, because the sun may not set or rise for month at a time **(C)**.

over the year. This changes towards higher latitudes, where daily and annual twilight duration, but also variability in that duration over the year, increases (Mcfarland, 1986, Mills, 2008, but see also Fig. 1).

The light environment is a key selective agent for evolutionary adaptations (Boyce, 1979, Conover & Present, 1990, Ejsmond *et al.*, 2018). Life has adapted to all shades and periodicities in light, but seasonal light environments require different life-history strategies, physiological, morphological and behavioural adaptations than aseasonal environments (e.g. Varpe, 2017). Adaptations to seasonality include using particular periods of the year for reproduction, maintenance and growth, often coupled with seasonal migrations (Shaffer *et al.*, 2006, Varpe & Fiksen, 2010), reduced activity (Hirche, 1996) and extensive energy storage (Hagen & Auel, 2001, Varpe *et al.*, 2009).

In environments with a distinct day-night cycle, light divides the day for most organism into a *"favourable"* and an *"unfavourable"* part. Therefore, one common adaptive strategy is to hide, digest and rest during parts of the day, and be active and forage during the other half. Temporal niche partitioning is as old, and might even predate, the evolution of the mammalian lineage (Schmitz & Motani, 2011, Angielczyk & Schmitz, 2014, Maor *et al.*, 2017).

The Biogeography of diel time partitioning on land is closely linked to the global distribution of light. Nocturnal and diurnal species dominate in the tropics and subtropics, while crepuscular and cathemeral behaviour (irregular activity at any time of day or night) is more prevalent at high latitudes, where hours of biologically useful twilight and seasonality in the light regime are greatest (Bennie *et al.*, 2014).

In high-latitude environments, where there is seasonally little variation in light intensity between day and night, diurnal partitioning of habitat and resources becomes impossible. Instead, the annual cycle is divided into a *"productive"* (summer) and *"unproductive"* (winter) seasons, selecting for a different set of adaptations. Only those who are able to survive both seasons during all life-stages will be able to persist here year-round. For this, timing is essential and the scheduling of annual events, i.e. annual routines, becomes an adaptation itself (McNamara & Houston, 2008, Varpe, 2012, Ejsmond *et al.*, 2015, Barta, 2016). There is a strong selection on when to reproduce, whether to produce offspring from stored resources or concurrent food (Varpe *et al.*, 2009), as well as when to enter or terminate a state of dormancy to conserve energy, or to migrate (Varpe, 2017).

Energy must, however, be acquired before allocated to growth, reproduction, or defence. Yet there are constraints on acquisition. For instance, seasonal environments have pulsed episodes of primary production (Schwartz, 1998, Winder & Cloern, 2010, Boyce *et al.*, 2017) limiting when grazers can feed. This illustrates the need to store energy, internally or externally, to match the duration of starvation periods. Another constraint on acquisition – and a pillar of my thesis – is that visual foragers might be seasonally constrained in their abilities to find food (Aksnes & Giske, 1993); a constraint not shared by tactile predators (Eiane *et al.*, 1999, 1997).

Organisms that cannot cope with seasonality have to leave before conditions become unfavourable. Hence, migration is another extremely successful adaptation to seasonality found in a wide range of taxa from mammals, to fish, insects and birds (e.g. Costa *et al.*, 2012). Importantly, migration can serve as an example that seasonality in light is not only a constraint but also a possibility. Take for example migratory birds, by migrating between hemispheres they integrate resources and favourable light conditions into one endless summer (Shaffer *et al.*, 2006). Further, breeding at high latitudes allows 24 hours foraging during a short but highly productive summer season, without the risk of nocturnal predation, providing juveniles with the best possible start. Recent observation of larval stages during the polar night (Berge *et al.*, 2015a) indicate that there might be an adaptive benefit to reproduction during the dark season, potentially because of reduced predation. In fact, the ability to reproduce during the polar night might be a key adaptation that allows only a few species to colonize the Arctic Ocean (Berge & Nahrgang, 2013). A similar mechanism has been suggested to increase survival of larval fish during phytoplankton blooms. Increased light scattering in turbid waters affects predators with long visual ranges before their prey with shorter visual ranges (Giske *et al.*, 1994, Fiksen *et al.*, 2002, Utne-Palm, 2002), explaining the positive effect of turbidity for some size groups.

## Understanding light and life in the pelagic realm: a fish-eye view

Oceans comprise 99.5 % of the Earth's liveable space (Cronin *et al.*, 2014) and the pelagic realm, commonly known as the blue ocean, is by far the largest of its habitats. Unlike on land, where physical objects, i.e. vegetation and topography, add to the habitat complexity, the pelagic zone far from the ocean bottom is featureless. Here, strong vertical gradients in temperature, oxygen, but above all light, structure biological processes. In aquatic habitats, light is best understood as a three dimensional lightscape, fundamentally different to the two dimensional experience of light in terrestrial systems. The closest analogy on land to the pelagic lightscape are possibly forest canopies, where light is filtered and its properties modulated when passing through layers of leaves and only a fraction of the light experienced in the treetops actually reaches the forest floor (Cronin *et al.*, 2014). This lightscape is the driver of marine primary production and the backdrop for most predator-prey interactions in the pelagic, thus shaping the entire ecosystem trough bottom-up and top-down control.

Most predators in the pelagic, such as bony fish (Vinyard *et al.*, 1976, Utne-Palm, 1999, Jönsson *et al.*, 2011), squids (Thomas *et al.*, 2017), seabirds (Johansen *et al.*, 2001, Martin & Prince, 2001, White *et al.*, 2008, Stempniewicz *et al.*, 2013) and even baleen whales (Cronin *et al.*, 2017) rely on vision for feeding. Other foraging strategies, such as tactical prey sensing (i.e. non-visual, for example using whiskers or the lateral line) or filter feeding exist and gain competitive advantage at reduced light levels (Eiane *et al.*, 1997, 1999, Batty *et al.*, 1990, Schnedler-Meyer *et al.*, 2016). Vision, however, depends on light, which in the ocean stems mainly from two sources: downwelling light (i.e. sunlight > moonlight > starlight) and bioluminescence (biological light) emitted by organisms themselves. Downwelling light intensity diminishes rapidly with depth due to absorption and scattering (Johnsen, 2012). Generally, below 200 m there will be too little light for photosynthesis, but still more than enough for many species that thrive at dim light and have eyes adapted to scotopic (*"twilight"*) vision (Evans, 2004, Warrant & Adam Locket, 2004, Turner *et al.*, 2009, De Busserolles & Marshall, 2017). Bioluminescence, as the other important source of light, spans all ocean depths but its relative importance and functions increases as surface light fades (Haddock *et al.*, 2010).

The dependence of visual foragers on light translates the lightscape into a predation landscape, where adjacent trophic levels from zooplankton to top-predators are locked in a game of hide and seek (Iwasa, 1982). The only chance to hide in the pelagic is in plain sight, driving a co-evolutionary arms race to select for the most efficient visual system (De Busserolles & Marshall, 2017), as well as counter measures to increase camouflage and evade detection, i.e. transparency, pigmentation, light ventral coloration, mirrors, or counter illumination (Fig. 2) (Sutton, 2013, Johnsen, 2014). Because smaller organisms are harder to spot than larger visual targets (given their optical properties are otherwise identical), the maximum attainable body size itself is subjected to selection through visual foragers (Brooks & Dodson, 1965).

Adaptive behavioural strategies are part of the visual arms race in the pelagic. Zooplankton grazers escape the prying eyes of visual predators by migrating vertically along gradients of light (Fiksen & Giske, 1995, De Robertis *et al.*, 2003, Hays, 2003), avoiding sunlit surface waters during daylight hours when planktivores are most efficient. By migrating to depth grazers trade-off foraging losses against increased survival. However, some of their predators will follow suit, triggering a cascade of interlinked migration patterns across multiple trophic levels, because the optimal distribution of an individual depends on the distribution of its prey, conspecifics, predators and competitors (Iwasa, 1982, Ohman *et al.*, 1983, Sainmont *et al.*, 2013, Pinti & Visser, 2019), as well as its own internal state. In fish, the internal state can represent for example the amount of food in the guts, energy reserves (Rosland & Giske, 1994), ontogenetic state (Rosland & Giske, 1997, Fiksen *et al.*, 1998) and swimbladder volume (Nero *et al.*, 2004).

The fact, that light structures predator-prey interactions in the pelagic through the prey-encounter of visually searching predators is widely acknowledged in freshwater lake systems (Brooks & Dodson, 1965, Kahilainen *et al.*, 2009, Mehner, 2012, Hansen & Beauchamp, 2015, Hedström *et al.*, 2017) and in the marine (Bollens & Frost, 1989, Ohman, 1990, Aarflot *et al.*, 2018)

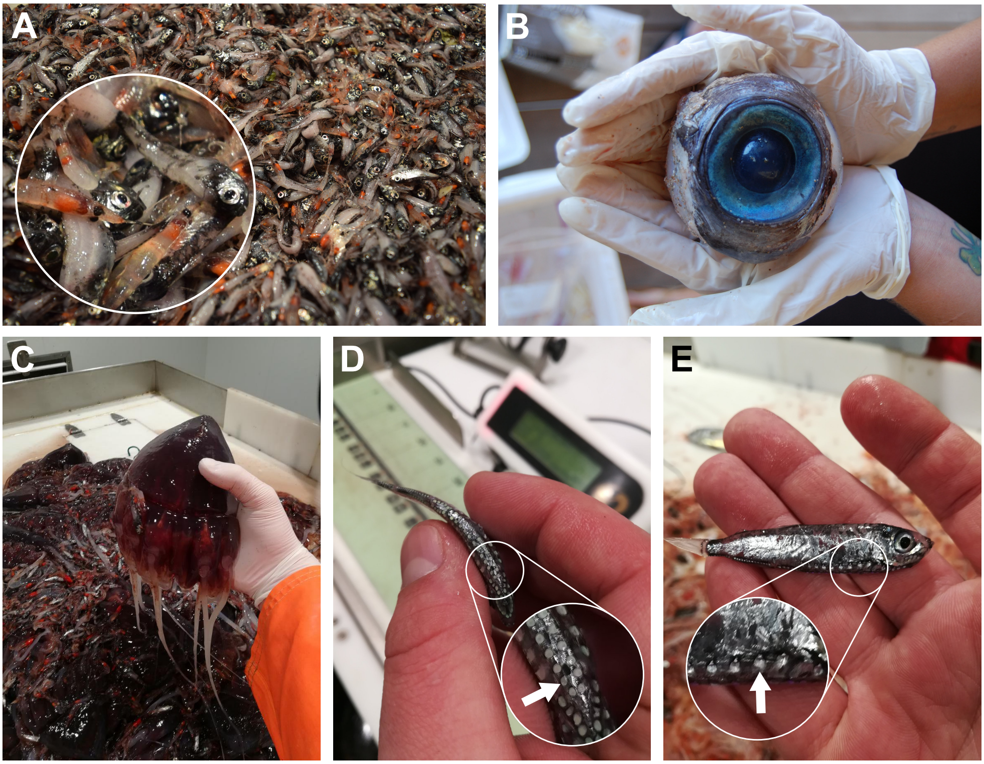

**Figure 2: Life in the pelagic is a game of hide and seek between micronekton and predators that drives an evolutionary arms race.** **(A)** Mesopelagic catch from a Norwegian Fjord close to Bergen (at 60°N) consisting mainly of glacier lanternfish *Benthosema glaciale* and the pelagic shrimps *Sergestes* and *Pasiphaea* spp. Mesopelagic mikronekton is abundant prey to both visual and tactile predators. **(B)** For example, the large eye of a swordfish (*Xiphias gladius*) allows them to predate on mesopelagic fish down to several hundred meters depth (photo by Carli Segelson from Florida Fish and Wildlife, made available under CC BY-ND 2.0 licence). **(C)** In Norwegian fjords, the mesopelagic jellyfish *Periphylla periphylla* can be a dominant predator. **(D, E)** To avoid predation from visual predators mesopelagic fish use counter illumination. Light organs (photophores) on the ventral side imitate the down-dwelling light to camouflage their silhouette against the surface from visual predators from below (here shown for adult pearlsides *Maurolicus muelleri*).

## Migration as a strategy

In marine pelagic ecosystems, migrations are a near universal strategy. Many of the large epipelagic fish stocks are known for their extensive horizontal migration between spawning, feeding and wintering grounds, extending into high latitude waters (Slotte & Fiksen, 2000, Varpe *et al.*, 2005, Tojo *et al.*, 2007, Jørgensen *et al.*, 2008). The Norwegian spring-spawning stock of herring (*Cupea harengus*) is one such predator, migrating into the Arctic every summer, and retreating to coastal overwintering areas as daylight becomes shorter and eventually disappears altogether (Varpe *et al.*, 2005). Similarly, Pacific herring (*Clupea pallasii*) closely tracks the ice edge, and winter feeding grounds have shifted northwestward during recent years (Tojo *et al.*, 2007).

The majority of biomass in the ocean, however, migrates vertically. Diel vertical migration undertaken by many zooplankton and other organisms, such as krill, jellyfish, fish and mammals, are the largest movement of biomass on the planet (Hays, 2003). We just begin to gauge importance of diel vertical migration in, for example, the global carbon cycle (Bianchi *et al.*, 2013, Davison *et al.*, 2013, Hudson *et al.*, 2014, Ariza *et al.*, 2015, Aumont *et al.*, 2018). Among the vertical migrators a taxonomic group of small fishes commonly referred to as mesopelagic fishes has attracted increased attention over the last couple of years because their abundance is estimated to be ca. 15 billion tons, or 10-20 times the biomass of all other fishes combined (Irigoien *et al.*, 2014). A focus has been on the potential to harvest this resource for human food or animal feed, which could relieve pressure on both fisheries and agriculture (SAPEA, 2017).

With some exceptions, mesopelagic organisms carrying out diel vertical migration appear to expose themselves to a limited range of light intensities throughout the diel cycle (Aksnes *et al.*, 2017, Bozman *et al.*, 2017, Kampa, 1971, Klevjer *et al.*, 2012, Norheim *et al.*, 2016). Organisms that track preferred light intensities across depth, i.e. inhabiting what appears a light comfort zone (Røstad *et al.*, 2016b,a), maintain a constant optical environment during the circadian light cycle, and diel vertical migration emerges as a consequence. One theoretical explanation for diel vertical migration is given by the *"antipredation window"*, denoting the relative distance between feeding- and mortality rates along a gradient of light (Clark & Levy, 1988, Scheuerell & Schindler, 2003); meaning, the range of light intensities where the prey organism has the edge over their predators because they can feed at lower light intensity.

The common perception of *"hide at day and feed at night"* often quoted to explain diel vertical migration, is not entirely correct for mesopelagic fish. Migrating within a fixed range of light intensities they are always equally well hidden to their predators, while their own prey encounter may vary, depending on the distribution of their prey. Consequently, for mesopelagic fish, and all other organism that occupy a light comfort zone, large variations over the circadian cycle occur in pressure, not light. Therefore, one true cost of diel vertical migration is buoyancy regulation.

## Light, temperature and climate change: will more fish enter the Arctic?

Globally, in response to rapid climate change species are shifting their distribution (and phenology), on land and in the sea (Parmesan, 1996, Thomas & Lennon, 1999, Parmesan & Yohe, 2003, Perry *et al.*, 2005, Hickling *et al.*, 2006). The general direction of temperature-driven range shifts is poleward, or to higher altitudes (Laurance *et al.*, 2011, Freeman *et al.*, 2018) in terrestrial and to greater depths in marine systems (Dulvy *et al.*, 2008).

In the marine, the velocity of climate change (i.e. isotherm shifts in $\mathrm{km\,decade^{-1}}$) is fastest in the polar and tropical regions (Burrows *et al.*, 2011). Marine taxa closely track those climate velocities (Pinsky *et al.*, 2013), and range shifts are most pervasive in bony fish with tens to hundreds of km per decade (Poloczanska *et al.*, 2016). With species, interactions and the functional trait biogeography are changing (Wiedmann *et al.*, 2014, Kortsch *et al.*, 2015, Frainer *et al.*, 2017), causing potential knock-on effects in food webs (Grebmeier *et al.*, 2006, Stempniewicz *et al.*, 2007, Crawford *et al.*, 2015), likely to become ever more important, given the current rates of climate change (IPCC, 2014).

Over the past decades, growing attention has been devoted to marine range shifts also because of its implications for human well-being (Pecl *et al.*, 2017) and because of its effects on future harvest potential and fisheries revenue (Sumaila *et al.*, 2011, Lam *et al.*, 2016), also in areas where, until today, no commercial fisheries exist. It has been suggested that several sub-arctic fish stocks may be able in the future to establish viable resident populations in the Arctic (Wassmann *et al.*, 2011, Hollowed *et al.*, 2013, Haug *et al.*, 2017), and the potential for the development of commercial fisheries in polar oceans is already being discussed (Christiansen *et al.*, 2014, McBride *et al.*, 2014, Misund *et al.*, 2016). The Arctic also stands out, because it is here that global models predict the highest species invasions and turnover rates (Cheung *et al.*, 2009, García Molinos *et al.*, 2015). The first newcomers with more southerly biogeographic affinities are already increasingly observed in Arctic waters (Berge *et al.*, 2015b), contributing to the rapid borealization of fish communities in the Arctic (Fossheim *et al.*, 2015). With declining sea-ice (Comiso *et al.*, 2017, Notz & Stroeve, 2018, Stroeve & Notz, 2018), that now forms a biogeographical boundary between the Pacific and the Atlantic, there is the potential for faunal exchange between the two oceans (Wisz *et al.*, 2015a).

While range shift studies have helped to gain a clearer picture of how climate change affects the distribution of life on earth, a mechanistic understanding of global change ecology and the role of species traits and evolution in range shift responses is still nascent (Sunday *et al.*, 2015, Diamond, 2018). The current focus is mostly on the drivers, and in particular on temperature, but only a few studies investigate the mechanisms that may slow or limit range shifts (Burrows *et al.*, 2014).

One such mechanism suggested to limit poleward range shifts pertains to the change in photoperiod with increasing latitude (Saikkonen *et al.*, 2012), with relevance for bottom-up (Sundby *et al.*, 2016) and top-down control (Kaartvedt, 2008, Kaartvedt & Titelman, 2018). The reasoning of the *"photoperiod constraint hypothesis"* (Kaartvedt, 2008) is intuitive: unlike temperature the latitudinal gradient of seasonal changes in daylength is a stable abiotic factor that will persist unaffected by climate change. But, because the seasonal change in daylength becomes extreme towards higher latitudes, species shifting poleward will experience a vastly different light environment, depending on their location on the latitudinal gradient. To keep up with climate velocities in the tropics, extensive range shifts might be required. Yet, the light environment changes only marginally. With increasing latitude, however, already small latitudinal changes in distribution, bring about large changes in the light environment (Fig. 3) (Saikkonen *et al.*, 2012, Poloczanska *et al.*, 2016). This matters when we recall the evolutionary adaptations to seasonality, and the *visual search* perspective discussed earlier.

The extreme photoperiod sets particular demands for the behaviour and life cycle of organism that make a living at high latitudes. Life-history traits and adaptations to seasonality, including adaptive behaviours, are acquired through evolution by natural selection (Darwin, 1859, Fisher, 1930) on timescales longer than contemporary climate-driven range shifts. Therefore, newcomers without the necessary adaptations to seasonality might be limited in their success at high-latitudes, unless they evolve or can adjust through behavioural plasticity. Another implication is that predictions from bio-climatic envelope models that do not account for dependencies, species interactions, and adaptations to extreme seasonality might be flawed near and beyond the polar circles.

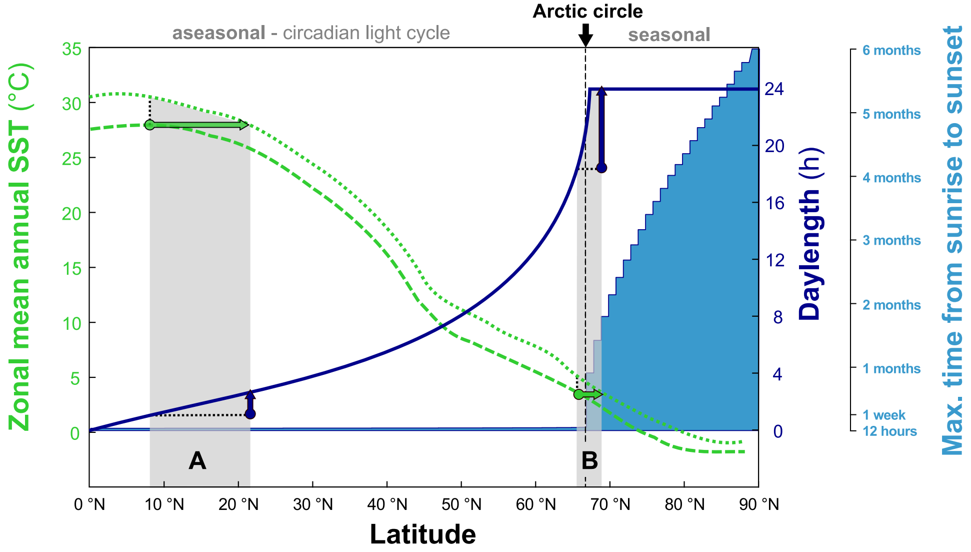

**Figure 3: Interaction between climate-driven range shifts and seasonality in light at different latitudes.** As ocean temperatures rise in response to climate-change, for tropical animals to track their thermal niche may require relatively large latitudinal shifts, but with little differences in the light regime (**species A**). Temperate or boreal species, however, need to change their distribution far less to achieve the same, but they will experience large changes in the light regime, in particular, when shifting across the polar circle from an aseasonal into a seasonal light environment (**species B**).

The reasoning for a proximate light mechanism that limits climate change-driven species' range shifts towards the poles (Saikkonen *et al.*, 2012), with the potential for multiple non-mutually exclusive ultimate pathways (Kaartvedt, 2008, Sundby *et al.*, 2016), is well developed verbally and the arguments have a solid theoretical foundation in life-history theory. However, the proposed hypotheses are based on limited evidence, with only a few examples from studies on biological invasion and insects pest (Urbanski *et al.*, 2012), finding e.g. that range expansion to high latitudes requires synchronization of overwintering behaviour and physiology with photoperiod (Lehmann *et al.*, 2014).

## Approach and aim of the thesis

To this point, I have introduced relevant concepts to understand the individual chapters. I have highlighted the importance of the light regime as a driver of evolutionary adaptations and behaviours, and the merits of thinking about vision and visual interactions along gradients of latitude and depth.

Although it is known for a long time that light affects the distribution and numbers of organisms in space and time (Fretwell, 1972, Tont, 1976), much effort is devoted to understanding the bottom-up effects, for example as consequences of sea-ice loss (Arrigo *et al.*, 2008, Leu *et al.*, 2011, Kortsch *et al.*, 2012, Clark *et al.*, 2013, Ji *et al.*, 2013). Plants and corals depend on light to grow. This makes it intuitive to understand why their distributions, and possible climate-driven range expansions, might be limited towards higher latitudes, where the dose of photosynthetically available radiation during the winter months is low (Muir *et al.*, 2015, Markkola *et al.*, 2016). The top-down effect of light, through vision, is more abstract and less intuitive. This may explain why the *"photoperiodic constraint hypothesis"* has remained untested since its publication ten years ago (Kaartvedt, 2008), despite the author outlining fjord studies suitable to test the hypothesis.

In this thesis, I have used evolutionary modelling based on explicit mechanisms of physiology and visual foraging, to explore the role of light in governing species distributions, vertically and along latitudinal gradients. Here, I focus on the visual search perspective (Eiane *et al.*, 1999, Aksnes *et al.*, 2004, Sørnes & Aksnes, 2006, Huse & Fiksen, 2010) and the hypothesis that inferior feeding conditions due to photoperiod and seasonal migration in zooplankton constrain mesopelagic fish distributions towards the poles (Kaartvedt, 2008). I include, however, other aspects that may act as photoperiod-mediated constraints, such as pulsed food availability and therefore the need for reserves (Sundby *et al.*, 2016) and the timing of life history events (Saikkonen *et al.*, 2012) in my reasoning.

The argument that photoperiod might filter climate change-driven species range shifts has emerged independently in the terrestrial (Saikkonen *et al.*, 2012) and marine literature (Kaartvedt, 2008, Sundby *et al.*, 2016), but the different ultimate explanations have not been linked yet.

The overarching research question in this thesis is:

***What are key biological mechanisms that limit the poleward distribution of fish stocks and how will they interact with climate change?***

I aim to unravel the role of light, i.e. photoperiod, and temperature in constraining pelagic species distributions towards high-latitudes. However, I will also think about, and elucidate the potentially wider systemic ecological and evolutionary implications in a climate-change context.

Based on this general objective I aim to answer the following, more specific research questions:

**Q1:** How will climate-driven sea-ice loss affect pelagic foraging interactions in high-latitude marine ecosystems? What are likely implications for top-down control and, consequently, eco-evolutionary dynamics? **(Paper I)**

**Q2:** Can we predict observed migration behaviour and vertical distribution of mesopelagic fish using a state-dependent life-history model? **(Paper II)**

**Q3:** What drives the observed poleward deepening and the parallel decrease in migration amplitude of mesopelagic scattering layers in the Norwegian Sea, light or temperature? **(Paper II)**

**Q4:** Can the extreme photoperiod at high latitudes,explain the global decline in mesopelagic fish towards high latitudes as suggested by Kaartvedt (2008)? What are the proximate and ultimate causes that limit the poleward distribution in mesopelagic fish? **(Paper III)**

In the following, I will provide a rationale why I use a modelling approach and then summarize the individual papers, highlighting the key findings, before moving to a brief general discussion that I will structure around future perspectives and ensuing research questions and hypothesis.

# Methods

## Methodological rationale: why modelling?

Experiments, observations, and models provide complementary and non-mutually exclusive approaches to test scientific hypothesis, and are most powerful when combined and supported by theory (Hilborn & Mangel, 1997, Cottingham *et al.*, 2016).

Field-measurements from the deep-ocean or high-latitudes, in particular when ice-covered and shrouded in darkness during the polar night, are costly and exceptionally difficult or even impossible to obtain due to technical and logistical challenges (e.g. Berge *et al.*, 2016). Further, while observations can provide substantial amounts of valuable data, observations in the field usually represent only a snapshot of the system in space and time, and drivers often correlate, making it difficult to identify the underlying mechanisms. In this case, another difficulty is that mesopelagic fish are efficient in avoiding trawls (Kaartvedt *et al.*, 2012). Therefore, most observations are made using acoustic tools, which are limited by design in the nature of the data they can provide (e.g. impossible to discriminate sex, age, body conditions or species). Therefore, acoustic observations with today's technology still require further ground-truthing (McClatchie *et al.*, 2000).

Lab-experiments provide controllable environments and therefore can offer answers about specific mechanism, but in this case are complicated, because in order to conduct experiments animals need to be caught and kept alive for extended periods while simulating their natural environment. This rarely succeeds for fragile mesopelagic organisms. Besides, multi-trophic level interaction experiments are notoriously difficult.

Historically, these constraints have led to a seasonal and spatial bias of observations, as well as an underrepresentation of studies pertaining these systems in the literature.

Only recently, studies have begun to unravel life in the darkness of the polar night (Berge *et al.*, 2015a,c), and pointed to the mesopelagic as the zone harbouring the majority of fish biomass in the oceans (Irigoien *et al.*, 2014, St. John *et al.*, 2016).

Here models can help. Models are useful for a few different reasons: (i) they help to build intuition and generate hypothesis, (ii) they allow us to fill in process and establish missing connections, and (iii) make predictions and answer *"what-if"* type of questions. One way to think about models is as numerical or virtual laboratories that replace experiments or field manipulations that are too expensive, risky, unethical, grandiose or otherwise impossible to conduct.

The largest advances in science often occur when data does not fit theoretical predictions, revealing fundamental gaps in our understanding. Hence, models do not replace work in the lab or the field, but rather allow us to generate hypotheses, which can be tested, the degree of fit used to refine models, which then in turn generate more accurate hypotheses, and so on in an iterative cycle of modelling-observation-modelling. Therefore, models cannot only be used to interpret observation (mostly using statistical models), but models, in particular when mechanistic in nature and build on theory, can also contribute to make fieldwork more targeted by providing a *priori* hypothesis to guide sampling design.

## Modelling distributions

A range of spatially-explicit approaches is currently used to model species distributions (for recent reviews see Peck *et al.*, 2018, Robinson *et al.*, 2017). Most commonly used is a family of statistical, correlative models that can be summarized under the umbrella term species distribution models (SDMs), also known as bio-climatic envelope-, niche- or habitat suitability models. The common denominator of these models is that they assume a fixed relationship between species occurrence and a set of abiotic predictors, in the sense of the ecological niche concept (Hutchinson, 1957). Typically, SDMs predict species distributions by correlating habitat parameters with known presence-absence data, and then, based on this relationship projected the probability of occurrence for e.g. future climate scenarios (e.g. Raybaud *et al.*, 2017). Because these models are built on correlations, their ability to teach us about general mechanisms is limited.

While SDMs can be insightful first-order means, their validity has been questioned, in particular because the link to ecological theory is often weak, they rarely account for biological interactions, environmental data is often remotely sensed and hence limited to the surface, and their predictive abilities critically depend on accurate species distribution data (Pearson *et al.*, 2003, Elith & Leathwick, 2009, Ingvaldsen *et al.*, 2015, Wisz *et al.*, 2015a,b, Brun *et al.*, 2016, Fourcade *et al.*, 2017). Some of these concerns have been addressed in second generation SDMs (Fernandes *et al.*, 2013, Duffy & Chown, 2017).

It is, however, concerning that despite the large and well-documented uncertainties and methodological challenges, SDMs are increasingly used in a management context, often predicting distributions into the distant future and at localities far from current occurrences (e.g. Cheung *et al.*, 2009, Lam *et al.*, 2016). I argue this is problematic, in particular when species envelopes are shifting from aseasonal into seasonal environments, not accounting for the need of adaptations to seasonality. Here, dynamic programming and mechanistic models can be more informative means because they distinguish causality from correlation and allow merging life-history theory and short-term behaviours based on evolutionary theory. However, I acknowledge that there are limitations to their spatial resolution.

## Dynamic modelling in behavioural ecology

In this thesis, I model explicit physical and biological mechanisms acting at the individual level and let patterns and predictions at the population level be emergent. For that, I embed mechanistic models of bioenergetics and visual encounter rates in a state-dependent optimization framework that imposes an evolutionary logic (Mangel & Clark, 1988, Houston & McNamara, 1999). The advantages of this approach are that assumptions are transparent, it allows being explicit about ecology and to formalize constraints and trade-offs (Clark & Mangel, 2000).

Dynamic optimization is a useful technique to model cases when individuals make a sequence of discrete behavioural choices over time, and past decisions will determine the options available in the future (McNamara, 2000, Kokko, 2007). In other words, given a set of circumstances, what is the behavioural decision that will lead to the best possible outcome over a set timeframe when all following decisions in the future are also optimal? The inherent evolutionary logic of dynamic optimization models helps us answers the question why animals behave the way they do by providing an ultimate explanation.

One fundamental assumption to optimality models in ecology is heredity (Maynard Smith, 1978), and therefore that the outcomes can be treated as adaptive behaviours shaped through evolution by natural selection (Darwin, 1859, Fisher, 1930). In the model, the best or optimal response (of the decision variable, in our case vertical migration) is selected based on an optimization criterion (a common currency). Lifetime reproductive output as a metric of Darwinian fitness is an obvious choice, but the optimization criterion might as well be for example size, as long as the behavioural decisions leading to the preferred outcome involve constraints that are beyond the control of the individual. Constraints, i.e. trade-offs, are the key to understanding life history variation and adaptive behaviour (Stearns, 1989, and references therein). When modelling foraging behaviour, trade-offs can be many things e.g. the conflicting need to forage and to shelter, or handling time limitations on larger, more rewarding food items (considerations that are the base of optimal foraging theory).

Following from this, the optimal choice at any given time is not necessarily the one that maximizes the immediate reward, but contributes most to fitness on the long-term. Hence, adaptive behaviour is inseparably linked to life history. Life history is the theoretical framework to explain patterns in growth, survival, and reproduction and the scheduling of important events through life, e.g. when to first reproduce, (Roff, 1992, 2002, Stearns, 1992, McNamara & Houston, 2008, Varpe, 2012, Barta, 2016). Or in other words: *"Life history theory predicts how natural selection should shape the way organisms parcel their resources into making babies"* (Reznick, 2010, p. 124).

The paradigm underlying much of life-history theory is that an individual's needs and therefore priorities are age- and state dependent, and consequently so are its behavioural decisions. State-dependent optimality models account for this complexity. As an example, consider the case of starvation and that the level of internal energy stores describes the state of an individual. When death from starvation is imminent for individuals with low reserves, they are more likely to accept high risk while foraging, compared to individuals with full stores that can afford to shelter. A similar argument applies to resource allocation, when the future prospects are bleak, more energy will be diverted away from growth and storage and towards reproduction in a last attempt to boost fitness (Stearns, 1992).

For a more technical and in-depth description, all while using illustrative examples from ecology, I refer to the excellent books by Mangel & Clark (1988), Houston & McNamara (1999) and Kokko (2007). Also, see the model description provided as a supplementary to Paper II in this thesis.

## Summary of papers: key findings & conclusions

In **Paper I**, we ask how the contemporary sea-ice decline will affect pelagic interactions in polar oceans; because less sea ice means less shading and hence more light (Varpe *et al.*, 2015), which consequently leads to better vision and a potential boost in foraging success for visual predators (Fig. 4 and **Q1**). Using decades of sea-ice measurements from locations across the Barents and Bering Sea, we model visual foraging efficiency of a generic *"herring-like"* planktivorous fish over the past 30 years, and make predictions for a future ice-free Arctic Ocean, along a pan-arctic transect. Our model indicates ongoing long-term changes, involving many non-linear processes, and predicts that once the ice is gone fish might be 16 times as efficient in finding food, compared to a situation with seasonal sea-ice cover. We discuss how minor changes in light could have disproportionately large ecological impacts in polar oceans, through increased top-down control. However, any feeding gains from sea-ice decline would be constrained to the summer months with 24 hours light during the midnight sun, because the polar night during winter remains relatively dark regardless. A seasonal light regime like this favours schooling seasonal migrants, i.e. herring, capelin or mackerel, but may limit the adaptive value of diel vertical migrations often found in mesopelagic fish (Kaartvedt, 2008). Both schooling and diel vertical migration are alternative behavioural solutions to the same problem, they minimize predation risk, but their effectiveness depends on the system.

We follow up on this in **Paper II** using a state-dependent dynamic optimization model to study vertical migration behaviour of the glacier lanternfish *Benthosema glaciale* (Myctophidae), along a latitudinal gradient from boreal to Arctic waters (63.7° - 68.8°N) during the onset of the midnight sun period (early May). We test the hypothesis that towards higher latitudes, longer and increasingly lighter summer nights prevent mesopelagic fish from migrating safely to the surface at night to feed, and that consequently their distribution is constrained to depths far below the surface during the summer (Fig. 4 and **Q2-3**). These predictions are compared to acoustic observations from the Norwegian Sea (Norheim *et al.*, 2016). Our modelling results align with the hypothesis, predicting vertical migration strategies for mesopelagic fish that in timing, amplitude and depth distribution are consistent with the acoustic observations. We show, that light is the proximate cause for the vertical distribution of mesopelagic fish in the Norwegian Sea, while temperature had only secondary effects. In our model, a light comfort zone for mesopelagic fish emerges from adaptive behaviour that is consistent with observation from the Norwegian Sea (Norheim *et al.*, 2016) and a circumglobal transect (Aksnes *et al.*, 2017).

Mesopelagic fish are found everywhere in the world's oceans, yet their abundance strongly decreases in polar waters, paralleled by changes in migration depth and amplitude as shown and discussed in **Paper II**. Why mesopelagic biomass decreases by several order of magnitude towards the poles is, however, unknown. Our findings in **Paper II** substantiate the *"photoperiodic constraint hypothesis"* suggesting that species with diel-vertical migration strategies might be constrained from establishing viable populations in polar waters, due to a shortage of appropriate light habitat overlapping with concentrations of potential prey as proposed by Kaartvedt (2008).

Therefore, in **Paper III** we analyse the evolutionary model developed in **Paper II** for a full annual cycle, and a latitudinal gradient spanning the transitional zone between aseasonal and strongly seasonal environments, to test the *"photoperiodic constraint hypothesis"* (Fig. 4 and **Q4**). Our model predicts, consistent with the hypothesis and observations, a negative population growth at latitudes beyond the polar circle, due to high predation mortality and less surplus energy that can be invested in growth or reproduction. We show that during summer, mesopelagic fish at high latitudes face a tough choice: starve at depth where it is safe but foraging is not efficient, or risk predation while feeding close to the surface. Starvation is aggravated towards higher latitudes, because the light environment becomes increasingly extreme. Starvation during the productive part of the year implies that individuals have only the winter month to refuel their reserves and build up capital for reproduction. During the polar night, however, production at high laltitudes is low and dim light, together with low prey concentration in the upper waters impedes foraging. Consequently, we provide modelled evidence to support the *"photoperiodic constraint hypothesis"* which is further supported by empirical studies, suggesting populations at the northern- and southernmost occurrences to consist of non-reproducing expatriates (Sameoto, 1989, Saunders *et al.*, 2017).

In conclusion, the picture painted by our modelling results for the Norwegian Sea and the Arctic Ocean is that of unique system, with an environmental regime found nowhere else on the planet, because the highest latitudes in Antarctica are on land, and similar latitudes in the Pacific are shallower. Although the species interactions in the polar waters are bound to change, it is unlikely that a warmer and eventually ice-free Arctic Ocean will resemble lower-latitude oceans, because of the systemic differences posed by the highly seasonal environment.

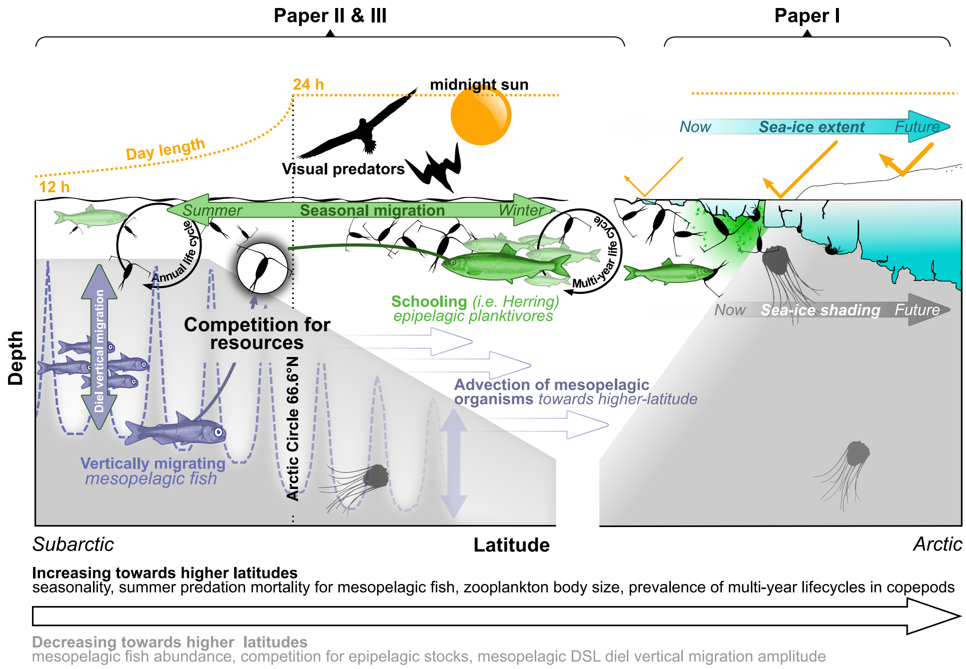

**Figure 4: An ecosystem perspective on light, visual foraging and climate change in the North Atlantic:** Extreme seasonality in light excludes diel vertical migrators, such as mesopelagic fish, from high latitudes because the window of safe crepuscular foraging disappears during the summer month **(Paper II, III)**. This means reduced competition for seasonal epipelagic migrants, such as herring or mackerel. While the extreme light regime will likely continue to constrain the poleward distribution of mesopelagic fish, climate-driven sea-ice loss may further benefit those migrants that can move in and out of polar waters. With less sea-ice shading the waters below, fish will experience a boost in visual foraging efficiency and a longer feeding season **(Paper I)**. Furthermore, the lack of predation from mesopelagic fish on overwintering stages of zooplankton may enable multi-year life cycles for Arctic copepods, forming an attractive resource for epipelagic planktivorous fish. Any alteration of foraging interaction and therefore top-down control has the potential to cause large-scale changes in eco-evolutionary dynamics with consequences for the entire food chain, that warrants future research.

# General discussion

The work presented in this thesis has tightened the link between theory and observations through modelling. I have advanced some untested hypotheses (e.g. Kaartvedt, 2008, Kaartvedt & Titelman, 2018) and common-sense logic by providing first model evidence that contributes to a better mechanistic understanding of how light shapes species distributions and may interact with climate change. The models that I have used and developed are simple, rest on certain assumptions, as they are for example oblivious to density dependence, and do not factor in feedback loops between the organism and the environment, hence there is much room for model pluralism. However, the quantitative fit of our predictions with empirical data is encouraging, and suggests that the model captures essential trade-offs and mechanisms relevant to the ecology of (meso-) pelagic fish that warrant further exploration. Working across both, polar night and mesopelagic research it becomes evident that there are many synergies between the two fields (e.g. eye sensitivity measures), but dots are too seldom connected.

## Confronting models with data

Throughout the thesis, I have aimed to use empirical data as environmental drivers and to confront my model predictions with data where possible (*sensu* Hilborn & Mangel, 1997). While temperature and sea-ice data is readily available, there is a need for more continuous in *situ* light measurements (Kaartvedt *et al.*, 2019). Given the importance of light in biological systems, in particular in the pelagic, it is surprising that light is not routinely measured in present-day studies, as it was done earlier in the pioneering work of mesopelagic research (Kampa & Boden, 1954, Clarke & Backus, 1957, Clarke & Kelly, 1965, Kampa, 1971). Similarly striking is the lack of consistent and open access zooplankton data-sets, covering more than one dimension (i.e. inter- and intra-annual changes, depth and along gradients of latitude and longitude), despite decades of zooplankton field research. In this respect, data collected at the weather ship stations is unique (Østvedt, 1955, Irigoien *et al.*, 1998, Irigoien, 2000, Hirche *et al.*, 2001).

Another caveat is units. I encourage fellow modellers to think about how their work can facilitate empirical work, e.g. by working with quantifiable units, and empiricists to think about how their data can feedback into models for example in terms of resolution but also units. For example, zooplankton biomass expressed as Ind·m$^{-2}$ is meaningful when studying productivity or energy fluxes over a certain area, however, is hardly interpretable for future studies with a different focus, e.g. requiring zooplankton concentrations as Ind·m$^{-3}$. Such consideration should influence sampling design but also reporting. To make the most of the costly data collected, it is desirable that non-aggregated data should be made publicly available along with meta-data.

Some of the predictions made in this thesis are easier to test than others, but clever empirical testing is the next logical step. Some of the acoustic data that can be used to confront the model predictions, mainly from **Paper II** and **III**, may already exist. This also points to the fact that with the rapidly advancing technologies in the field, we are often amassing data faster than we can analyse it, highlighting the need for good *a priori* hypotheses about causality to make sense of what we see, and not fall into the trap of trawling data for patterns, i.e. correlations. I further suggest to asses variation in stomach and lipid content in mesopelagic fish during summer north and south of the Arctic Circle and to do dissection and histological analysis to detect changes in gonads and reproductive effort with and without midnight sun. These results would be invaluable to test our predictions in **Paper III**, and refine the model in a modelling-observation-modelling cycle.

## Future perspectives and open questions

Based on the research presented in this thesis I see the following pertinent research questions for the future that can, but do not have to, be answered using modelling:

1) **What is the role of mesopelagic advection in sustaining high-latitude marine ecosystems?**

   Observations from the Arctic and Antarctic suggest that substantial mesopelagic biomass reaches these high-latitude systems through advection (Fig. 4, Dunbar & Hildebrand, 1952, Gjøsæter *et al.*, 2017, Knutsen *et al.*, 2017, Saunders *et al.*, 2017), sustaining high-latitude sink populations **(Paper III)**. To what degree do polar marine food webs depend on this flux of energy? Which species benefit, and how does it affect their life histories? How, and with what effects, does climate change modulate this potential link?

2) **Does the lack of predation from mesopelagic fishes at high latitudes enable large body size and multi-year zooplankton life cycles?**

   From life history theory, it is known that increased survival means a longer future horizon can be expected, which through natural selection favours slower life history strategies that may take several years to complete. Under the ice and during the polar night, Arctic zooplankton is safe from planktivores with eyes adapted to photic vision **(Paper I)**, but not from mesopelagic fish with scotopic vision. Yet, because the long summers exclude mesopelagic fishes from polar waters **(Paper III)**, predation on overwintering stages of calanoid copepods at depth is consequently also reduced (Fig. 4). This is an alternative explanation to low temperature, slow development, and short productive seasons as evolutionary drivers of large copepods, with multi-year life cycles such as *Calanus glacialis* and *C. hyperboreus* in the Arctic.

3) **Does the absence of mesopelagic fish facilitate a unique niche for migratory epipelagic stocks at high latitudes?**

   The absence of mesopelagic fishes from high latitudes (**Paper III**) may directly benefit migratory planktivores through reduced food competition and indirectly by enabling multi-year zooplankton life cycles (Fig. 4). Sea-ice retreat will further boost visual search efficiency during summer, extending the feeding season for those horizontal migrants (**Paper I**). What does that mean for stock productivity and what are the eco-evolutionary feedbacks from this change in selection regime?

4) **Can (and will) climate change cause counter-intuitive, i.e. equatorward, shifts in the mesopelagic biogeography?**

   In fish, higher water temperatures increase metabolic demands. Without additional acquisition, this reduces energy available for stores but also reproduction, translating into negative population growth (**Paper III**). The only way to make the reserves last for the winter without taking excessive risk may then be to shift towards lower latitudes where the seasons are shorter. If mesopelagic fish, however, were to forage more to meet the demands of increased metabolic costs and store enough resources to survive and reproduce, they would have to migrate to the surface more often, thus increasing their risk exposure and further reducing their survival (**Paper III**). Again, this may exclude mesopelagic fish from latitudes where they are currently found and restrict their distribution to a more southerly range where the summer season is shorter.

5) **Do different buoyancy strategies (gas-filled vs. lipid-filled swim bladder) reflect adaptions to differences in water light penetration, i.e. water clarity?**

Clear water allows light to penetrate deeper, and therefore water clarity has a significant effect on mesopelagic depth distributions (**Paper II**). Gas-filled swim bladders, become compressed with depth and buoyancy decreases, affecting swimming and energy budgets (Nero *et al.*, 2004). Further, the rates at which gas is regulated in the swimbladder to attain neutral buoyancy then determines vertical migration speed (Godø & Michalsen, 2000), limiting the time that can be spent foraging. Therefore, a higher prevalence of lipid-filled swim bladders can be expected in clearer waters (further offshore) than in coastal waters where water is murkier and hence allows for shallower migration depth. This may also help to explain species-specific distribution patterns. For example, *Maurolicus muelleri* with eyes uniquely adapted to mesopic (*dim but not quite dark*) light conditions, and therefore shallow distributions, generally disappears offshore, where *Benthosema glaciale* with lipid-filled swim bladders and scotopic vision (adapted to *twilight* conditions) can evade predation by diving deeper.

6) **Is starvation resistance the explanation to “Bergmann clines” in southern ocean myctophids?**

Saunders & Tarling (2017) find that southern ocean myctophids comply with the Bergmann rule, i.e. suggesting a poleward increase in body size. The authors conclude that greater attainable body size is a necessary attribute to reach colder regions at higher latitudes and suggest starvation resistance as a possible explanation. Additionally, the authors hypothesize that climate-driven warming will alleviate constraints resulting in a reduction of average body size with the potential to cause ripple effects to adjacent trophic levels. This reasoning rests on a causal relationship between body size and temperature and therefore between body size and latitude.

Our modelling results from **Paper III**, however, show that starvation occurs because mesopelagic fish are excluded from entering near-surface waters at high latitudes during light summer nights where their prey is. Daylength is independent of climate change, and hence, unless climate change increases productivity, warmer waters will likely not weaken but increase starvation because of higher metabolic demands (see the reasoning developed under point 4. above). Strikingly, the exception to the Bergmann clines in southern ocean myctophids were species that did not migrate vertically, and instead predominantly fed on prey with deeper distributions (Saunders & Tarling, 2017). Given that starvation resistance is the mechanism that leads to the observed Bergmann clines, this would be a pattern expected from the visual search mechanism and reasoning proposed in **Paper II-III**.

In **Paper III** we also show that myctophids at higher latitudes are unable to build up the same reproductive capital as their congenerics at lower latitudes, which could explain why mesopelagic fish at high-latitudes appear unable to reproduce successfully (Saunders *et al.*, 2017, Saunders & Tarling, 2017), contributing to the evident absence of smaller juveniles (Sameoto, 1989).

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# PAPER I

**Langbehn TJ & Varpe Ø** (2017) Sea-ice loss boosts visual search: fish foraging and changing pelagic interactions in polar oceans

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# Sea-ice loss boosts visual search: fish foraging and changing pelagic interactions in polar oceans

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## Abstract

Light is a central driver of biological processes and systems. Receding sea ice changes the lightscape of high-latitude oceans and more light will penetrate into the sea. This affects bottom-up control through primary productivity and top-down control through vision-based foraging. We model effects of sea-ice shading on visual search to develop a mechanistic understanding of how climate-driven sea-ice retreat affects predator–prey interactions. We adapt a prey encounter model for ice-covered waters, where prey-detection performance of planktivorous fish depends on the light cycle. We use hindcast sea-ice concentrations (past 35 years) and compare with a future no-ice scenario to project visual range along two south–north transects with different sea-ice distributions and seasonality, one through the Bering Sea and one through the Barents Sea. The transect approach captures the transition from sub-Arctic to Arctic ecosystems and allows for comparison of latitudinal differences between longitudes. We find that past sea-ice retreat has increased visual search at a rate of 2.7% to 4.2% per decade from the long-term mean; and for high latitudes, we predict a 16-fold increase in clearance rate. Top-down control is therefore predicted to intensify. Ecological and evolutionary consequences for polar marine communities and energy flows would follow, possibly also as tipping points and regime shifts. We expect species distributions to track the receding ice-edge, and in particular expect species with large migratory capacity to make foraging forays into high-latitude oceans. However, the extreme seasonality in photoperiod of high-latitude oceans may counteract such shifts and rather act as a zoogeographical filter limiting poleward range expansion. The provided mechanistic insights are relevant for pelagic ecosystems globally, including lakes where shifted distributions are seldom possible but where predator–prey consequences would be much related. As part of the discussion on photoperiodic implications for high-latitude range shifts, we provide a short review of studies linking physical drivers to latitudinal extent.

KEYWORDS
photoperiod, predator–prey interaction, range shift, tipping points, visual ecology

## 1 | INTRODUCTION

The effects of environmental change are mediated through responses of individuals. Besides physiological responses, predator–prey interactions are a key mechanism through which climate-driven change affects populations and ecosystems (Sydeman, Poloczanska, Reed, & Thompson, 2015). Foraging behaviour and predator–prey interactions affect structure and function of ecological systems (Ripple & Beschta, 2012; Schmitz, Krivan, & Ovadia, 2004). Global and local climate change will modify physical foraging constraints, some will be relieved or become void, others will be strengthened and novel ones are likely to arise. Foraging constraints in animal systems operate via restricted or time-limited access, reduced ability to locate food, or trade-offs between acquired and spent energy during foraging. Many studies have reported altered foraging performance and reconfiguration of trophic interactions in response to climate-driven change of the physical habitat. Ungulates encounter ice-locked pastures (Hansen, Aanes, Herfindal, Kohler, & Sæther, 2011), murkier water caused by increased river run-offs limit visual prey detection in fish (Jönsson et al., 2011), sea level rise narrows the temporal exposure of tidal flats to foraging waders (Galbraith et al., 2002), change in wind speed and patterns paralleled by change in wave action affects foraging effort in seabirds (Lewis, Phillips, Burthe, Wanless, & Daunt, 2015), while sea-ice loss deprives mammalian predators of access to their prey (Stirling & Derocher, 2012). These examples highlight the importance of trophic interactions as link between environmental changes, individual fitness and population and community level patterns and processes.

Climate change effects are exacerbated in polar marine ecosystems (Hoegh-Guldberg & Bruno, 2010), where the highly seasonal light environment is a key characteristic and a driver of many adaptations and ecological interactions (Berge et al., 2015; Regular, Davoren, Hedd, & Montevecchi, 2010). Most prominently, Arctic temperatures rise at twice the global average (Hoegh-Guldberg & Bruno, 2010; Pörtner et al., 2014), paralleled by a significant long-term reduction in sea-ice extent (SIE) and thickness (Comiso, 2012; Stroeve et al., 2012), and much altered sea-ice phenology. Without the shading effect of sea ice, more light will reach the water column (Varpe, Daase, & Kristiansen, 2015; Figure 1), affecting both bottom-up control through primary productivity (Arrigo, van Dijken, & Pabi, 2008) and top-down control through visual foraging (Aksnes, Nejstgaard, Saedberg, & Sørnes, 2004). Increased light due to less ice can change polar benthic communities towards autotrophic and macroalgae dominance (Clark et al., 2013; Kortsch et al., 2012). The underpinning mechanism of climate-induced pelagic regime shifts (Beaugrand et al., 2014) and the role of top-down control by visual predators (Varpe et al., 2015) is however elusive. Seasonality in photoperiod is, in contrast to temperature, decoupled from climate change and constitutes a stable abiotic environmental factor but with a marked latitudinal gradient. Hence, the Arctic light regime provides the unique opportunity to disentangle the dynamic effects of climate change from underlying static mechanisms.

With this study, we merge several recent conceptual ideas on high-latitude fish foraging and distributions (Kaartvedt, 2008; Saikkonen et al., 2012; Sundby, Drinkwater, & Kjesbu, 2016; Varpe et al., 2015) and advance from the stage of conceptual work to a mechanistic and fully parameterized model framework. We quantify, for the first time, the potential increase in visual search efficiency in a generic high-latitude pelagic fish over the annual photic cycle, along gradients of latitude and intra- and interannual sea-ice cover. Estimates of change in visual search are provided for sea-ice conditions over the period 1978–2015 and compared to an Arctic Ocean (AO) void of sea-ice. We contextualize our findings by discussing light as a biological mechanism defining species range margins in a changing climate and tie it to the ongoing borealization of Arctic fish communities (Fossheim et al., 2015). Climate driven sea-ice retreat, and the resultant change to the amount of light reaching the waters below includes a range of known nonlinear dynamics (i.e. ice-albedo feedbacks and exponential

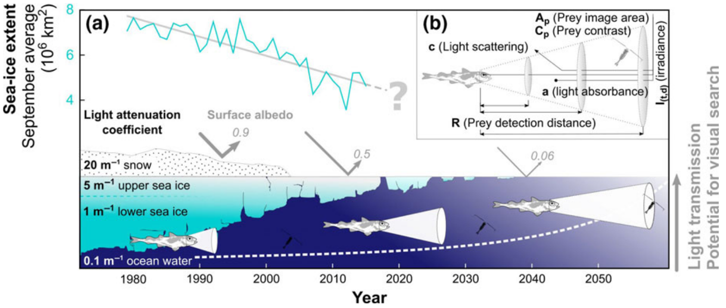

**FIGURE 1** Visual search in a changing Arctic Ocean: (a) Less sea ice means increased light, which results in more efficient visual search. Sea-ice extent has retreated in the past (turquoise line) and is projected to continue in the future (extended linear trend line, grey) with consequences for the pelagic lightscape (dashed white line). Prey items, here depicted as a copepod of equal size and distance to the predator, will become more likely to be visually detected with decreasing sea-ice thickness because the visual range of predators scales with incoming light. (b) The distance at which a predator can spot its prey depends on many factors, including incoming light and the optical properties of prey and water. For visual purposes, visual range and fish size are not drawn to scale

light transmission with decreasing ice and snow thickness, Fig S5). Therefore, we expect strongly nonlinear responses of visual search, both in space and time, with effects likely to propagate through the food web.

## 2 | MATERIALS AND METHODS

### 2.1 | Model framework

We model the visual prey detection range of planktivorous fish over the annual cycle and along gradients of latitude and sea-ice conditions. Visual range was modelled as described by Aksnes and Giske (1993) and Aksnes and Utne (1997), except that the model was forced by photosynthetically available solar radiation (PAR), in the range of visible light between 400-700 nm, under clear sky conditions (Figs. S1–S3). PAR calculations (W m$^{-2}$) for solar irradiance at the ocean surface, accounting for the angle of incidence, are based on an analytical formula by Frouin, Lingner, Gautier, Baker, and Smith (1989), implemented for R in the "fishmethods" package (Nelson, 2016). Details can be found in the "astrocalc4r" documentation by NOAA (Jacobson, Seaver, & Tang, 2011). Transmission calculations for light availability at depth, applying the Lambert-Beer law, were made in relation to the sea-ice cover (Fig. S4). A similar model set-up has previously been used to study the effects of light on predation-related zooplankton mortality (Aksnes et al., 2004), energy flux in marine food chains and seasonal foraging by migratory fish (Varpe & Fiksen, 2010). Therefore, we limit the model description here to a summary of all equations and parameters (Table 1), and refer to Aksnes and Giske (1993), Aksnes and Utne (1997), Huse and Fiksen (2010), Varpe and Fiksen (2010), van Deurs, Jørgensen, and Fiksen (2015) for detailed model descriptions. See also studies by O'Brien and Evans (1992) and Eggers (1977) for pioneering work on the visual ecology of planktivorous fish. Our model provides hourly estimates of visual range as a function of sea-ice conditions and latitude. The underlying principle is that ambient light scales the distance at which a visual predator can locate its prey, termed visual range. With less sea ice, more light will reach the water and prey becomes detectable at larger distance for fish, increasing foraging efficiency (Figure 1a).

Prey and predator size act only as scaling parameters without affecting the relative integrity of model estimates. We parameterized the model to represent a generic forage fish of 20 cm body length (BL), selectively preying on planktonic copepods with total body length of 4 mm (image area of 3 × 10$^{-6}$ m$^2$). The selected size exceeds the body size of *Calanus finmarchicus* (Leinaas, Jalal, Gabrielsen, & Hessen, 2016) dominating total copepod biomass in the sub-Arctic North Atlantic Ocean (Planque & Batten, 2000), but represents a conservative size estimate in respect of some larger high-Arctic copepods, such as *Calanus hyperboreus* (Leinaas et al., 2016).

### 2.2 | Scenario building

We compiled daily sea-ice concentration scenarios based on a time series from the National Snow and Ice Data Center (NSIDC) that provides satellite-derived daily sea-ice concentration (SIC) on a grid of 25 × 25 km from 1978 to 2015 (Cavalieri, Parkinson, Gloersen, & Zwally, 1996). We excluded 1978, 1987, 1988 as they lack full seasonal coverage. From 1978 to 1987, SIC is only available for every second day. We extracted SIC for intervals of 1° latitude along two transects, a North Pacific transect (55–85°N, 169°W) and a North Atlantic transect (70–85°N, 35°E). The former spanning from the

**TABLE 1** Model summary, including a list of all equations, units and references, used to describe visual range of pelagic fish along latitudinal gradients that include sea ice in the north

| # | Explanation (units) | Equations | Parameter description |
|---|---|---|---|
| 1 | Visual range (m)[a] | $R^2_{(t,d)}\exp^{(cR_{(t,d)})} = {}^{\sim}C_pA_pE'\frac{I_{(t,d)}}{K_e+I_{(t,d)}}$<br>or if R <~<br>0.05 m$R_{t,d} = \sqrt{C_pA_pE'{}^{\sim}\frac{I_{(t,d)}}{K_e+I_{(t,d)}}}$ | $c$ = beam attenuation coefficient = 0.3[b]<br>$C_p$ = prey contrast = 0.3[b]<br>$A_p$ = prey image area (m$^2$) = 3 × 10$^{-6}$ [b]<br>$t$, $d$ = time (h) and Julian day<br>$I$ = ambient irradiance (Eq. 3)<br>$E'$ = visual capacity<br>$K_e$ (μE m$^{-2}$ s$^{-1}$) = composite saturation parameter<br>$E'$ and $K$ are scaled such that $R$ = 1 BL when light is not limiting and prey image area (Prey length × prey width × 0.75) = 3 × 10$^{-6}$ m$^2$<br>$I_0$ = irradiance at the water surface |
| 2 | Irradiance corrected for local surface albedo (W m$^{-2}$) | $I_{a_{(t,d)}} = {}^{\sim}I_{0_{(t,d)}}(1-\alpha)$ | α = local surface albedo = 0.5 for sea ice[c], 0.9 for fresh snow[c] and 0.06 for open ocean water[c] |
| 3 | Ambient irradiance (W m$^{-2}$) | $I = {}^{\sim}I_{a_{(t,d)}}\exp^{(-k*z)}$ | $k$ = diffuse attenuation coefficients (m$^{-1}$) = 20 for snow[d], 5 for upper 10cm of sea ice[d], 1 for sea ice interior[d] and 0.1 for ocean water[b].<br>$z$ = light path length in medium |

[a] Aksnes and Utne (1997).

[b] Varpe and Fiksen (2010).

[c] Perovich (1996).

[d] Grenfell and Maykut (1977).

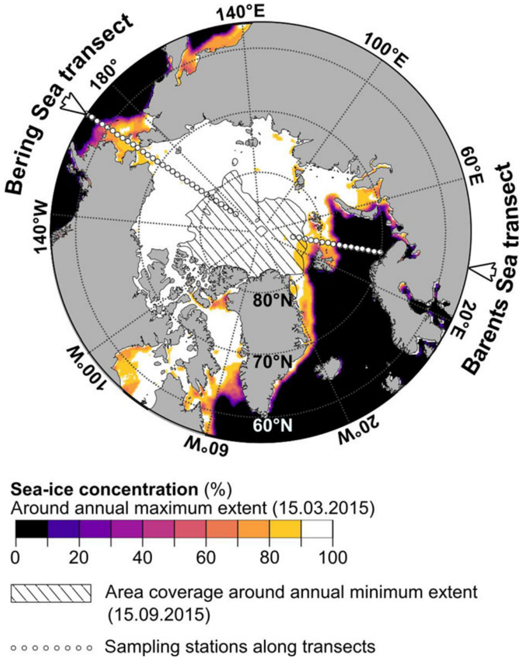

**FIGURE 2** Exemplary map of Arctic sea ice (in 2015) illustrating the seasonal range in sea-ice extent. Sea ice at its maximum annual extent (mid-March) is colour-coded based on 10% concentration increments from ice-free (black) to total cover (white). The hatched area marks the minimal annual extent (<75% sea-ice concentration) during mid-September. Circles along two transects (Bering Sea and Barents Sea) indicate point source location of sea-ice concentrations used to build daily sea ice. Sea-ice concentrations are based on satellite-born Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (*Cavalieri et al.*, 1996)

Bering Sea, through the Bering Strait into the Arctic proper and the latter crossing the Barents Sea and entering the AO between Svalbard and Franz Josef Land (Figure 2). The choice of transects attempts to capture the large-scale contrast between the Pacific and Atlantic side of the AO. Sea ice occurs at higher latitudes and thus in a more extreme light environment, in the Atlantic than the Pacific Arctic (Barnhart, Miller, Overeem, & Kay, 2015; Parkinson, 2014).

For each transect, daily, empirical pan-arctic sea-ice concentration scenarios over a period of 35 years were established. We excluded latitudes above 85°N as accurate coverage within this sector cannot be warranted (Cavalieri et al., 1996).

To explore the change in visual range in response to a changing physical environment, we compared hindcast estimates under past sea-ice conditions against the extreme—yet predicted—scenario of an ice-free AO. Arguments are developed for an all-else-equal scenario, omitting feedback loops of increased light transmission, subsequent phytoplankton growth and hence increased turbidity. Here, we consider the conservative case of uniform, 120 cm thick sea ice, covered by 10 cm of fresh snow (see Fig. S5 for the effect of snow and ice thickness), representative for a first-year ice (FYI) situation (Tilling, Ridout, & Shepherd, 2016) along the transects. All calculations were made for fish foraging at 30 m depth.

## 3 | RESULTS

### 3.1 | Latitudinal variability in visual range under a no-ice scenario

In the absence of sea ice, our model predicts a sattle-shaped pattern where interannual variation of the average visual range increased with increasing latitude; reflecting the transition from a predominantly circadian lightscape at low latitudes to a more seasonal, and less circadian, light regime at higher latitudes (Figure 3). At high latitudes (~75–85°N), visual range peaked around summer solstice with a daily average of 6 cm and declined to an average of <1 cm during the polar night. At low latitudes (0°–20°N), average visual range is only marginally influenced by the seasonality in solar radiation (Figure 3).

### 3.2 | Seasonal effects of sea ice on visual range

We found sea ice to fundamentally restructure the visual foraging landscape, and because sea-ice properties (phenology, concentration and lowest-latitude of occurrence) differ across the Arctic (see Figure 2 for reference), the light environment is spatially variable beyond the constraints dictated by photoperiod (Figure 4). Along the

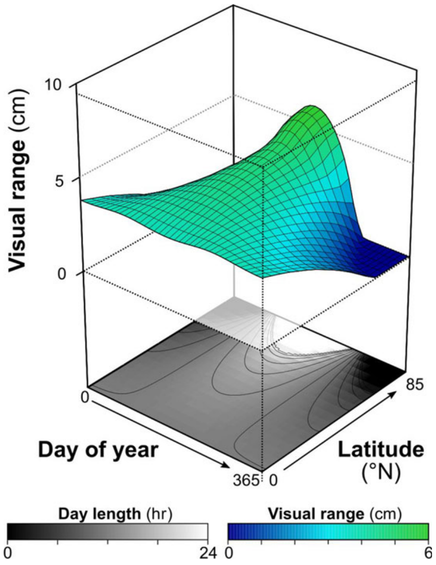

**FIGURE 3** Mean visual range (cm) varies by day of the year and latitude (°N) in relation to the surface light regime, here plotted as day length in hours when the sun reaches above the horizon. For this no-ice scenario, there are smooth latitudinal transitions

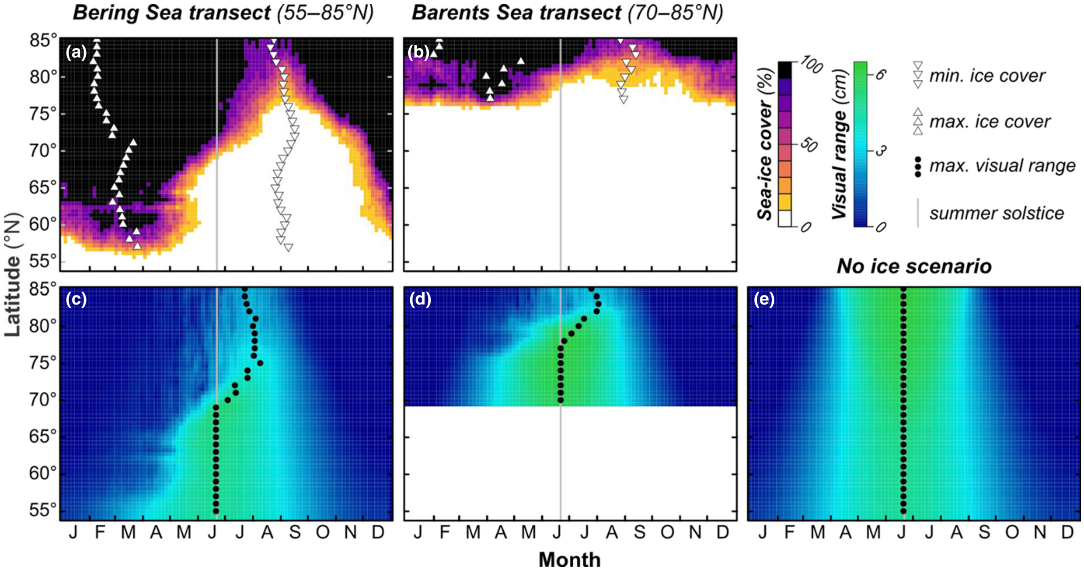

**FIGURE 4** Sea-ice extent and phenology (a and b), here averaged for the period 2010–2015, dictates visual range of fish below the sea ice (c and d). Comparison to visual range under a no-ice scenario (e) (see also Figure 3) reveals that shadowing of the water column by sea ice impedes vision in fish and shifts peak visual range towards later in the season. Grey lines mark summer solstice, black dots the annual maximum in visual range and upward and downward pointing white triangles sea-ice maximum and minimum respectively. Maximum or minimum sea ice values were calculated as median of values falling within a 10% increment around the minimum and maximum value.

Bering Sea transect, sea ice extends to latitudes below the Arctic Circle. Ice retracts by about 20° latitude during the melting season, with a window of about 330 ice-free days (<10% ice cover) at its southern margin. The window of sea-ice minimum gradually narrows towards the pole until 80–85°N where >90% ice cover reigns for nearly three quarters of the year (Figure 4a). Along the Barents Sea transect, sea ice exhibits a similar phenology as in the Bering Sea, but with a less pronounced amplitude and therefore with a steeper spatial gradient at higher latitudes and ice extending less far south onto the shelf (Figures 4b and 2).

Importantly, the seasonal window of sea ice minimum is not synchronized with the window of available solar light. Whereas surface irradiance is at its minimum at the winter solstice, the lid as represented by sea ice can last far into the light season, in particular at high latitudes (Figure 4a, b). Sea-ice minimum and maximum were found on average to be offset from summer solstice by 73 (±7 *SD*) and -110 (±24 *SD*) days across both transects. Sea-ice melt past summer solstice causes peak light availability at depth to be delayed relative to surface irradiance, which translates into a shift of the predation landscape towards later in the season.

### 3.3 | Temporal and spatial variability in hindcast visual range estimates

In an ice-free future, our model predicts a gradual decrease of yearly averages in visual range towards the pole. Hindcast estimates of visual range fall below future projections. Towards higher latitudes, the divergence between projections and hindcast estimates increases, as the period of seasonal ice-cover lengthens (Figure 5a). Changes in ice cover from 1979 to 2015 have already resulted in an increased visual range, except for around 60°N along the Bering Sea transect where visual range has slightly decreased. Year-to-year change in visual range is spatially variable, but highest percent change per decade is found around 76°N in the Pacific Arctic and around 81°N in the Atlantic Arctic (Figure 5b). In the Barents Sea, changes in visual range have accelerated during the last decade (Figure 5a). With receding sea ice, visual range is eventually bound to converge with projected values made under an ice-free scenario, representative for the terminal stage of observed sea-ice loss. In the central Arctic basin, this will result in a fourfold increase of current visual range (Figure 5b).

The visual range of planktivorous fish is predicted to have changed significantly over the past 35 years (Figure 6) at a similar rate between the Atlantic and Pacific side of the AO.

## 4 | DISCUSSION

We demonstrate for the first time through mechanistic modelling how a new subaqueous lightscape, emerging as Arctic sea ice declines, should seasonally boost visual search of planktivorous fish. We show conclusively that seasonal sea-ice occurrence and its timing

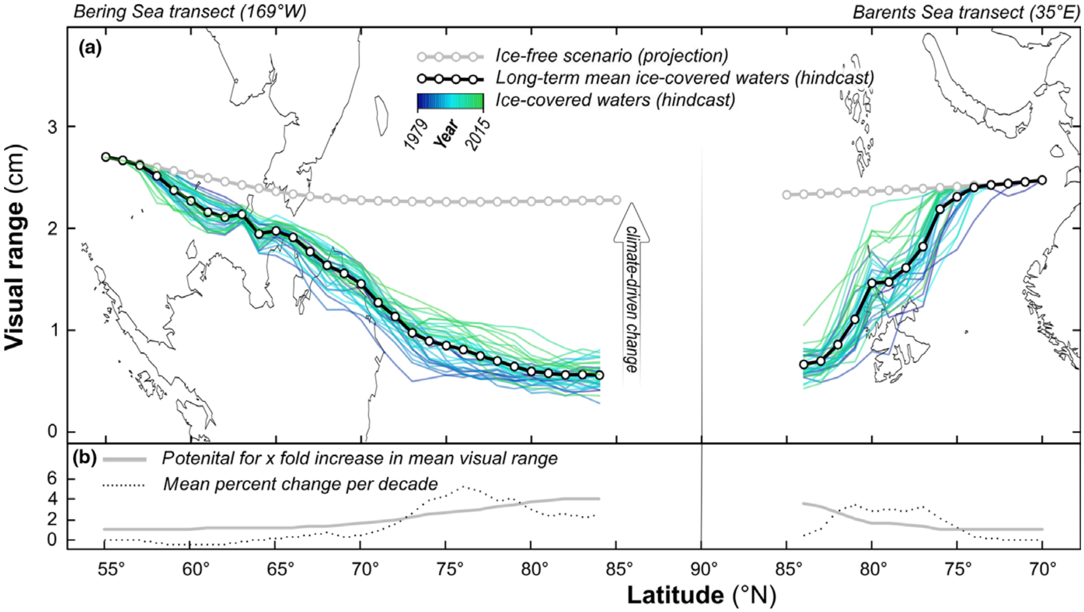

**FIGURE 5** Climate-driven sea-ice decline unlocks potential for visual predation at high latitudes. (a) Hindcast visual range, given as yearly averages by increments of 1° latitude, for the years 1979–2015 are depicted by coloured lines, in comparison to projected estimates of visual range made for a future ice-free AO, marked by grey lines with open circles. (b) The potential for increase in visual range was calculated as the ratio between estimates derived under the ice-free scenario and the average of hindcast estimates across the past 35 years, marked by black line with open circles. Underlying maps serve the orientation and are centred around the transect longitudes

relative to photoperiod affects visual foraging efficiency, and that sea ice creates a heterogenic pan-arctic landscape of foraging opportunities. In its current state, sea ice acts as a lid that shields the water below and thus constrains vision-dependent prey search in high-latitude oceans. The shading effect is particularly strong when sea ice is consolidated and prevalent for extended periods during the light season. Hindcasting visual range over the past four decades exposes that climate-driven sea-ice retreat has already begun to release visual foraging constraints. Here, we provide quantitative predictions under an all-else-equal scenario, which suggest that the Arctic pelagic ecosystem is on a nonlinear trajectory to become a hot-spot for high latitude summer feeding (Figure 7).

## 4.1 | The sea-ice lid and consequences for fish performance and distributions

Our results show that sea ice is an important contributor in shaping the pelagic lightscape, and that ice causes constraints beyond the scope of photoperiod (Figure 4). Therefore, sea-ice phenology is pivotal to the visual predation landscape. Earlier ice break-up, or a shift in ice-free days towards midsummer, means that light at depth is available over a period with more daylight hours. The nonlinearity of this relationship increases towards the poles, making ice-free days around summer solstice at high latitudes increasingly beneficial to visual predators, whereas the role of ice-cover closer to winter solstice loses in importance towards the poles (see Clark et al., 2013 for a detailed graphical derivation).

Based on hindcast estimates of visual range, we present evidence that declining sea ice eliminates those limitations (Figure 5), opening a window for much improved summer feeding (Figure 3). Feeding migrations into the high Arctic are then expected, given sufficient food availability. Current projected changes of AO primary production (PP) are inconsistent regarding the sign of change, yet the underpinning mechanisms are consistent (Vancoppenolle et al., 2013). While increased light transmission due to reduced and thinning sea-ice cover is expected to increase PP (Arrigo et al., 2008) but also to change the timing (Ji, Jin, & Varpe, 2013) and the extent of (sub-ice) phytoplankton blooms (Horvat et al., 2017), depletion of nitrate and enhanced stratification may increasingly limit productivity towards the end of the century (Slagstad, Wassmann, & Ellingsen, 2015; Vancoppenolle et al., 2013). However, sea-ice retreat off the Arctic shelf may cause winter upwelling at the shelf-break, which in combination with a prolonged growth season can fuel production (Falk-Pedersen et al., 2015). Despite the general agreement that PP in the central AO will remain low (Slagstad et al., 2015), key mesozooplankton species might benefit on a pan-arctic scale. Particular increases of *C. finmarchicus* are expected along the Eurasian perimeter of the AO, while *C. glacialis* is predicted to expand its distribution

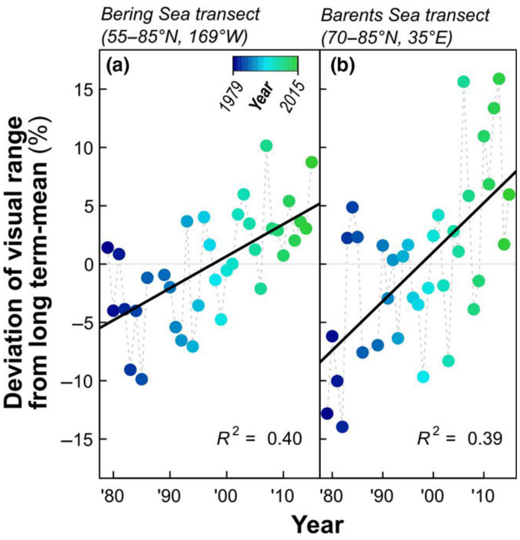

**FIGURE 6** Modelling results predict a significant change in visual range of fish in the period 1979–2015, with a similar rate of change in the Pacific and Atlantic Arctic. Yearly averages of visual range (coloured dots) are shown as deviation from the long-term mean across all study years (grey horizontal line). Decadal rate of change is 2.7% and 4.2% for the Bering Sea and Barents Sea transect, respectively. The linear fit (black line) had slopes different from 0 ($p < .001$) for both transects.

poleward (Feng, Ji, Campbell, Ashjian, & Zhang, 2016; Slagstad et al., 2015).

Besides fish, receding sea ice will change the foraging habitat for most Arctic seabirds and whales. Ice can act as a barrier for air breathers and shelter to their prey, limiting foraging to the ice edge environment (Brierley, 2002). Given the nonlinear latitudinal distribution of the foraging landscape (Figure 3), mobile, fast swimming predators able to cover long distances will have most to gain from feeding forays into high latitudes oceans. These predictions coincide with increased high-latitude incidences of known pelagic migrants with temperate or boreal biogeographic affinities such as Atlantic Salmon *Salmo salar* (Jensen et al., 2014), Chinook Salmon *Oncorhynchus tshawytscha* (Logerwell et al., 2015), Atlantic mackerel *Scomber scombrus* and Atlantic herring *Clupea harengus* (Berge et al., 2015). In the south-eastern Bering Sea, the migration of Pacific herring (*Clupea pallasii*) closely tracks the ice edge, and winter feeding grounds have shifted north-westward during recent years. Tojo, Kruse, and Funk (2007) suggest predator avoidance and reduced basal metabolic rates as likely explanations. In general, an overall northward displacement of pelagic traits has been observed in Arctic shelf-seas (Fossheim et al., 2015; Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015). This community change is further reflected in the dietary shift from invertebrates to fish in some Arctic top-predators (Crawford, Quakenbush, & Citta, 2015).

## 4.2 | Photoperiodic implications for high-latitude range expansion

Species respond to changing climate by changes in their distribution range (Lenoir & Svenning, 2015). This pattern is global, largely coherent and observed across a wide range of taxa (Hickling, Roy, Hill, Fox, & Thomas, 2006; Sorte, Williams, & Carlton, 2010). Climate-induced shifts in distribution are generally assumed to occur unidirectionally along gradients of temperature, due to thermal control of physiological processes (Clark, Sandblom, & Jutfelt, 2013; Pörtner, 2012). Therefore, range shifts are typically poleward (Parmesan & Yohe, 2003; Perry, Low, Ellis, & Reynolds, 2005; Poloczanska et al., 2013) or towards higher altitudes in terrestrial systems, and towards greater depth in the case of global ocean warming (Dulvy et al., 2008; Fossheim et al., 2015).

The logic of latitudinal range shifts driven by thermal limits dictates that under continuous warming the tropics face a net loss of species (as local extinction > local invasion) while the polar regions will experience high invasion rates paralleled by local extinction of the endemic cold stenotherm fauna (Cheung et al., 2009). However, this concept neglects the role of photoperiod as part of a species fundamental niche. For phototrophs, light is inherently accepted as part of their environmental niche and an acknowledged driver of their latitudinal distribution (Muir, Wallace, Done, & Aguirre, 2015), the same practice is generally not adopted for heterotrophs. Marine range shift theory is largely informed by studies from temperate regions where seasonality in light is minor (Figure 3) but seasonality in temperature is major (Mackas et al., 2012). Temperature is the most common explanation suggested for observed range shifts (Table 2).

However, light is a central driver of biological systems at high latitudes. As the seasonality of light increases with latitude, so does its relevance as a structuring factor, and in high latitude oceans, the extreme photoperiod may synergistically with temperature act as the key factor defining species range margins (Kaartvedt, 2008; Sundby et al., 2016; Varpe et al., 2015). Biological rhythms and activity patterns of polar organisms are highly influenced by the light regime (van Oort et al., 2005) and photoperiodic responses are central to fitness (Varpe, 2012). The shorter the favourable season, the more important does the precise timing of crucial life-history events such as migration, growth and reproduction become (Conover, 1992), all of which at some stage depend on successful foraging in order to have energy and resources to allocate to vital body functions (Figure 2 in Enberg et al., 2012). Therefore, the failure to account for light seasonality in climate-niche models might yield unrealistic projections for species distributions at high latitudes. Yet, recent work concludes a moderate to high likelihood for several sub-Arctic pelagic species (e.g. Atlantic herring and capelin) to expand into the AO with unlimited extent beyond the shelf edge (Haug et al., 2017). Although built upon life-history considerations, vision-based feeding and vision-based predation risk (sensu Kaartvedt, 2008) are still being disregarded.

In contrast to temperature, seasonality in surface light is detached from climate change. Hence, photoperiod will persist to be

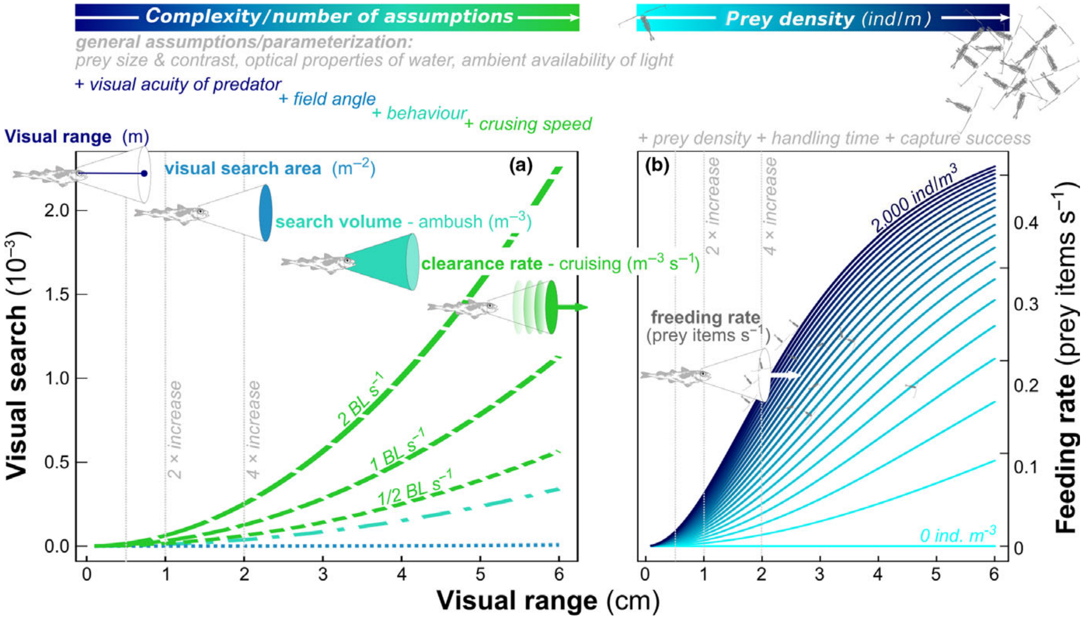

**FIGURE 7** Visual range is the fundamental metric of visual search. Moving from visual range to more complex descriptors of visual search (visual search area [m$^{-2}$] ➡ search volume [m$^{-3}$] ➡ clearance rate [m$^{-3}$ s$^{-1}$] ➡ feeding rate [prey items s$^{-1}$]), ecological relevance and interpretability comes with an increased number of model parameters and related assumptions, both of which are often uncertain. (a) The dependencies of visual search area (relevant for cruising predators) and search volume (relevant for ambush predators) on visual range are nonlinear. Visual area (m$^{-2}$) scales to the power of two and search volume (m$^{-3}$) to the power of three with visual range. A fourfold increase in visual range (marked by grey dotted vertical lines) as projected for the Arctic Ocean at latitudes >80°N (but see Figure 5) will result in a 16-fold increase in visual search area and a 64-fold increase in search volume. (b) Feeding rates at low prey densities are not constrained by handling time and thus scale with visual range. With increasing prey densities, prey handling limits feeding and increasing visual range will not increase predation rates any further. Here, we consider the case of a predator swimming at a speed of 2 BL s$^{-1}$, with a prey handling time of 1 s$^{-1}$ and a prey capture success of 0.5, for prey densities between 0 and 2000 ind. m$^{-3}$. We refer to Aksnes and Utne (1997) and Varpe and Fiksen (2010) for calculations of clearance rates and feeding rates

a stable abiotic ecological filter (Saikkonen et al., 2012) selecting against nonadapted life histories. Clearly, seasonal environments require different strategies as they impose a different selection regime (e.g. sufficient energy storage to overcome starvation periods) than nonseasonal environments. Only species with behavioural strategies and life histories adapted to complete a full life cycle under the constraints of seasonally varying food availability, foraging environment, predation pressure and abiotic conditions will be able to pass that filter and colonize high latitudes. Behavioural strategies will affect to what extent different fish species can benefit from the boost in light. Any substantial foraging gains from the boost in light will be limited to the summer months as the polar night persists to be relatively dark and visual foraging is consequently expected to remain low, regardless of sea-ice loss. Although, some native polar organisms are able to detect and utilize low levels of irradiance during the polar night (Cohen et al., 2015). Planktivores also have predators, some of them being visual. In accordance with the antipredation window hypothesis (Clark & Levy, 1988), summer foraging gains of planktivores related to sea-ice loss are traded-off against an increase in predation risk through larger visual predators. In this case, fish that perform diel vertical migrations do not gain an adaptive advantage, as they have to minimize the time at the surface to reduce predation risk, which will consequently limit prey encounter. Schooling fish on the other hand, such as herring or capelin, can forage more safely even in the presence of piscivores, and therefore make better use of the long days.

The life histories and behavioural strategies of some boreal species may be maladapted to the change in day length associated with a relatively small latitudinal shift from the sub-Arctic to the Arctic (Figure 4 in Poloczanska et al., 2016). Limited prey encounter on copepods during winter time and increased predation risk during summer, as supported by our findings and as argued for mesopelagic fish by Kaartvedt (2008), are the main regulatory mechanisms making the seasonal light regime of the Arctic a possible zoogeographical filter. If seasonal light is slowing or constraining further poleward range expansions at high-latitude, longitudinal distribution-shifts towards comparable habitats with colder temperatures but at similar latitudes are conceivable

**TABLE 2** Examples of contemporary distribution changes in marine fish and associated physical drivers

| Suggested physical driver | Max. lat. | Studied system and species | Type of range shift | References |
|---|---|---|---|---|
| | 61°N | Anchovies and sardines | Leading edge range | Alheit et al. (2012) |
| | 62°N | North and Baltic Seas | Expansion | Beare et al. (2004) |
| | 61°N | Demersal North Sea fish assemblage | Shift of community centre of distribution, northward boundary shifts | Perry et al. (2005) |
| | 62°N | Demersal North Sea fish assemblage | Deepening of the North Sea fish assemblage | Dulvy et al. (2008) |
| Δ Temperature | 82°N | Fish communities of the Barents Sea | Shift of community centre of distribution | Fossheim et al. (2015) |
| | 46°N | 36 fish stocks on the Northeast United States continental shelf | Poleward shift in their centre of biomass, deepening | Nye, Link, Hare, and Overholtz (2009) |
| | 44°N | 7 fish species of the Northwest Atlantic Ocean | Poleward shift of maximum latitude of occurrence | Murawski (1993) |
| | 61°N | Marine assemblages from North American seas | Species track local climate velocities | Pinsky, Worm, Fogarty, Sarmiento, and Levin (2013) |
| Δ Temperature$^{SIE}$ | 61°N | Bering Sea Arctic-sub-Arctic ecotone | Increases in total biomass, species richness, and average trophic level | Mueter and Litzow (2008) |
| Δ Salinity$^{T}$ | 45°N | 6 most common juvenile marine species in the Gironde estuary | Increase in abundance | Pasquaud et al. (2012) |
| Δ Wind$^{T}$ | 62°N | North Sea cod stock | Northward shift in distribution of juveniles and centre of gravity | Rindorf and Lewy (2006) |
| Δ Ocean currents | Global | Larval dispersal through means of advection | Flow direction can hinder or assists species dispersal at poleward range edges | van Gennip et al. (2017) |
| Δ Light$^{SIE}$ | High | latitudes | Pelagic fish | Suggested mechanisms are limits to visual search and life histories not adapted to pulsed food availability |
| Varpe et al. (2015)<br>Sundby et al. (2016)<br>this study | | | | |

Superscript letters indicate covariance with other drivers, T, Temperature; SIE, Sea-ice extent.

(Saikkonen et al., 2012). The Fram Strait as a likely invasion gateway to the Arctic provides an illustrative example for such a scenario with two closely linked systems, the Northeast Greenland shelf and the coastal waters of Svalbard, but differentiated by a steep gradient in temperature (Christiansen et al., 2016). In this case, a northward shift west of Svalbard would allow species to track ocean temperature changes, but require them to cope with a more seasonal environment; an equidistant shift westward however would maintain seasonality and keep experienced temperatures below critical limits.

### 4.3 | Ecological interactions, evolution and ecosystem effects

Our findings show a large, yet unrealized potential for visual predators at high latitudes related to sea-ice decline (Figure 5). Small changes in Arctic sea-ice conditions invoke complex nonlinear responses: Ice-albedo feedbacks accelerate the melt process nonlinearly (Curry, Schramm, & Ebert, 1995; Landy, Ehn, & Barber, 2015), reduced snow cover and ice thickness will increase light penetration exponentially (Fig. S5), the contribution of daily irradiance to the annual light budget becomes increasingly nonlinear at high latitudes (Clark et al., 2013) and visual search scales nonlinearly with increasing visual range (Figure 7). Hence, a quadrupling of the visual range following the loss of the high-Arctic perennial ice cover (Figure 5) will increase clearance rate of cruise predators by a factor of 16. Increased search efficiency, especially at low prey densities, is therefore very likely to increase zooplankton mortality.

Consequently, the ecological impacts of minor changes in light can be expected to be disproportionately large and are tightly interwoven with prey availability. Hence, we argue that a basin wide change to the visual foraging landscape following sea-ice loss can contribute to climate-driven regime shifts in the Arctic marine ecosystem. Projections foresee a transition to a nearly ice-free ($SIE < 1$ M km$^2$) AO during summer before mid of the century. But sea-ice extent is declining even faster than models predict (Overland & Wang, 2013). Therefore, not only the effect of increased light on productivity but also top-down effects of visual foraging should be regarded as a candidate mechanisms along with the range of identified environmental and biological tipping elements (Duarte et al., 2012).

A reorganizations of the Arctic marine food web seems imminent, given the anticipated phenological shifts (Ji et al., 2013) the potential for ecological mismatches (Søreide, Leu, Berge, Graeve, & Falk-Pedersen, 2010), the large-scale loss of the sea-ice habitat (Stirling & Derocher, 2012), and the changes in species interaction strength as boreal species are shifting northwards (Fossheim et al., 2015). In the Arctic and sub-Arctic pelagic ecosystems, planktivorous fish such as polar cod *Boreogadus saida* and capelin *Mallotus villosus* are central to the food web (Kortsch et al., 2015), because they channel the energy transfer from lipid-rich invertebrates at the base of the food chain, to higher trophic levels (Hop & Gjøsæter, 2013). Therefore, any change in forage fish abundance and distribution, or change in interaction strength, is thought to redirect energy flows (Stempniewicz, Błachowiak-Samołyk, & Węsławski, 2007) with cascading effects along the food chain (Frank, 2005; Kortsch et al., 2015). In the pacific Arctic, the northward shift of the pelagic-dominated ecosystem of the southern Bering-Sea has been linked to a weakened pelagic-benthic coupling (Grebmeier et al., 2006). This change in energy fluxes highlights the importance to understand the role of visual predation in the pelagic to anticipate the complex evolution of future food webs in a changing AO.

Predation by visual planktivores affects the size structure and trait distribution of zooplankton communities, both on short time-scales, such as after introductions to fish-less lakes, and on evolutionary time-scales. Large-bodied and conspicuous individuals are vulnerable to predation from planktivorous fish (Brooks & Dodson, 1965). Copepod species within the Arctic *Calanus* complex exhibit intra- and interspecific Bergmann clines (Leinaas et al., 2016) accompanied by life-history differences for traits such as generation time and energy reserves (Sainmont, Andersen, Varpe, & Visser, 2014). Kaartvedt (2000) relates the success of large Arctic copepods with slow life histories (e.g. *C. hyperboreus* with a 5-year life cycle) to a reduced visual predation pressure at high latitudes. While further south, under higher predation pressure from abounding visual predators, the smaller sized congeneric *C. glacialis* and *C. finmarchicus* with shorter life cycles perform better. If boreal planktivores enforce a size selective predation regime, this will be to the detriment of the large native copepods, while small boreal newcomers might expand northwards under predatory release. Life histories preadapted to a lengthening of the ice-free season and increasing temperatures might further facilitate the northward expansion of the boreal zooplankton community.

## 4.4 | Outlook and concluding remarks

Our mechanistic reasoning and modelling can also be applied to investigate the inverse effect on optical conditions under climate change, namely an increase in turbidity, as it might be expected due to higher chlorophyll concentrations (Arrigo et al., 2008) or changes in water clarity related to river discharge as discussed in Dupont and Aksnes (2013). Further, the insights of this study can be generalized and applied to other visual predators in the pelagic realm, such as large zooplankton (krill and amphipods) and seabirds. The mechanistic link between changed optical conditions, light and foraging is equally relevant to other aquatic systems (e.g. Hedström, Bystedt, Karlsson, Bokma, & Byström, 2017). Alpine and high latitude lakes, where species across several trophic levels also are governed by extreme light regimes (Kahilainen, Malinen, & Lehtonen, 2009), experience changes to ice cover (Magnuson et al., 2000) similar to those in the oceans. Although few lake systems are large enough to experience lateral migratory shifts, changes in optical conditions will alter vision-based foraging and vision-based predation risk, with ecological and evolutionary consequences.

To confront our large-scale projections with observation (sensu Hilborn & Mangel, 1997), we deem case studies where model data are compared against spatially and temporally resolved field data, paired with field or aquarium experiments, to be the most promising approach. Lakes in the sense of semiopen and controllable environments with limited room for range expansions can provide suitable natural laboratories.

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## SUPPORTING INFORMATION

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# PAPER II

**Langbehn TJ, Aksnes DL, Kaartvedt S, Fiksen Ø & Jørgensen C**

Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient

in review *Marine Ecology Progress Series*

# Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient

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***Keywords*** — Antipredation window | deep scattering layer | photoperiodic constraint hypothesis | high-latitude | Myctophidae | ocean twilight zone | Norwegian Sea

## Abstract

Throughout the oceans, small fish and other micronekton migrate between daytime depths of several hundred meters to near surface waters at night. These diel vertical migrations of the acoustic deep scattering layer formed by mesopelagic organisms structure pelagic ecosystems through trophic interactions, and are a key element in the biological carbon pump. However, depth distributions and migration amplitude vary greatly. Suggested proximate causes of the migration such as oxygen, temperature, and light often correlate and therefore the causal underpinnings have remained unclear. Using mesopelagic fish and the Norwegian Sea as a study system, we developed a dynamic state variable model that finds optimal migration patterns that we validate with acoustic observations along a latitudinal gradient. The model allows us to disentangle the drivers of migration and make predictions about depth distribution and related fitness consequences along a latitudinal trajectory with strong gradients in environmental drivers and vertical distribution of scattering layers. We show that a light comfort zone similar to that observed emerges from ultimate factors involving survival and maximization of Darwinian fitness and that temperature regime, in comparison with light regime, has little effect on distributional patterns. According to the model, water clarity, which limits how deep light can penetrate into the ocean, structures daytime depths, while surface light at night controlled the depth of nocturnal ascents. This has implications for the distribution in seasonal light environments. Identifying drivers of the observed acoustical distribution of mesopelagic fish in

further datasets requires that surface light and light attenuation be measured accurately and routinely.

# Introduction

The mesopelagic is the daytime twilight zone in the world oceans. The ecology here is a game of hide and seek, where organisms with limited swimming ability, e.g. micronekton such as small fish, crustaceans, and siphonophores, try to avoid encounters with larger predators, mainly bigger fish and squid. Mesopelagic micronekton are an important link in the pelagic food web (Dagorn *et al.*, 2000, Connan *et al.*, 2007, Naito *et al.*, 2013) and might play a crucial role in mediating climate change effects through the sequestration of carbon into the deep ocean (Davison *et al.*, 2013, Aumont *et al.*, 2018). Revised estimates suggest that the mesopelagic zone, from ca. 200-1000 m depth, harbours the majority of the global fish biomass (Irigoien *et al.*, 2014). These diverse midwater assemblages make up the deep scattering layer (DSL), which distribute across all major oceans from the tropics to sub-Arctic latitudes (Gjøsaeter & Kawaguchi, 1980, Sutton *et al.*, 2017).

In synchrony with the day-night cycle, the DSL rises and falls in the water column (Bianchi & Mislan, 2016), often spanning several hundred meters in depth (Klevjer *et al.*, 2016). About half of all mesopelagic micronekton, possibly more than 5000 million tons, takes part in this diel vertical migration (Irigoien *et al.*, 2014, Klevjer *et al.*, 2016). This makes the daily vertical movement of mesopelagic organisms the largest migrations of living biomass on the planet.

The depth range of the DSL migration varies greatly (Bianchi *et al.*, 2013a, Klevjer *et al.*, 2016). The daytime sound scattering layer is closer to the surface in the northern Indian Ocean, the central Atlantic Ocean, and the North and eastern tropical Pacific, than in the subtropical gyres, the central Indian Ocean, the western tropical and southeast Pacific, and the Pacific sector of the Southern Ocean (Bianchi *et al.*, 2013a, Klevjer *et al.*, 2016). Some studies suggest these basin-scale patterns can be explained by the distribution of dissolved oxygen, with shallower migration depth in hypoxic areas (Koslow *et al.*, 2011, Bianchi *et al.*, 2013a, Netburn & Anthony Koslow, 2015). Mesopelagic organisms forming the DSL, however, did not avoid oxygen-depleted waters. In contrast, in areas with oxygen minimum zones, these mesopelagic organisms appeared at hypoxic or even anoxic depths (Tont, 1976, Bianchi *et al.*, 2013b, Klevjer *et al.*, 2016, Aksnes *et al.*, 2017), suggesting no direct causation between their depth distribution and dissolved oxygen.

Light penetration offers a parsimonious, mechanistically comprehensible, and universal explanation for DSL depth distribution. Light was among the first drivers suggested to structure DSL depth (Kampa, 1975, Dickson, 1972, Tont, 1976). Since then, various lines of evidence have converged, pointing towards light being a first-order driver of DSL behaviour and therefore the most defining environmental factor for mesopelagic ecosystem structure (Kaartvedt *et al.*, 2019). This relates to short-term perturbations in surface light like changes in weather (Barham, 1957, Balino & Aksnes, 1993, Kaartvedt *et al.*, 2017) and solar eclipses (Backus *et al.*, 1965, Tont & Wick, 1973, Kampa, 1975), small-scale spatial variations in waters of changing transparency (Abookire *et al.*, 2002, Norheim *et al.*, 2016), as well as global relations between water clarity and DSL distributions (Aksnes *et al.*, 2017). When corrected for light attenuation, DSL along a circumglobal transect were found within a narrow range of light intensities (Aksnes *et al.*, 2017), also referred to as optical depth or light comfort zone (Røstad *et al.*, 2016b,a). With better vision at dim light and smaller prey than their predators, mesopelagic fish might be able to exploit light comfort zones as an antipredation window, so that their search efficiency is maximized relative to the mortality risk from visually feeding piscivores (Clark & Levy, 1988, Scheuerell & Schindler, 2003). A proximate light comfort zone mechanism has been suggested to control DSL depth in the Norwegian Sea, but the potential role of temperature in governing DSL distribution patterns could not be excluded (Norheim *et al.*, 2016).

Deep scattering layer depth also varies with latitude (Beklemishev, 1981). There are strong latitudinal gradients in seasonality of surface light irradiance and day length. Moving poleward, the 24 h light cycle gradually changes into a seasonal light regime with little variation in light intensities over the diurnal cycle. During the Arctic summer, the sun never sets, and it may not rise for months at a time during the polar night. These patterns have strong implications for the vertical extent of the twilight zone (Kaartvedt *et al.*, 2019). Consistent with the assumption that light penetration structures vertical migration depth (Aksnes *et al.*, 2017), the DSL was deeper during summer at higher latitudes, where migration was of smaller amplitude and not as distinct (Sobolevsky *et al.*, 1996, Norheim *et al.*, 2016).

In this study, we aim to unravel the role of light in structuring the depth distribution of mesopelagic fishes, with a particular emphasis on latitudinal gradients and the associated change in light regime towards high latitudes, using the Norwegian Sea as a case study. We use dynamic programming (Mangel & Clark, 1988, Houston & McNamara, 1999) to predict optimal migration behaviour of mesopelagic fish, here parametrized for the myctophid *Benthosema glaciale*. We first run the model for the environment observed during a cruise along a latitudinal transect where diel vertical migration of the DSL changed depth and amplitude (Norheim *et al.*, 2016). Since temperature affects metabolic rates in ways that can affect vertical distributions (Rosland & Giske, 1994, Sims *et al.*, 2006), and temperature and light often co-vary across depth and latitude, a primary aim is to disentangle the role of light and temperature in how they influence and constrain mesopelagic organisms. We then rerun the model while varying surface irradiance, temperature, and light attenuation to contrast the effects of these drivers. Our model is built on simple, well-understood and quantifiable mechanisms (Fig. 1), i.e. visual encounter of prey and predators (Eggers, 1977, Aksnes & Giske, 1993) and temperature-dependent bioenergetic processes (Killen *et al.*, 2010).

# Material & Methods

## Study location and latitudinal gradients in the environment

We use a detailed dataset of vertical CTD profiles and continuous (day and night) surface light measurements (Norheim *et al.*, 2016) as direct drivers of the model (Fig. 1). Measurements were taken from May 1 to June 14, 2013, along a cruise track across the Norwegian Sea (63.77°- 68.8° N), from the Norwegian shelf break in the southeast, across the Arctic Circle, to the Icelandic plateau in the northwest (Fig. 2A). Water temperature, water clarity and surface light intensities all showed marked south to north gradients

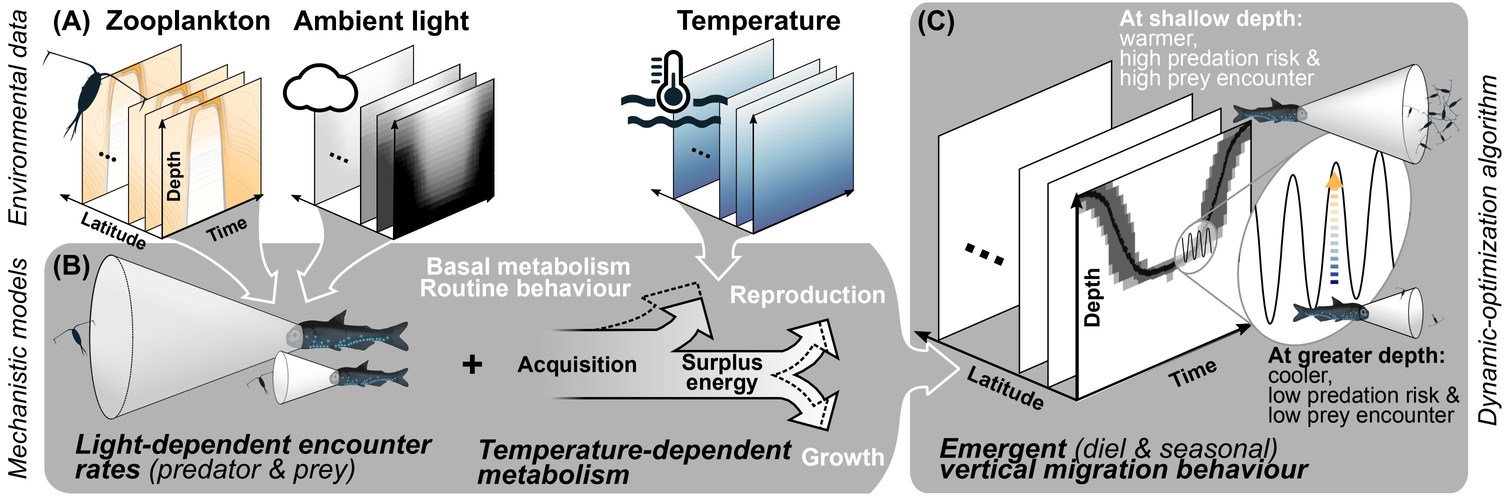

**Figure 1:** Schematic model overview showing the links between environmental data **(A)**, two mechanistic models **(B)** and the dynamic optimization algorithm **(C)**. Mesopelagic fish need to forage to avoid starvation and their encounter rates, both with predators and prey, depend on the ambient light and the abundance of prey and predators. Temperature controls how fast ingested food can be digested, how much acquired energy is needed for routine metabolism, and consequently how much can be allocated to surplus resources. Optimal diel and seasonal vertical migration strategies then emerge from the model as individuals solve these trade-offs in order to maximize fitness.

(Fig. 2B-D), and the timing was right before the onset of the midnight sun period in the northernmost part of the transect. The gradient in the hydrography and light regime was associated with a deepening of the DSL and a decrease in the diel vertical migration amplitude at higher latitudes (Fig. 2E, echogram in the background).

## Model overview

We use dynamic programming (Mangel & Clark, 1988, Clark & Levy, 1988, Houston & McNamara, 1999) to find state-dependent optimal life-histories and vertical migration behaviour of mesopelagic fish throughout the annual cycle in a 1D water column environment (Fig. 1). We run the model for the full annual cycle. The model is fully mechanistic and consists of two primary components. First, a backwards iteration procedure where optimal behavioural decisions are identified assuming that individuals maximize surplus energy as a proxy for Darwinian fitness. Thereafter we track single individuals in a forward simulation as they follow the optimal behavioural strategies, and these emergent behaviours and the associated state dynamics are visualized.

A full model description with all equations presented in detail is provided in the supplementary material, along with model terms and parameters summarized in Tab. S1. Below, we provide a verbal summary.

## State dynamics

We use two physiological states to describe mesopelagic fish; 1) reserve size - a metabolically active long-term energy store, and 2) gut fullness - the energy contained in the digestive system. State values are updated every time step, which in the current analysis is one hour. The gut dynamics are governed by consumption and digestion. Mesopelagic fish fill their guts by foraging and the gut size constrains how much food can be consumed. Gut evacuation is temperature dependent, as higher temperatures increase the rate at which consumed food is digested and energy is made available to the organism. Instantaneous metabolic demands, i.e. metabolic rate, also increase with temperature. If the net energy balance is negative then energy stores are drained, and individuals that have depleted their reserves die from starvation. If, however, the net energy balance is

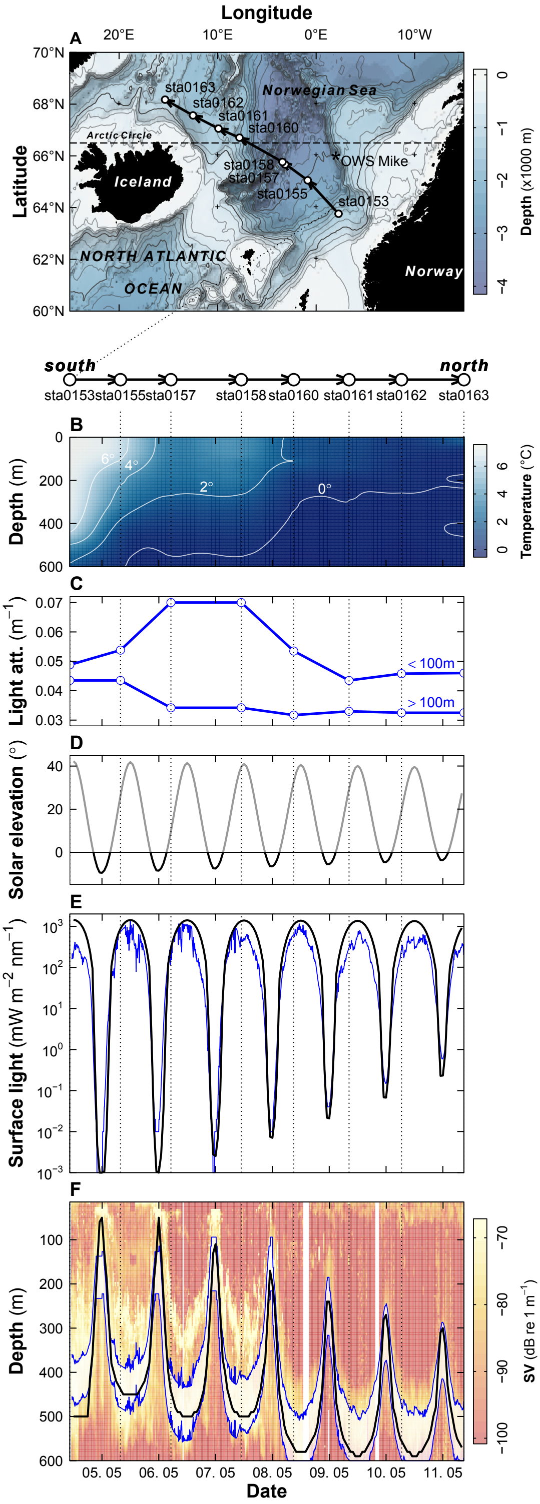

**Figure 2:** Observations along a southeast to northwest cruise track across the Norwegian Sea during May 2013 **(A)** there was variation in temperature **(B)**, water clarity, here displayed as light attenuation, **(C)**, the angle of the sun relative to the horizon **(D)**, surface light **(E)** and depth of the mesopelagic scattering layer (**F**, underlying echogram ). Using the empirical observations as environmental drivers, our model predicts optimal migration depth for the glacier lanternfish *Benthosema glaciale* (**E**, fat black lines) that fit the observed backscatter distribution and predictions about the light comfort zones (envelop marked by thin blue lines). Blue lines in panel C to F denote observations from Norheim *et al.* (2016) and black lines our model predictions.

positive, reserves are replenished and once they are filled, remaining energy is allocated to surplus which in our model is the fitness proxy and thus what is maximized.

## Trade-offs

Encounters with both prey and predators are dependent on vision (Eggers, 1977, Aksnes & Giske, 1993). Steep vertical gradients, particularly in light, which declines exponentially with depth, characterize the pelagic habitat. Visual foraging is therefore more efficient close to the surface. Foraging where or when there is more light to maximize encounter rates will, inherently, also increase the efficiency of other visual predators such as birds and predatory fish, resulting in increased predation risk.

This trade-off is state-dependent. Life history theory predicts that starving individuals with empty guts and low reserves are more likely to accept risks, and expose themselves to higher light intensities and predation risk, while a satiated individual can afford to shelter in the dark and digest its meal. Digesting in deep and dark waters reduces predation risk, but the deep is usually colder, which prolongs the time between foraging events. There is thus a trade-off between safe versus fast digestion, which affects survival and net energy gain and therefore is crucial to fitness.

## Backwards optimization and forward simulation

Foraging and life history theory predicts that mesopelagic fish should reside at the depth that resolves the trade-offs arising along the depth axis. The common currency underlying behavioural decisions is fitness. Here, we define fitness as expected surplus energy gain – the energy the individual potentially could channel towards reproduction if it avoids predation and remains alive. The optimal state- and time-dependent depth position maximizes this fitness measure. We work out optimal depth choices for all state and time combinations through backward iteration, starting from the end of the season when no future surplus is expected and fitness becomes zero. This allows us to calculate fitness in the previous time step, and we continue to iterate this process backwards from the final to the first time step, by replacing the terminal fitness function with fitness in the previous time step and so on. The backwards iteration procedure results in a complete matrix with optimal depth choices for all state combinations. Repeating the backwards procedure multiple times allows behavioural strategies to converge and become independent of terminal effects due to the time horizon (see e.g. Houston & McNamara, 1999).

Vertical migration strategies then emerge from the model once we simulate the optimal state-dependent depth positions found in the backwards procedure forward in time, using observation from the cruise as environmental drivers. We run 100 years in the forward simulation and show the last one to avoid effects of assumed initial states.

## Resolution

One time step of the model corresponds to one hour and we model the behaviour for a full annual cycle from the beginning of January to the end of December. Fish can migrate and adjust their vertical position by up to 100 m in one time step (corresponding to a vertical migration speed of $0.03\,\mathrm{m{\cdot}s^{-1}}$, and the model is constrained between the surface and 1000 m depths. We compute the light environment for every time step, whereas we update zooplankton densities and their vertical distribution daily. Aside CTD casts taken along the cruise track we lack temperature observations. Therefore, we resorted to the simplifying assumption that temperature profiles were constant through the year.

## Model validation

The observational dataset (Norheim *et al.*, 2016) provides a unique opportunity to test the influence of light on DSL depth and to validate our model for a range of environmental settings. Continuous light measurements, including nocturnal illumination, alongside acoustic observations and other relevant environmental factors (e.g. temperature) allowed for the rare opportunity of a one-to-one comparison of model predictions with observations, across environmental gradients and down to an hourly resolution. Here, we combine eight model runs to cover the full latitudinal gradient from 63.77 to 68.8° N (Fig. 2A). At each discrete latitude, we run the model for the full annual cycle of 365 days. We then select a single day from every run, beginning with May 3 and progressing to May 11 with increasing latitude, and merge them to a continuous transect to compare with observations. Because we can anchor our model to observations, at different time resolutions, latitudes and environmental settings such as the increasingly lighter nights above the Arctic Circle, this increases the confidence in future predictions made for other localities and times of the year.

### Sensitivity analysis

We run two types of sensitivity analyses. First, we use one-factor-at-a-time sensitivity analysis with ±20 % variation in default parameter values to confirm that our predictions were robust to variation in environmental, ecological, and physiological parameters. In total, we tested model sensitivity to 26 parameters, resulting in 70 model runs (doubling occurs because some parameters, such as eye sensitivity, describe both predators and prey). Secondly, we tested the effect of removing latitudinal gradients in the environment, which will help us disentangle the relative effects of specific drivers on the predicted vertical migration behaviour. We used a $2 \times 3$ full factorial design with temperature, water clarity, and surface light as factors. We removed latitudinal gradients by substituting the changing environments along the cruise track with the same temperature, light or optical conditions for all latitudes. For that we used the light and optical conditions from the start of the transect, and fixed temperature to 7 °C, which consequently also removed the vertical temperature gradient.

## Results

### Confronting model predictions with observations

The model predicts the depth and vertical movements of the DSL with high fidelity to observations (Fig. 2F), and was robust to variation in initial parameter choice (Fig. S2). We predict a gradual deepening of the DSL from around 450 m daytime depth at latitudes <65° N, to almost 600 m at 68° N. At the same time, nighttime ascents reached 50 m in the south, but where halted at 300 m depth at the northernmost station. Consequently, the migration amplitude was truncated by around 100 m at higher latitudes, because the deepening of the scattering layer distribution was more pronounced at night than during day (Fig. 2F).

The deepening of the DSL correlated with a latitudinal change in light regime (Fig. 2D). During the eight-day cruise crossing the Arctic Circle, nights grew shorter, from around 7 hours between sunset and sunrise in the south to around 4 hours in the north. In part, this increase in day length was seasonal. North of the Arctic Circle, civil twilight persisted through the night, with nocturnal light intensities three orders magnitude higher than at the beginning of the transect (Fig. 2E).

## Deep scattering layer depth in relation to light

The migration depth of the modelled fishes was highly responsive to changes in the environment; particularly light (Fig. 3). Along the cruise track there was clearer water towards the north (Fig. 2C), and light therefore penetrated deeper, which explained change of the observed daytime depth of the DSL. When the more turbid water from the southernmost station was applied in the model throughout an otherwise equal transect, the observed day-time deepening towards higher latitudes no longer occurred in the simulation (Fig. 3C). Another effect of light was the arrest of nighttime ascents at greater depths with increasing latitude, which in the model resulted from lighter nights (Fig. 3B). In a scenario run where we controlled for both light and water clarity, nighttime depth shifted closer to the surface under higher temperatures (Fig. 3D). Although we adopted the light environment from one specific latitude, including its diel and seasonal variation, across all latitudes, the shallowest nighttime depth slightly decreased with increasing latitude, which in this case can be attributed to progressing date and therefore lighter nights closer to midsummer.

On average, our model predicts the DSL to deepen by 68 m for each order of magnitude increase in surface light at midnight, which is consistent with observations (Fig. 4A, solid versus broken regression lines). The model predicted crepuscular migrations that were synchronized with incoming solar radiation. This resulted in constant ambient light levels of the fishes (Fig. 4B) despite several orders of magnitude variation in surface light. The model predict a relatively narrow light comfort zone between $1.6 \times 10^{-6}$ and $2.1 \times 10^{-6}\,\mathrm{mW{\cdot}m^{-2}{\cdot}nm^{-1}}$ at 486 nm, calculated as light intensity in the 25 % to 75 % quantile range, and an average of $1.9 \times 10^{-6}\,\mathrm{mW{\cdot}m^{-2}{\cdot}nm^{-1}}$ at 486 nm.

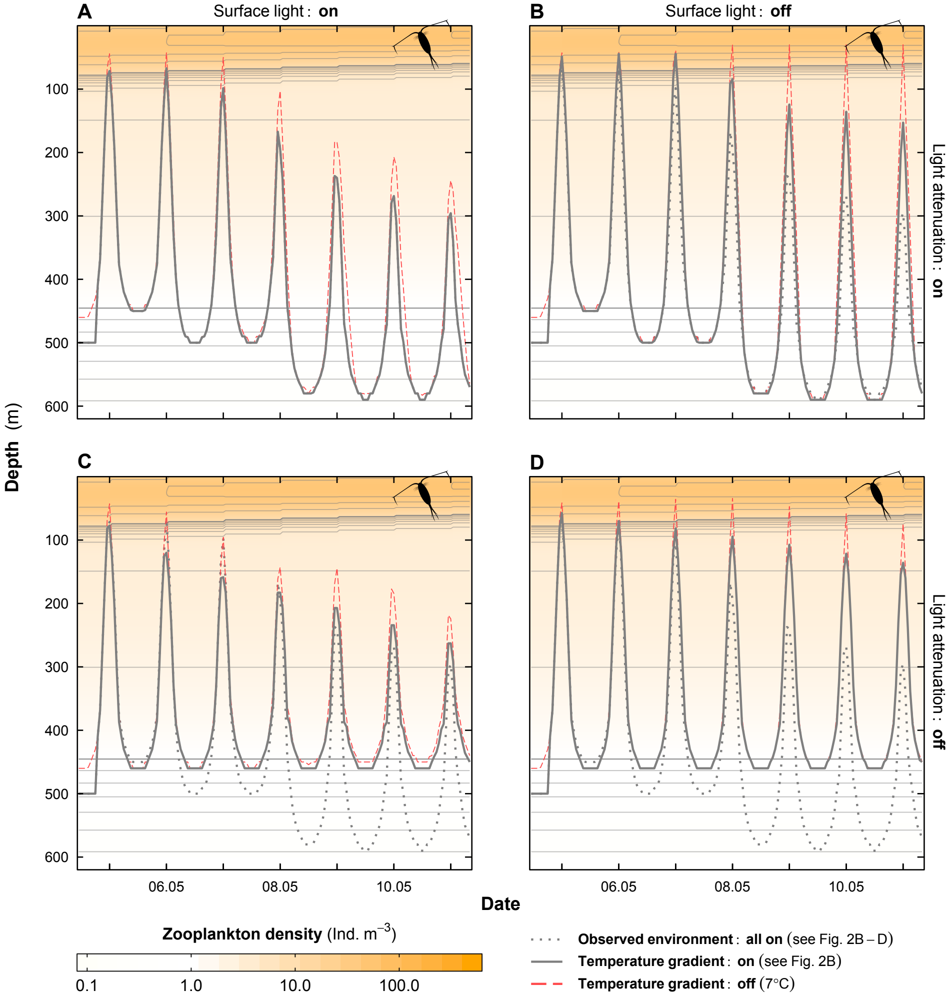

**Figure 3:** Predicted migration depth of *Benthosema glaciale* with (solid grey lines) or without (dashed red lines) latitudinal temperature gradients, for the default light environment **(A)** in comparison with model runs where latitudinal gradients in either surface light **(B)**, or light attenuation **(C)**, or both **(D)** where eliminated. This full factorial setup shows that surface light intensities explain nighttime depth, while daytime depth was dependent on water clarity, i.e. light attenuation. Temperature had only a secondary effect on the deep scattering layer depth distribution. The deeper distribution of the mesopelagic scattering towards the end of the transect shows that mesopelagic fish above the Arctic Circle are prevented from approaching near-surface layers where their food is (see also Fig. S1).

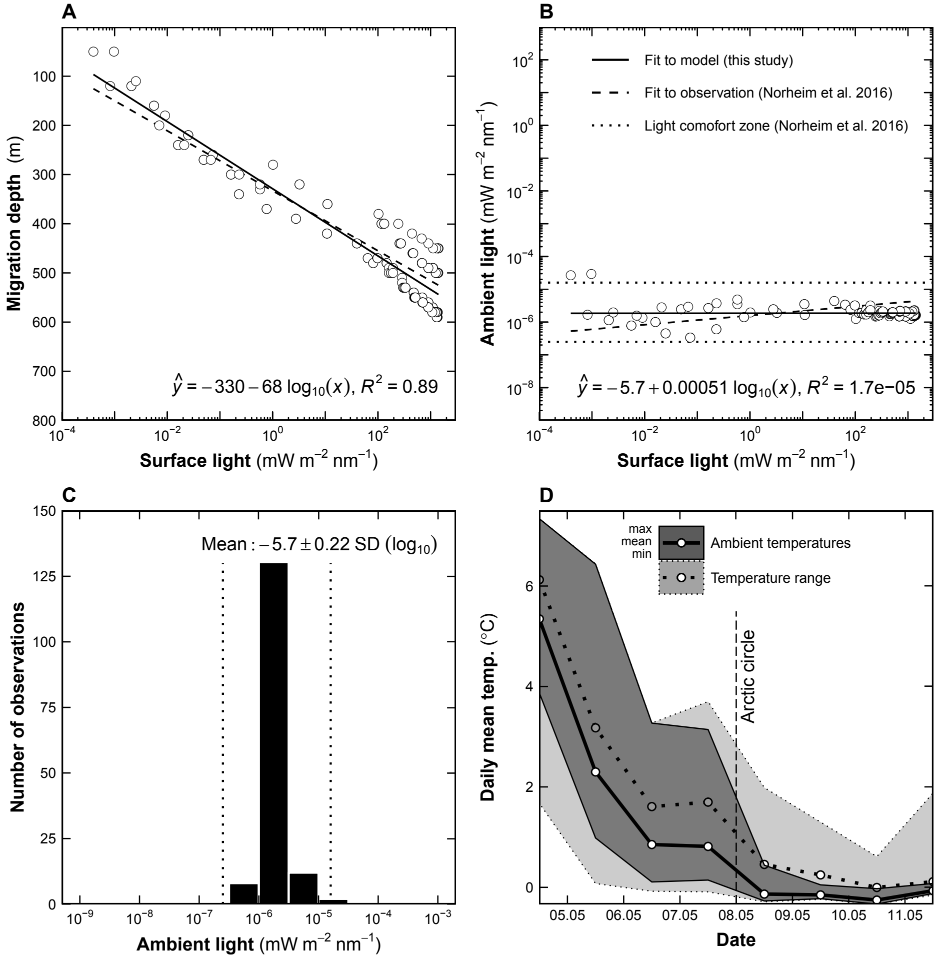

**Figure 4:** Predicted vertical migration depth of *Benthosema glaciale* **(A)**, and ambient light for a given depth **(B)** as a function of surface light (mW·m$^{-2}$·nm$^{-1}$ at 486 nm). The model predicts mesopelagic fish to inhabit a narrow range of light intensities around $1.9 \times 10^{-6}$, or $10^{-5.7}$, mW·m$^{-2}$·nm$^{-1}$ at 486 nm. **(C)**. On average, vertical distribution deepened by 68 m for every order of magnitude increase in surface light (solid regression line and equation in panel A). The average ambient, i.e. experienced, temperatures during a diel vertical migration cycle where close to the daily average temperature environment **(D)**. Modelling results (solid regression line) are compared with observations (dashed regression line) from Norheim *et al.*, 2016 (see their Fig. 4).

### Deep scattering layer depth in relation to temperature

Our simulations show that temperature was of minor importance in controlling depth distribution of the observed DSL (Fig. 3A). Temperature had practically no influence on the simulated DSL daytime depth and minor influence on nighttime depth. Only in a stratified water column, as found at the southernmost part of the transect (Fig. 2B, see May 4), did the model suggest that there was an opportunity for mesopelagic fish to exploit temperature gradients by descending below the thermocline. This would bring them deeper than what could have been expected from ambient light and the light comfort zone (Fig. 2B and F, Fig. 3), to reduce metabolic loss in cold water. Migrations below the thermocline were, however, not evident from the observations. With increasing temperatures, nighttime depth distributions shifted closer to the surface, particular at times when light summer nights constrained mesopelagic fish to greater depth at night (Fig. 3).

Predicted ambient temperatures, averaged over a full 24 h diel vertical migration cycle, closely tracked the general decline in temperatures towards the north (Fig. 3D). The range of experienced temperatures during diel vertical migration differed for latitudes below and above the Arctic Circle. Below the Arctic Circle, experienced temperatures reached the upper temperature extremes in the environment but never extended into the coldest waters. The opposite was true for latitudes above the Arctic Circle (Fig. 3D).

## Discussion

Our results show that ambient light is the main factor determining the DSL depth, substantiating earlier studies pointing to light as a first-order driver. Our dynamic optimization approach allowed us to disentangle the relative importance of co-varying environmental factors. The model thus preempts temperature and confirms light as a first-order driver controlling migration amplitude and depth in mesopelagic fish. Variation in ambient light of the DSL organisms depends on surface light and water column light penetration, and these two have different effects on vertical distributions and migrations.

Our model predicts vertical migration strategies for mesopelagic fish that in timing, amplitude, and diel depth distribution are consistent with acoustic observations of the DSL

Fig. 2F). We predict the scattering layer depth to deepen by 68 m for each 10-fold increase in surface light, which is close to an estimate of 61 m based on acoustic observations from the same trajectory in the Norwegian Sea (Norheim *et al.*, 2016). Observations from the northern end of the transect further support our predictions that with increasing latitude, the DSL during summer becomes increasingly constrained to greater depth, and vertical ascents at night are arrested several hundred meters below the surface, a behaviour that has been observed in previous studies (Sameoto, 1989, Sobolevsky *et al.*, 1996, Siegelman-Charbit & Planque, 2016, Gjøsæter *et al.*, 2017, Knutsen *et al.*, 2017).

The simulations predict optimal ambient light intensities for our parameterization of the myctophid *B. glaciale* around $1.9 \times 10^{-6}\,\mathrm{mW{\cdot}m^{-2}{\cdot}nm^{-1}}$ at 486 nm, which is near identical to ambient irradiance of $2.0 \times 10^{-6}\,\mathrm{mW{\cdot}m^{-2}{\cdot}nm^{-1}}$ at 486 nm at the median DSL depth calculated based on observations (Norheim *et al.*, 2016). When integrated over the spectrum, this corresponds to a total ambient irradiance of $1.9 \times 10^{-7}\,\mathrm{\mu mol{\cdot}m^{-2}{\cdot}s^{-1}}$ (Norheim *et al.*, 2016), which matches observations from a global transect, predicting a LCZ around $10^{-7}\,\mathrm{\mu mol{\cdot}m^{-2}{\cdot}s^{-1}}$ with a span from $10^{-6}$ to $10^{-9}\,\mathrm{\mu mol{\cdot}m^{-2}{\cdot}s^{-1}}$ at the 25 % to 75 % quantile DSL depths (Aksnes *et al.*, 2017).

Our predictions about a narrow light comfort zone could lead to the misguided interpretation that mesopelagic organism should form dense aggregations. One caveat of optimality models is, however, the difficulty to account for density-dependence (Houston & McNamara, 1999). In an environment with limited resources, and where aggregations make the prey an easier target for predators, deviating from the apparent optimal strategy might increase fitness. Therefore, predicted optimal strategies must be understood as population means, and observed light comfort zones might be wider than our predictions when such density-dependent effects are factored in. Additionally, light comfort zones will differ between species, length classes, and different predator-prey pairings due to differences in the light thresholds of their visual systems, of which we model only one. These differences contribute to the broad DSLs as seen from acoustic observations and may explain the co-occurrence of multiple scattering layers with discrete vertical distributions (Røstad *et al.*, 2016b,a).

Temperature is certainly the environmental factor most widely invoked in explaining species distributions (Burrows *et al.*, 2011, Sunday *et al.*, 2012), and has been shown, among others, to be a proximate cause for vertical migration depth in fish (Levy, 1990, Sims *et al.*, 2006, Busch *et al.*, 2011) and copepods (Fiksen & Giske, 1995, Bandara *et al.*, 2018, and referecnes therein). Here we find, however, little evidence for a temperature optimum or a bioenergetic basis of migration depth in mesopelagic fish. The DSL depth was largely independent of temperature, and diel vertical migration emerged as the optimal fitness-maximizing strategy in the absence of vertical or latitudinal temperature gradients (Fig. 2B and F, Fig. 3). Environments with steep temperature gradients might be the exception. In this case, migrating to the cold side of the thermocline could add to fitness by reducing metabolic costs, in particular if prey is limiting (Fig. 2B, see 4 May).

Species in terrestrial and marine systems respond to global warming by shifting their distribution, not only laterally but also to higher elevations or greater depth in the oceans (Dulvy *et al.*, 2008, Pinsky *et al.*, 2013, Fossheim *et al.*, 2015). The predicted shift to shallower and warmer waters under increased temperatures (Fig. 3) may hence seem counter-intuitive at first, but can be explained by the interaction of light and temperature in the Norwegian Sea. One implication of tracking a light comfort zone is that mesopelagic fish maintain the same search efficiency over time, day and night. However, at polar latitudes, there is little circadian variation in light levels during summer and winter. The relative diel change in surface light during light summer nights in the Arctic is sufficient to shift light comfort zones and therefore induce diel vertical migration, but mesopelagic light preferences prevent them from coming close to the surface during much of the productive season (Fig. 2). Since their prey remain close to the surface, mesopelagic fish may struggle to find sufficient food at increasing latitudes with a deepening of the mesopelagic zone during summer. This finding is consistent with the photoperiodic constraint hypothesis, suggesting that the lack of overlap between mesopelagic light comfort zones with prey depth distributions (Kaartvedt, 2008, Kaartvedt & Titelman, 2018), and not necessarily just temperature constraints (Escobar-Flores *et al.*, 2018), may exclude mesopelagic fish from polar latitudes.

Understanding mesopelagic distribution has also been the focus of recent attempts to classify the global biogeography of the mesopelagic zone (Sutton *et al.*, 2017, Proud *et al.*, 2017, Sayre *et al.*, 2017, Reygondeau *et al.*, 2018). These papers have focused on the environmental drivers primary production, temperature, and surface wind stress, but have not included light despite a long history of compelling observational studies (i.a. Kampa, 1971, Dickson, 1972, Tont, 1976, Aksnes *et al.*, 2017). Therefore, one important insight that follows from our model analysis is that we currently do not routinely measure and consider what emerges as the first order driver of mesopelagic ecology, namely ambient light (Kaartvedt *et al.*, 2019). Because temperature is routinely measured or is easily available from hydrographic data bases and models it is, almost without exception, included as an explanatory variable in all contemporary marine studies. Light data is, in contrast, sparsely available, and particularly nighttime values (Kaartvedt *et al.*, 2019). There is consequently a need for *in situ* light measurements, at the surface and down to mesopelagic depths, and for studying visual capacity and particular spectral sensitivity of mesopelagic organisms.

We conclude by repeating Dickson (1972): *"it is clear in each case that these controls* [referring to temperature and oxygen] *are no more than modifying influences on migration patterns that are primarily influenced by illumination"*.

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# Supplementary figures

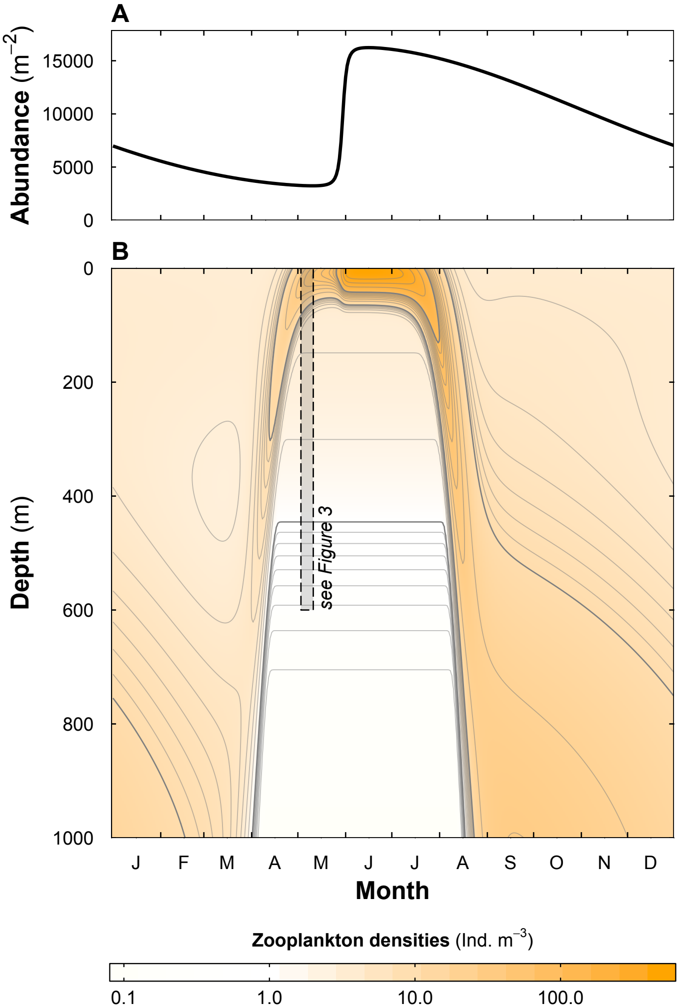

**Figure S1:** Idealised zooplankton prey-field for the southern Norwegian Sea used as model input. Seasonally fluctuating zooplankton abundances (Ind·$m^{-2}$, summed over the upper 1000 m) **(A)**, and zooplankton densities (Ind·$m^{-3}$) **(B)** are compiled from Østvedt, 1955, Heath, 2000, Melle *et al.*, 2004, 2014, Gislason & Silva, 2012 and Gislason, 2018. Note that zooplankton densities are presented on a *log*-scale. The 0.1, 1 and 10 Ind·$m^{-3}$ isoclines are marked with thick grey lines and the shaded area with a dashed outline indicates the timeframe and depth range in Fig. 3.

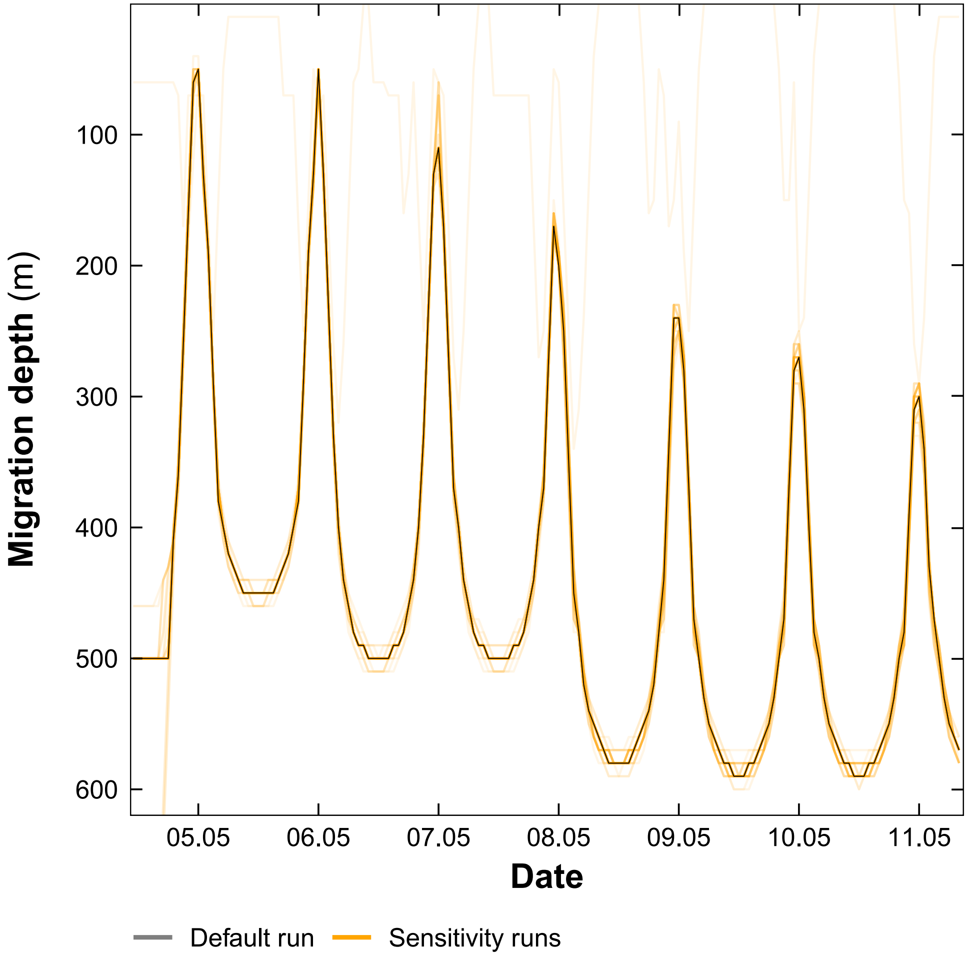

**Figure S2:** Sensitivity analysis, comparing vertical migration depth for the default parametrisation (solid grey line) with 70 runs where 26 environmental, ecological, and physiological parameters were varied, one at a time, by ±20 %.

# SUPPLEMENTARY INFORMATION TO: Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient

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## Supplementary methods

We use state-dependent dynamic programming to model vertical migration behaviour of mesopelagic fish in a 1-D water column environment from the surface to 1000 m depth. We consider a full year divided into hourly increments such that time $t$ is easily calculated from the *day* of the year and the *hour* of the day:

$$t = (day - 1) \cdot 24 + hour \tag{1}$$

It follows that $t = 1$ is 1:00 a.m. on the first day of the year and that the time horizon $T = 8760$ is midnight on day 365.

### State dynamics and survival

Mesopelagic fish are in our model characterized by two dynamic state variables describing the physiological state of the organism: energy reserves and gut fullness. We run the model for a fish of adult body size, so there is no growth. We focus on how individuals with different states face different needs and will therefore make different behavioural decisions in order to maximize fitness.

The state variables are:

**(i)** Energy stores or reserves $R$ [Joules, J] at time $t$, which are a metabolically active long-term storage of energy acting as a buffer that can be used to overcome periods of starvation. Absolute reserve size $R_{\max}$ is a fixed proportion of the energy content of the organism, such that the size of the energy stores is constraint to the range $0 \leq R_t \leq R_{\max}$

for all $t$. The state value of $R$ at $t+1$ depends on the net energy balance $\Delta E$ [J] at time $t$:

$$R_{t+1} = \min[0, \min(R_t + \Delta E_t,\ R_{\max})] \tag{2}$$

Accordingly, reserves are depleted when the net energy balance $\Delta E_t$ is negative, and then $R_{t+1} < R_t$. If, however, $\Delta E_t$ is positive, meaning more food is assimilated than required to fuel routine behaviour and basal metabolism, then reserves are replenished $R_{t+1} > R_t$. Once the reserves are filled $R_t = R_{\max}$ the remainder is *surplus*$_t$ [J] energy:

$$surplus_t = \max[0, \Delta E_t - (R_{\max} - R_t)] \tag{3}$$

We keep track of surplus energy because this energy can be used for growth or reproduction and thus contributes to fitness if the individual is alive.

**(ii)** Gut or stomach fullness $G$ [J] at time $t$. The absolute gut capacity is proportional to body weight such that the size of the gut is constraint to the range $0 \le G_t \le G_{max}$ for all $t$. The gut dynamics from one time step to the next are governed by consumption $C_t$ and digestion $D_t$:

$$G_{t+1} = \max[0, \min(G_t + C_t - D_t)] \tag{4}$$

In every time step we check whether reserves are depleted such that $R_t = 0$, if so the fish dies. However, also fish with $R_t > 0$ may die, if they encounter a predator. We calculate this as a risk of dying following from exposure to predators:

$$survival_{t+1} = \begin{cases} 0, & \text{if } R_t = 0 \\ e^{-M_{t,z}}, & \text{if } R_t > 0 \end{cases} \tag{5}$$

where $e^{-M_{t,z}}$ is the survival probability to the next time step for a given depth $z$, and $M_{t,z}$ is the instantaneous predation rate from visual predators and therefore depends on the ambient light level which varies with depth and time (see below).

## Strategy

The objective of mesopelagic fish in the model is to choose a vertical migration strategy that maximizes their fitness for the period between $t = 1$ and $T$. At every time step $t + 1 < T$, mesopelagic fish choose a new depth $z'$, which is constrained by a maximum vertical migration distance $z_{\Delta\max}$ for every time interval, such that $(z - z_{\Delta\max}) \leq z' \leq (z + z_{\Delta\max})$.

The model environment is vertically structured, with light and temperature decreasing with depth. Fish at different depths will consequently face different fitness trade-offs, e.g. foraging gains vs. predation risk. Hence, any chosen depth $z$ will affect both, its current $survival_{z,t}$ and its state variables in the next time step $G_{t+1}$ and $R_{t+1}$.

We define the fitness function $F_{G,R,z,t}$ as the expected surplus from the current time $t$ until $T$ for any mesopelagic fish at depth $z$, with reserves $R_t$ and gut fullness $G_t$, given that the fish behaves optimally from timestep $t + 1$ onward. Expected surplus is the current surplus and the sum of future surplus, discounted by the chance of mortality.

## Optimization and population simulation

The optimal state- and time-dependent depth position $z$ is that which maximizes the state-related fitness $F_{G,R,z,t}$ at time $t$:

$$F_{G,R,z,t} = \max_{z}[survival_{z,t} \cdot (surplus_{z,t} + F_{G',R',z',t+1})] \tag{6}$$

where $G'$,$R'$,$z'$ are the new state and depth values at the end of time step $t$ and thus the values at the start of timestep $t + 1$.

The stochastic dynamic programming equation (6) is solved by iterating backwards through time from $T$ to $t = 1$ and solving for the suite of depth values to find the strategy (choice of depth) that maximizes fitness, and this is repeated for each of the different state combinations of the mesopelagic fish. We assume that the terminal fitness for all states of $G_T$ and $R_T$, at any depth $z$ at the time horizon $T$ is:

$$F_{G,R,z,T} = 0 \tag{7}$$

because no future surplus can be expected after the season has ended. Since $F_{G,R,z,t}$ depends on $F_{G',R',z',t+1}$ and the terminal fitness at time $T$ is known we can calculate the fitness at time $T-1$.

By replacing the terminal fitness function $F_{G,R,z,t}$ with the fitness function for $T-1$, $F_{G,R,z,T-1}$ we can then also calculate the fitness at $T-2$. Repeating this process to the beginning of the season at time $t = 1$ results in a complete set of optimal depth choices for all state and time combinations. The backwards iteration procedure is then repeated for a second season, $T = 8760$ to $t = 1$, using the fitness function at $t = 1$ from the previous year as terminal fitness function to start with. Repeating the backwards procedure for many years allows behavioural strategies to converge and become independent of the initial terminal reward function and the effects of the time horizon (see Houston & McNamara, 1999).

Finally, state-dependent optimal depth choices derived in the backwards iteration are simulated forwards in time for single individuals, starting at time $t = 1$ until $T$.

## Visual encounter rates and associated trade-offs

In our model, encounters with both prey and predators are dependent on vision, and therefore the ambient light conditions. Foraging where or when there is more light to maximize food intake will, inherently, also increase the sighting distance of predators resulting in increased predation mortality.

We model visual encounter rates $\iota_{z,t}$ as a *Holling type II* functional response:

$$\iota_{z,t} = \frac{\beta_{z,t} \cdot N_{\text{prey},z,t}}{1 + h \cdot \beta_{z,t} \cdot N_{\text{prey},z,t}} \tag{8}$$

where the encounter rates depend on clearance rate $\beta_{z,t}$ [m$^3$·s$^{-1}$·predator$^{-1}$], handling time $h$ [s·prey item$^{-1}$] of the predator and the local prey density $N_{\text{prey},z,t}$ [Ind·m$^{-3}$]. Knowing the weight $W_{\text{prey}}$ [g] and energy content $j_{\text{prey}}$ [J·g·wet weight$^{-1}$] of the prey organism, consumption $C$ [J] then follows given that a fixed prey capture success $p_c$ (proportion) is assumed:

$$C = p_c \cdot \iota_{z,t} \cdot W_{\text{prey}} \cdot j_{\text{prey}} \tag{9}$$

The clearance rate or search rate $\beta_{z,t}$ [m$^3$·s$^{-1}$] depends on the visual range $r_{z,t}$ [m], the swimming speed $v$ [m·s$^{-1}$] and the reactive field angle $_r$ [radians] of the predator:

$$\beta_{z,t} = \pi(r_{z,t} \cdot \sin\theta_{\text{r}})^2 \cdot v \tag{10}$$

We apply a mechanistic model as described by Aksnes & Giske (1993) and Aksnes & Utne (1997) to model visual prey detection range $r_{z,t}$ [m], the distance at which a predator spots its prey, given by the non-linear equation:

$$r_{z,t}^2 \cdot e^{(c \cdot r_{z,t})} = C_{\text{prey}} \cdot A_{\text{prey}} \cdot E' \frac{I_{z,t}}{K_{\text{e}} + I_{z,t}} \tag{11}$$

which can be solved by means of Newton Raphson iteration and derivation, or approximated if $r_{z,t} \leq 0.05\,\text{m}$ using:

$$r_{z,t} \approx \sqrt{C_{\text{prey}} \cdot A_{\text{prey}} \cdot E' \frac{I_{z,t}}{K_e + I_{z,t}}} \tag{12}$$

where $c$ is the beam attenuation coefficient [m$^{-1}$], and the optical properties of the prey organism are: prey contrast $C_{\text{prey}}$ [dimensionless] and the image area $A_{\text{prey}}$ [m$^2$]. $E'$ characterizes the visual capacity [dimensionless], which together with the composite saturation parameter $K_{\text{e}}$ [mW·m$^{-2}$·nm$^{-1}$ at 486 nm] scales the visual range of the predator, and $I_{\phi,z,t}$ is the ambient light for a given latitude $\phi$ [radians], depth $z$ [m], and time $t$.

The eye sensitivity parameter $K_{\text{e}}$ determines the threshold light intensities for efficient search, both in mesopelagic fish as well as in their predators, and therefore is instrumental in calibrating the model predictions to observations as it controls the upper and lower values of the antipredation window. However, $K_{\text{e}}$ is unknown and therefore we here used a value of $10^{-8}$ for mesopelagic fish and $4 \times 10^{-4}$ for piscivores that correspond to the upper and lower ambient light observed for the scattering layer in Norheim *et al.* (2016, see Fig. 4B therein).

We introduced a threshold for non-visual detection to ensure that the prey cannot escape predation completely. Any prey organism closer than the threshold $r_{\text{min}}$ will be detected irrespective of ambient light, assuming non-visual prey sensing:

$$r_{z,t} = \max[r_{\text{min}}, r_{z,t}] \tag{13}$$

The coefficient $E'$ [dimensionless] was calculated such that the visual range $r_{t,z}$ for a given prey organism reaches $r_{\text{max}}$ under optimal light conditions:

$$E' = \frac{r_{\text{max}}^2}{C_{\text{prey}} \cdot A_{\text{prey}}} \tag{14}$$

The image area of the prey organism $A_{\text{prey}}$ [m$^2$] is given by:

$$A_{\text{prey}} = L_{\text{prey}}^2 \cdot S_{\text{prey}} \cdot 0.75 \tag{15}$$

assuming an elliptical body shape, calculated from the length $L_{\text{prey}}$, and length to width ratio $S_{\text{prey}}$ [dimensionless] of the prey organism.

Given that the prey capture success $p_c$ [proportion], the clearance rate $\beta_{z,t}$ [m$^3$·s$^{-1}$] and density of piscivorous predators $N_{\text{prey}}$ [Ind·m$^{-3}$] are known, the instantaneous predation mortality of myctophids $M_{z,t}$ [Ind·timestep$^{-1}$] can then be calculated as:

$$M_{z,t} = p_{\text{c}} \cdot \beta_{z,t} \cdot N_{\text{prey}} \tag{16}$$

## Surface light, light transmission and ambient light

### *Surface light*

The light reaching Earth's surface varies with latitude, time of day, and season. Various degrees of overcast may further modify the incoming light. We calculate irradiance $I$ [W·m$^{-2}$], the solar energy radiation reaching the earth surface, in dependence of the incident or solar elevation angle $\alpha_t$ [°], latitude $\phi$, and time $t$. Remember that time $t$ is defined as a continuous measure of time from $t = 1$ to $T = 8760$, covering a full year in hourly time increments. At low elevation angles, e.g. at higher latitudes or during dusk and dawn, more light is reflected back to the atmosphere and when the sun sinks below the horizon twilight gradually fades into starlight:

$$I_{\Phi,t} = \begin{cases} (i_\mathrm{b} + i_\mathrm{d}) \cdot (1 - 0.62 \cdot c_\mathrm{clouds} + 0.0019 \cdot \alpha_\mathrm{noon}), & \text{if } \alpha > 0 \\ 10^{\left(\frac{1}{e^{-18\cdot-0.07}}\right)}, & \text{if } -18 \leq \alpha_t \leq 0 \\ i_\mathrm{s}, & \text{if } \alpha_t < -18 \end{cases} \tag{17}$$

For $\alpha_t$ when the sun is above the horizon, we adopt calculations used in the HYbrid Coordinate Ocean model HYCOM (Bleck, 2002). Here, $i_\mathrm{b}$ and $i_\mathrm{d}$ denote the beam and diffuse component of the irradiance, respectively, and $c_\mathrm{clouds}$ is the fraction of the sky covered by clouds. Once the sun sets, we interpolate twilight values for $-18° \leq \alpha \leq 0°$ using an exponential decay function, scaled between surface light $I_{\alpha=0}$ and starlight $i_\mathrm{s}$. If the sun sinks lower than 18° below the horizon twilight fades into night and we assume starlight to be the only constant source of background light. We do not account for lunar light. Here, we assumed starlight to be $10^{-9}$ times that of daylight (Ryer & Olla, 1999).

The beam component of the solar radiation $i_\mathrm{b}$ is given by:

$$i_\mathrm{b} = I_\mathrm{E} \cdot 0.07^{\min\left[100, \left(\frac{1}{\cos\theta_\mathrm{z} + 10^{-9}}\right)\right]} \tag{18}$$

where the extra-terrestrial radiation $I_\mathrm{E}$ is calculated from the solar constant 1366.1 $\mathrm{W \cdot m^{-2}}$, the Earth eccentricity $\varepsilon_0$, and the zenith angle $\theta_\mathrm{Z}$:

$$I_\mathrm{E} = 1366.1 \cdot \varepsilon_0 \cdot \cos\theta_\mathrm{Z} \tag{19}$$

The diffuse component of the solar radiation $i_\mathrm{d}$ is given by:

$$i_\mathrm{d} = [(i_0 - i_\mathrm{b}) \cdot (1 - \alpha_{H_2O})] \cdot 0.5 \tag{20}$$

where $a_{H_2O}$ accounts for the absorption by water vapour and ozone.

In this study, we are interested in a narrow band of wavelengths. Light in the ocean becomes increasingly monochromatic with depth, and blue light at  penetrates the deepest.

Here we consider only 486 nm, a wavelength presumably relevant to the visual system of myctophids. We therefore multiply surface irradiance by 0.001, which accounts for the relative contribution at 486 nm to the standard solar spectrum AM0 (ASTM E490) with an integrated value of 1366.1 W·m$^{-2}$. To match observation by Norheim *et al.* (2016), we apply an additional correction factor of 2.05.

### *Astronomical quantities*

Irradiance calculations are based on the sun's position in the sky throughout the year. We calculate the declination angle of the sun $\delta$ [radians] and the earth eccentricity $\varepsilon_0$ [dimensionless] accounting for variation in the distance between the sun and earth over the course of the year as described by Spencer (1971) in e.g. Duffie & Beckman (1991) or Vignola *et al.* (2012):

$$\begin{aligned}\delta = 0.006918 &+ 0.070257\sin(\Gamma) - 0.399912\cos(\Gamma)\\ &+ 0.000907\sin(2\Gamma) - 0.006758\cos(2\Gamma)\\ &+ 0.001480\sin(3\Gamma) - 0.002697\cos(3\Gamma)\end{aligned} \tag{21}$$

$$\begin{aligned}\varepsilon_0 = 1.00011 &+ 0.001280\sin(\Gamma) + 0.034221\cos(\Gamma)\\ &+ 0.000077\sin(2\Gamma) + 0.000719\cos(2\Gamma)\end{aligned} \tag{22}$$

where the day angle $\Gamma$, is derived for a given day $1 \leq d \leq 365$):

$$\Gamma = \frac{2\pi(d-1}{365} \tag{23}$$

The zenith angle $\theta_\mathrm{Z}$ [radians] for a given a latitude $\phi$ [radians] can then be calculate as follows because the declination angle $\delta$ is known:

$$\cos(\theta_\mathrm{Z}) = \sin(\phi)\cdot\sin(\delta) + \cos(\phi)\cdot\cos(\delta)\cdot\cos(\omega) \tag{24}$$

where $\omega$ is the hour angle [radians]:

$$\omega = 2\pi\cdot\frac{hour}{24} \tag{25}$$

For every *hour* of the day the hour angle, i.e. the angular motion of the sun in the sky, changes by 15° or ≈ 0.263 radians because the earth completes a full revolution during a 24 h period.

The elevation angle $\alpha_t$ [°], also used interchangeably with altitude angle, is the height of the sun above the horizon at a particular time of year:

$$\alpha_t = \arcsin\left(\cos\theta_{\mathrm{Z}}\right) \cdot \frac{360}{2\pi} \tag{26}$$

***Light transmission and light at depth***

We calculated the ambient light $I_{z,t}$ at depth $z$ and time $t$ in dependence of the reflective loss $\psi$ at the water surface, and light attenuation $K$ [$\mathrm{m}^{-1}$]:

$$I_{z,t} = \begin{cases} I_{\phi,t} \cdot \psi_\alpha \cdot e^{-(z \cdot K_{\mathrm{upr}})}, & \text{if } z \leq 100\ m \\ I_{\phi,t} \cdot \psi_\alpha \cdot e^{-(100 \cdot K_{\mathrm{upr}} + (z-100) \cdot K_{\mathrm{lwr}})}, & \text{if } z > 100\ m \end{cases} \tag{27}$$

here, we assume different attenuation coefficients for the upper 100 m $K_{\mathrm{upr}}$ and all depth below 100 m $K_{\mathrm{lwr}}$.

The reflective loss $\psi$ caused by reflection and refraction, i.e. the change in angle that occurs when light passes through the water air-interface is calculated using Fresnel equations and Snell's law (see Kirk, 1994, Mobley, 1994):

$$\psi_\alpha = \begin{cases} 1 - \left(\frac{1}{2} \cdot \frac{\sin\left(\theta_{\mathrm{Z}} - \theta_{\mathrm{w}}\right)^2}{\sin\left(\theta_{\mathrm{Z}} + \theta_{\mathrm{w}}\right)^2} + \frac{1}{2} \cdot \frac{\tan\left(\theta_{\mathrm{Z}} + \theta_{\mathrm{w}}\right)^2}{\tan\left(\theta_{\mathrm{Z}} - \theta_{\mathrm{w}}\right)^2}\right), & \text{if } \alpha > 0 \\ 1 - 0, & \text{if } \alpha < 0 \end{cases} \tag{28}$$

where $\theta_{\mathrm{Z}}$ [radians] is the zenith angle, $\theta_{\mathrm{w}}$ [radians] is the angle of the downwards transmitted beam in water, following if Snell's law is written as:

$$\theta_{\mathrm{w}} = \arcsin\left(\frac{n_{\mathrm{a}} \cdot \sin(\theta_{\mathrm{z}})}{n_{\mathrm{W}}}\right) \tag{29}$$

here, $n_{\mathrm{W}}$ and $n_{\mathrm{a}}$ are the reflective indices of water and air, respectively.

## Bioenergetics and gut evacuation

Our bioenergetic calculations are in large parts based on the generalized bioenergetics model of fish growth by Hewett & Johnson (1992).

The net energy balance $\Delta E$ [J] of an individual determines how much *surplus* resources are available for allocation to somatic growth, including structures and stores, and reproduction. The net energy balance $\Delta E$ is determined by the rate at which energy is assimilated through digestion $D$ [J·h$^{-1}$] after subtracting the 'running costs' ($RMR$ and $S$) and the 'waste losses' ($F$ and $U$):

$$\Delta E_t = D_t - (RMR_t + S_t) - (F_t + U_t) \tag{30}$$

where $RMR$ [J·h$^{-1}$] is the routine metabolic rate, $S_t$ [J·h$^{-1}$] is the energy accounted for by specific dynamic action, and $F_t$ and $U_t$ denote egestion or faecal waste [J·h$^{-1}$] and excretion or nitrogenous waste [J·h$^{-1}$], respectively. We modelled egestion $F_t$ as a constant proportion $F_\mathrm{a}$ of digested food $D_t$:

$$F_t = F_\mathrm{a} \cdot D_t \tag{31}$$

and excretion $U_t$ and specific dynamic action $S_t$ as constant proportions $U_\mathrm{a}$ and $S_\mathrm{a}$ of assimilation:

$$U_t = U_\mathrm{a} \cdot (D_t - F_t) \tag{32}$$

$$S_t = S_\mathrm{a} \cdot (D_t - F_t) \tag{33}$$

Digestion $D_t$ is temperature-dependent. We adopted an exponential model for gastric evacuation rate fraction of the gut content h$^{-1}$ from Hudson *et al.* (2014), based on an earlier study by Pakhomov *et al.* (1996):

$$GER_{z,t} = 0.0942 \cdot e^{(0.078 \cdot \tau_{z,t})} \tag{34}$$

where $\tau_{z,t}$ denotes ambient water temperatures [°C], for a given depth $z$ and time $t$.

Digestion is then calculated as:

$$D_t = G_t \cdot \left(1 - e^{GER_{z,t}}\right) \tag{35}$$

The routine metabolic rate $RMR$ [J·h$^{-1}$] of fish was defined as the standard metabolic rate $SMR$ [J·h$^{-1}$] scaled by an activity constant $y$ [dimensionless]:

$$RMR_t = SMR_t \cdot y \tag{36}$$

where $SMR$ is calculated following Killen *et al.* (2010, see Fig.1 therein, but for comparison see also Davison *et al.*, 2013). Here we, however, scale $SMR$ for a $Q_{10} \approx 2.5$:

$$SMR = 8.52 \cdot 10^{10} \cdot \left(\frac{W}{1000}\right)^{0.83} \cdot e^{\left(\frac{x'}{B \cdot (273.15 + \tau_{z,t})}\right) \cdot \left(\frac{e^{\left(\frac{x}{B \cdot 273.15}\right)}}{e^{\left(\frac{x'}{B \cdot 273.15}\right)}}\right)} \tag{37}$$

where $W$ [g] is the body weight and $B$ [eV·K$^{-1}$], $x$, $x'$ are constants.

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**Table S1**: Definitions, values, units and references of the terms used in the model. Abbreviations denote parameter values for *Benthosema glaciale* (Bg), piscivorous fish (Pf) and zooplankton (Zp), respectively.

| Term | Definitions | Value | Unit | Ref. |
|---|---|---|---|---|
| $A_{\mathrm{prey}}$ | Prey image area | | m$^2$ | |
| $C_{\mathrm{prey}}$ | Prey contrast | Zp = 0.5, Bg = 0.5 | Dimensionless | |
| $C_t$ | Consumption rate | | J h$^{-1}$ | 1 |
| $D_t$ | Digestion rate | | J h$^{-1}$ | 1 |
| $F_{\mathrm{a}}$ | Proportion of consumption lost to egestion | 0.16 | Constant | 1 |
| $F_{G,R,z,T}$ | Terminal fitness function | | Dimensionless | |
| $F_{G,R,z,t}$ | Fitness function | | Dimensionless | |
| $F_t$ | Egestion rate or faecal waste | | J h$^{-1}$ | 1 |
| $G_{\mathrm{ER},t}$ | Gastric evacuation rate | | Fraction of gut content h$^{-1}$ | 2,3 |
| $G_{\max}$ | Absolut gut size | 0.03 | Fraction of body mass ind$^{-1}$ | 4–6 |
| $I_{\mathrm{E}}$ | Extra−terrestrial radiation | | W m$^{-2}$ | |
| $I_z$ | Ambient light at depth $z$ | | W m$^{-2}$ | |
| $K_{\mathrm{e}}$ | Composite saturation parameter | Bg = $1\cdot10^{-8}$, Pf = $4\cdot10^{-4}$ | mW m$^{-2}$ nm$^{-1}$ at 486 nm | |
| $K_{\mathrm{lwr}}$ | Light attenuation coefficient, z>100m | See Fig. 2C | m$^{-1}$ | 7 |
| $K_{\mathrm{upr}}$ | Light attenuation coefficient, z≤100m | See Fig. 2C | m$^{-1}$ | 7 |
| $M_t$ | Predation mortality rate | | Ind. h$^{-1}$ | |
| $N_{\mathrm{pred}}$ | Predator (piscivorous fish) density | $5.0\cdot10^{-6}$ | Ind. m$^{-3}$ | |
| $N_{\mathrm{prey}}$ | Prey density | See Fig. S1 | Ind. m$^{-3}$ | |
| $R_{\max}$ | Absolute reserve size | 0.2 | Fraction of energy density ind$^{-1}$ | |
| $RMR_t$ | Routine metabolic rate | | J h$^{-1}$ | 8,9 |
| $S_{\mathrm{a}}$ | Proportion of assimilated energy lost to specific dynamic action | 0.175 | Constant | 1 |
| $S_{\mathrm{prey}}$ | Prey length−to−width ration | Zp = 0.2 , Bg = 0.2 | Ratio | |
| $SMR_t$ | Standard metabolic rate | | J h$^{-1}$ | |
| $S_t$ | Energy accounted for by specific dynamic action | | J h$^{-1}$ | 1 |
| $U_{\mathrm{a}}$ | Proportion of consumption lost to excretion | 0.1 | Constant | 1 |
| $U_t$ | Excretion rate or nitrogenous waste | | J h$^{-1}$ | 1 |
| $W_{\mathrm{prey}}$ | Weight of the prey | $1.08\cdot10^{-3}$ | g | 10,11 |
| $a_{H_2O}$ | Water vapour and ozone absorption coefficient | 0.09 | Dimensionless | |
| $c_{\mathrm{clouds}}$ | Cloud cover | 0 | Fraction | |
| $i_{\mathrm{b}}$ | Beam component of the solar radiation | | W m$^{-2}$ | |
| $i_{\mathrm{d}}$ | Diffuse component of the solar radiation | | W m$^{-2}$ | |
| $i_{\mathrm{s}}$ | Starlight | $1.5\cdot10^{-6}$ | W m$^{-2}$ | 12 |
| $j_{\mathrm{prey}}$ | Energy density of the prey | Zp = 3500, Bg = 5900 | J g wet weight$^{-1}$ | 13–16 |
| $n_{\mathrm{a}}$ | Reflective indices of air | 1.0 | Dimensionless | 17 |
| $n_{\mathrm{w}}$ | Reflective indices of sea water | 1.33 | Dimensionless | 17 |
| $r_{\max}$ | Max. visual range | Bg = 0.06, Pf = 1.5 | m | |
| $r_{\min}$ | Non−visual detection threshold | Bg = $3\cdot10^{-3}$, Pf = $1\cdot10^{-1}$ | m | |
| $z_{\Delta max}$ | Max. vertical migration distance | 100 | m h$^{-1}$ | |
| $\alpha_{\mathrm{noon}}$ | Solar elevation angle at noon | | Radians | |

| | | | | |
|---|---|---|---|---|
| $\beta_{z,t}$ | Clearance rate | | m$^3$ s$^{-1}$ predator$^{-1}$ | 18,19 |
| $\varepsilon_0$ | Earth eccentricity | | Dimensionless | 20–22 |
| $\theta_\mathrm{r}$ | Fraction of visual field scanned | Bg = 0.6, Pf = 0.6 | Radians | |
| $\theta_\mathrm{w}$ | Angle of the downwards transmitted beam | | Radians | |
| $\theta_\mathrm{Z}$ | Solar zenith angle | | Radians | |
| $\iota_{z,t}$ | Encounter rates | | Ind. h$^{-1}$ | 18,19 |
| $\tau_z$ | Ambient temperature | See Fig. 2B | °C | 7 |
| $\Delta E$ | Net energy balance | | J | 1 |
| $h$ | Handling time | Bg = 2.0, Pf = 15.0 | s ind$^{-1}$ | |
| $hour$ | Hour of the day | | hour | |
| $surplus$ | Surplus energy | | J | |
| $t$ | Current time step | $1 \leq t \leq T = 8760$ | h of the year | |
| $B$ | Bolzmann constant | $8.62 \cdot 10^{-5}$ | eV K$^{-1}$ | |
| $E'$ | Visual capacity | | Dimensionless | |
| $G$ | Gut fullness state variable | $0 \leq G \leq G_\mathrm{max}$ | J | |
| $G'$ | New gut state | | J | |
| $I$ | Irradiance | | W m$^{-2}$ | |
| $L$ | Body length | Zp = $2.7 \cdot 10^{-3}$, Bg = 0.06, Pf = 0.5 | m | 6,23 |
| $R$ | Internal reserve state variable | $0 \leq R \leq R_\mathrm{max}$ | J | |
| $R'$ | New reserve state | | J | |
| $W$ | Body weight for $L = 0.06$ | 2.45 | g WW ind$^{-1}$ | 23 |
| $c$ | Beam attenuation coefficient | 0.3 | m$^{-1}$ | |
| $day$ | Day of the year | | day | |
| $pc$ | Prey capture success | Bg = 0.7, Pf = 0.7 | Probability | |
| $r$ | Visual range | | m | 18,19 |
| $survival$ | survival probability | | Probability | |
| $v$ | Swimming velocity | Bg = 0.06 , Pf = 0.25 | m | |
| $x$ | Normalization constant | −0.4568 | eV | 8 |
| $x'$ | Normalization constant, modified to yield a $Q_{10} \approx 2.5$ | −0.655 | eV | |
| $y$ | Activity constant | 1.25 | Constant | |
| $z$ | Current depth | $1 \leq z \leq 1000$ | m | |
| $z'$ | New depth | | m | |
| $\Gamma$ | Day angle | | Radians | |
| $\Phi$ | Latitude | $63.77° \leq \Phi \leq 68.8°$ | Degrees | |
| $\alpha$ | Solar elevation angle | | Radians | |
| $\delta$ | Declination angle | | Radians | 20–22 |
| $\psi$ | Reflective loss | | Fraction | 17,24 |
| $\omega$ | Hour angle | | Radians | |

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# PAPER III

**Langbehn TJ, Aksnes DL, Kaartvedt S, Fiksen Ø & Jørgensen C**

Poleward distribution of mesopelagic fish is constrained by seasonality in light

manuscript, prepared for *Nature Ecology & Evolution*

# Poleward distribution of mesopelagic fish is constrained by seasonality in light

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## Abstract

Mesopelagic fishes are the most abundant vertebrate group on the planet. They are distributed worldwide from tropical to sub-Arctic waters, yet their biomass and abundance decrease markedly poleward and viable populations seem excluded from polar oceans. Given their ubiquity elsewhere, the absence from high latitudes begs for an explanation rooted in ecology and the environment. Here we use an evolutionary model for adaptive behaviour to provide evidence that seasonality in light is the mechanism that constrains the distribution of mesopelagic fishes at high latitudes. During the period with midnight sun, these fishes are trapped in the deep and do not risk visiting the productive water masses near the surface, where visual predators are abundant. Instead, they depend on stores to wait for darker nights so they can resume feeding.

## Introduction

The evolutionary and ecological mechanisms that govern species' range margins are often unexplored, and remain a pertinent question in ecology (Sutherland *et al.*, 2013). One striking example is provided by mesopelagic (midwater) fishes, which are found everywhere in the world's oceans, yet their abundance strongly decreases in polar waters, both in the southern (Escobar-Flores *et al.*, 2018b,a) and northern hemispheres (Sameoto, 1989, Kristoffersen & Salvanes, 1998, Norheim *et al.*, 2016, Siegelman-Charbit & Planque, 2016, Gjøsæter *et al.*, 2017, Knutsen *et al.*, 2017). For species groups with high abundance and near-global distributions, the most relevant question might not be why they occur where they do, but rather what explains their lack of success in certain places.

Mesopelagic fishes inhabit the ocean's twilight zone (Kaartvedt *et al.*, 2019) and are extremely abundant with a global biomass on the order of 1,000 to 10,000 million tons (Gjøsaeter & Kawaguchi, 1980, Irigoien *et al.*, 2014, Proud *et al.*, 2018b), maybe 10-20 times that of all other fishes combined. Mesopelagic fishes therefore play an influential role in oceanic food webs (Horning & Trillmich, 1999, Connan *et al.*, 2007, Cherel *et al.*, 2010, Naito *et al.*, 2013) and for biogeochemical cycling (Bianchi *et al.*, 2013, Davison *et al.*, 2013, Aumont *et al.*, 2018). There is also renewed interest in their commercial exploitation (St. John *et al.*, 2016).

Where distinct day-night cycles exist, diel vertical migrations structure the pelagic. Here visual predators and their prey engage in a game of hide and seek that often spans several hundred meters in depth (Hays, 2003). Small fishes in well-lit waters are an easy prey for visual predators such as piscivorous fishes, marine mammals (Levenson & Schusterman, 1999, Stewart *et al.*, 2018), and, closer to the surface, seabirds (Connan *et al.*, 2007). Therefore, planktivorous mesopelagic fishes seek the best trade-off between visual feeding aided by their light-sensitive eyes (De Busserolles & Marshall, 2017, Warrant & Adam Locket, 2004, Turner *et al.*, 2009), and staying undetected by predators whose eyes work best with higher illumination. The resulting behaviour is that mesopelagic fishes are found in a narrow interval of ambient light intensities, and track this apparent light comfort zone (LCZ) over time (Langbehn *et al.*, in review, Aksnes *et al.*, 2017). Consequently, about half of all mesopelagic organisms, globally on the order of 5,000 million tons, rise to the surface at night to feed where zooplankton is more abundant and sink to depth during daytime where predation from epipelagic predators is reduced (Irigoien *et al.*, 2014, Klevjer *et al.*, 2016).

The environmental drivers and mechanisms that limit the poleward distribution of mesopelagic fishes remain unclear. Here, we investigate the hypothesis that the extreme photoperiod at polar latitudes constrains the distribution of mesopelagic fishes (Sameoto, 1989, Kaartvedt, 2008, Kaartvedt & Titelman, 2018). Variable light regimes constantly

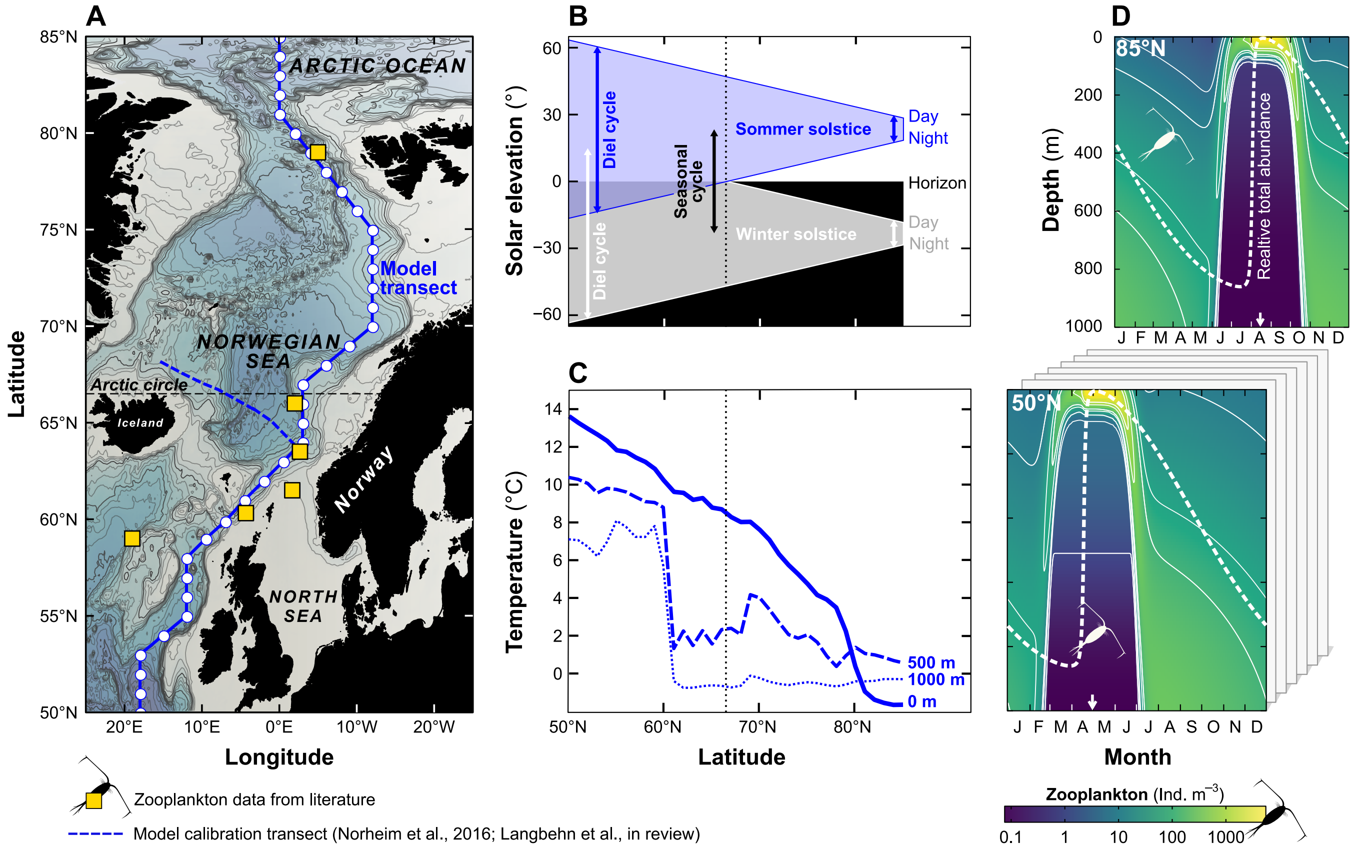

**Figure 1: Map of the study area and relevant environmental drivers in the model**. In the Norwegian Sea (**A**), seasonality in light (**B**), water temperature (**C**) and zooplankton distribution (**D**) vary along latitudinal gradients.

change the rules of the game for pelagic predator-prey interactions. In particular, the extended duration of polar night and midnight sun constitute forcing that is radically different from low latitudes where there are regular circadian light cycles. At latitudes above the polar circle, midnight sun during summer implies bright nights during which mesopelagic fishes cannot migrate safely to the surface to feed, as they can be easily detected by epipelagic predators (Sameoto, 1989). Conversely, during the polar night in winter, there is little or no production at the surface and most of the potential *Calanus* prey hibernate at depth where it is pitch black. The constant darkness may thus limit successful foraging of mesopelagic fish on overwintering *Calanus* in deep waters (Kaartvedt, 2008), although a rare encounter may suffice to cover metabolic requirements in the cold, Arctic waters.

Our approach is dynamic state modelling of migratory behaviour in a seasonal environment, rooted in evolutionary ecology and including explicit mechanisms of temperature-dependent physiology and foraging interactions (Material and Methods). We have previously calibrated and favourably tested the model with acoustic observations along a latitudinal transect in the Norwegian Sea (Langbehn *et al.*, in review). Here we run the model along a latitudinal gradient from temperate to Arctic waters (50°- 85° N, Fig. 1A) to identify the bottlenecks that set the poleward range margin for mesopelagic fishes.

## Results & Discussion

Our model predicts that waters beyond the polar circle are a population sink for mesopelagic fishes. Specifically, our model results show that annual survival drops markedly, by ca. three quarters, when crossing from sub-arctic to Arctic latitudes (Fig. 2A), while the decrease in surplus energy is more gradual (Fig. 2B). At high latitudes, only 20 % of the 6 cm length-class, representative for mature adults age 4-6 (Gjøsæter, 1981), survives to the end of the year according to our model. High summer predation mortality and a reduction in annual surplus energy, and hence less capital for growth or reproduction, together explain the negative population growth (Fig. 2). The marked nick in survival and surplus energy around 60°N (Fig. 2) is due to cooler deep waters associated with the transition from the Rockall basin to the Norwegian Sea basin (Fig. 2A, C).

The extreme light regime at high latitudes can explain the lack of success of mesopelagic fishes in polar waters, because the sun-lit summer nights leave them with two poor options: starvation or predation. At higher latitudes, daylight hours become increasingly seasonal, with periods of winter darkness during the polar night that can last for months, and corresponding periods with midnight sun (Fig. 1B). This creates a challenging environment for diel vertical migrators, which normally exploit a nocturnal window of safe foraging in surface waters during night before sinking back to depth where they can stay safe from most visually hunting piscivores as the light returns. Acoustic observations during summer, from the transitional zone around the Arctic circle (63.7°- 68.8° N, Fig. 1A), show a deepening of the deep scattering layer with increasing latitude, mostly because mesopelagic micronekton no longer migrated into surface waters at night (Sobolevsky *et al.*, 1996, Norheim *et al.*, 2016). This is consistent with observations from further north (67°- 82° N), where mesopelagic scattering layers were located below 200 m through the day during summer, with weighted mean depth increasing poleward (Siegelman-Charbit & Planque, 2016, Gjøsæter *et al.*, 2017, Knutsen *et al.*, 2017). The consequence of remaining in the deep during daytime, far away from the productive surface waters, is reduced foraging and potential starvation.

Our model predicts depth distributions that align with those observed (Fig. 3). Towards higher latitudes, where light intensities during summer allow piscivorous predators to hunt efficiently in surface waters round the clock, the model predicts mesopelagic fish distributions at depths far from the surface, although the surface is where food is abundant during the short productive season (Fig. 3, Fig. 1D).

During winter, dim light compresses the twilight zone towards the surface in polar regions (Kaartvedt *et al.*, 2019), and north of 80°N our model predicts optimal depth for mesopelagic fishes to shift into the epipelagic, shallower than 200 m, both day and night (Fig. 3A). Surface observations of the mesopelagic jellyfish *Periphylla periphylla* at 78.9°N (Geoffroy *et al.*, 2018), which is known to have light preferences similar to mesopelagic fish (Bozman *et al.*, 2017), suggest suitable light conditions near the surface during midwinter. At that time of the year, most zooplankton, however, will already have left the

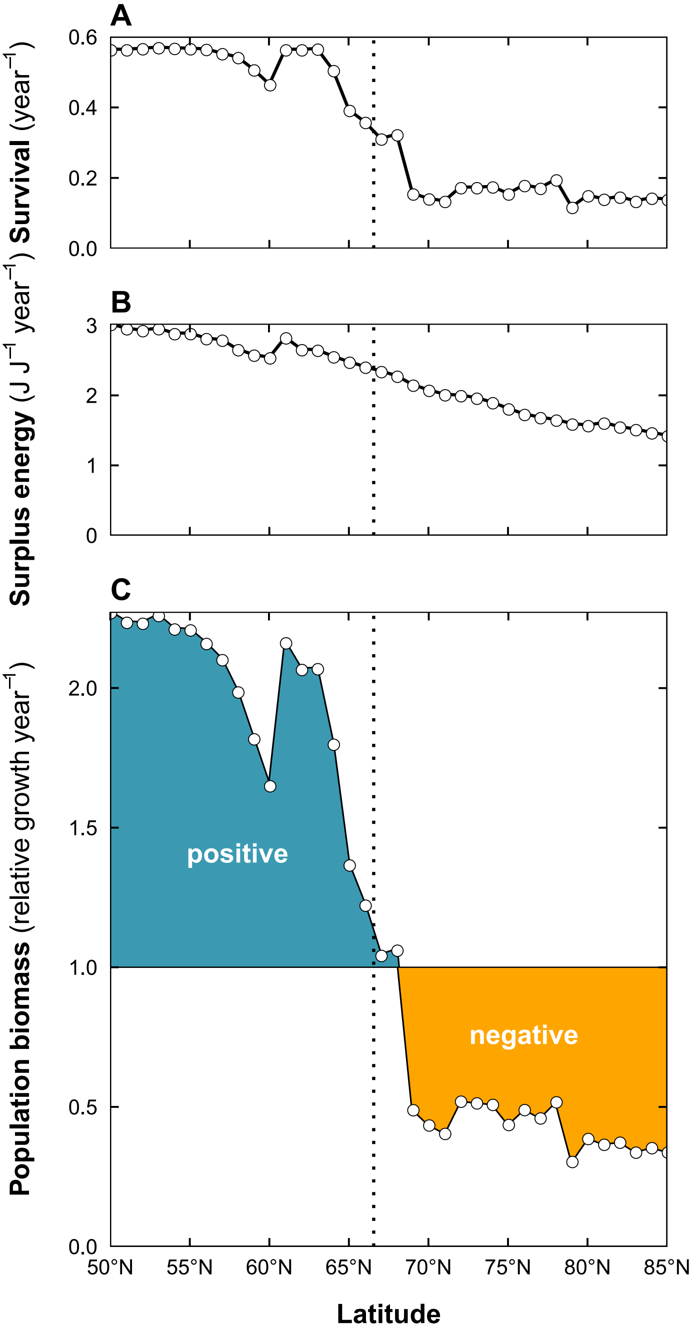

**Figure 2: Arctic waters are population sinks for mesopelagic fish**. Our model predicts that annual survival **(A)** and surplus energy **(B)** decrease poleward, explaining the negative population growth at latitudes beyond the Arctic Circle **(C)**

surface waters (Fig. 3B) and descended for hibernation at depths of  (Østvedt, 1955, Melle *et al.*, 2004, Gislason, 2018), thus dispersed and diluted where it is too dark for visual predators, even mesopelagic fish, to feed efficiently. Even though recent studies have shown ongoing biological activity in the upper water during the polar night (Berge *et al.*, 2015, Hobbs *et al.*, 2018), at that time of the year, most copepods are in diapause at great depth (Falk-Pedersen *et al.*, 2009, Baumgartner & Tarrant, 2017, Gislason, 2018).

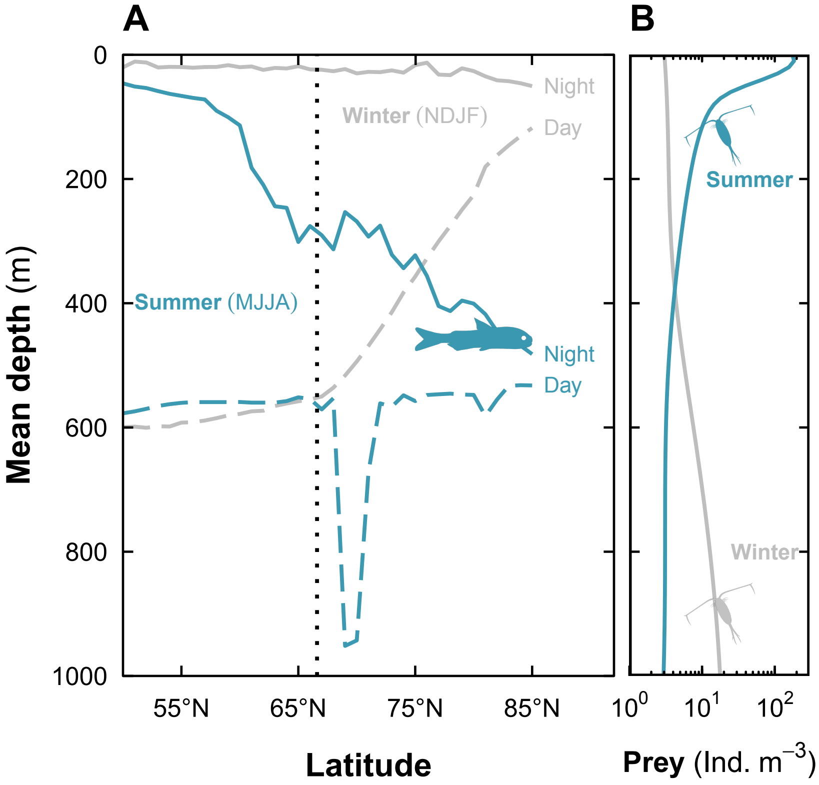

**Figure 3: Seasonality in light creates a spatiotemporal mismatch between mesopelagic fish and their prey**. Midnight twilight and midnight sun at high latitudes make it too risky for mesopelagic fish to forage safely in surface waters, constraining them to depth during summer **(A)**, far from their prey **(B)**. During the darkness of the polar night, while it is safe near the surface, it is too dark to forage at greater depth **(A)**, causing an increasing spatiotemporal mismatch between mesopelagic fish and their prey **(B)** towards higher latitudes.

Consequently, our results show that both the summer and winter season at high latitudes are challenging for mesopelagic fish, because there is little overlap between appropriate light habitat and concentrations of potential prey (Fig. 3). According to the model, this is particularly critical during the productive period in summer, when light, a zooplankton burst, and seasonally high temperatures co-occur, favouring rapid ingestion and growth.

Because of the increasing spatiotemporal mismatch between mesopelagic fish and their prey towards higher latitudes (Fig. 3), starvation occurs during the summer months where nights are light and copepods concentrated near the surface (Fig. 4A). Midnight twilight, with the disk of the sun remaining less than 10° below the horizon all night, causing nautical twilight from sunset to sunrise, emerges a good predictor for where summer starvation begins to occur. The longer the period with twilight or sun at midnight, the longer are mesopelagic fishes trapped in barren deep-water, and the higher is the potential for starvation.

The antipredation window hypothesis (Clark & Levy, 1988) provides a theoretical explanation for why some light levels are particularly beneficial for foraging. The antipredation window is where the ratio of predation risk over feeding rate is minimal (Fig. 4B); for mesopelagic fishes this is where light permits feeding on zooplankton but constrains visual detection by piscivores. This partly arises from differences in eye sensitivity between species, but also because small mesopelagic fishes detect the much more numerous small prey on short distances, which is hampered less by light scattering than piscivores that search for larger visual objects over larger distances (Giske *et al.*, 1994, Fiksen *et al.*, 2002, Utne-Palm, 2002, De Robertis *et al.*, 2003).

Our model predicts a behaviour where mesopelagic fishes stay mostly within a narrow range of light levels throughout the day and across seasons. This preference for a constant light regime matches observations of mesopelagic scattering layers in the Norwegian Sea (Fig. 4B) (Norheim *et al.*, 2016), and along a circumglobal transect (Aksnes *et al.*, 2017). The light interval inhabited by mesopelagic fish, as derived from acoustic observations, has been referred to as a light comfort zone (LCZ) (Røstad *et al.*, 2016b,a).

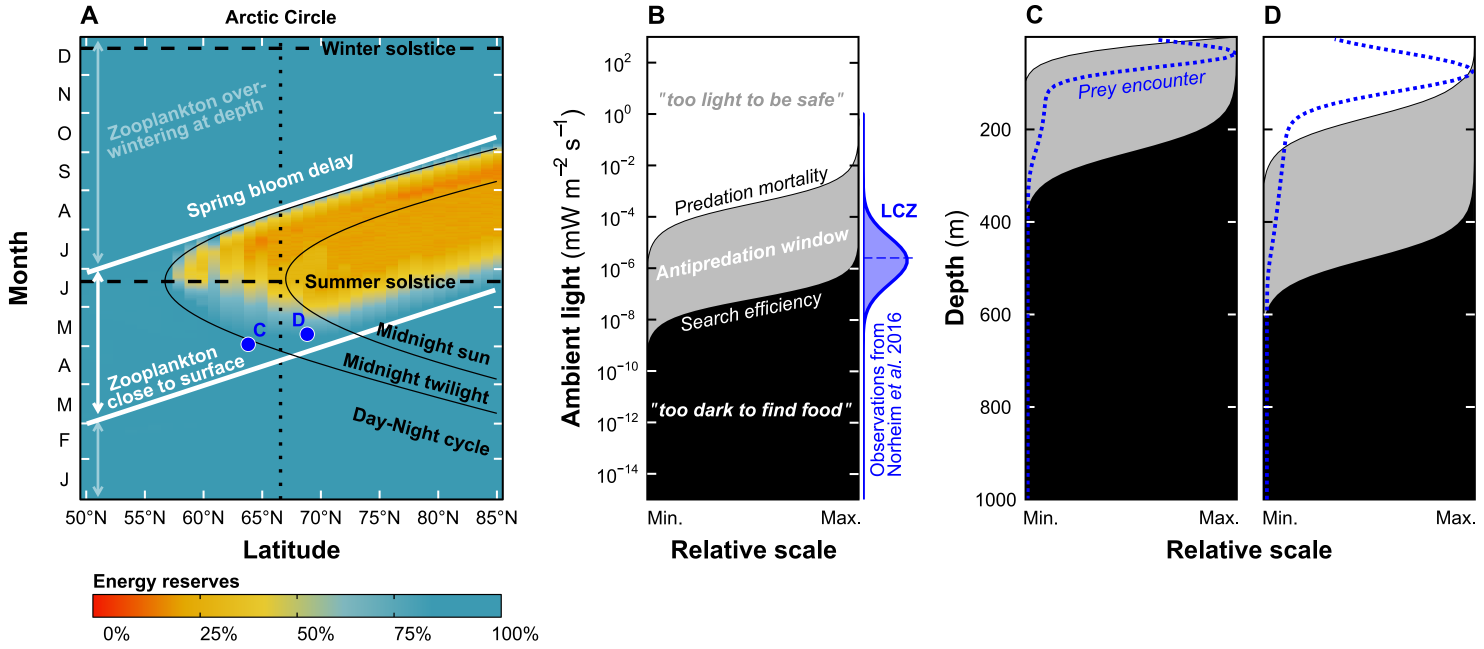

**Figure 4: The lack of overlap between appropriate light habitat with prey explains summer starvation of mesopelagic fish at high latitudes.** Mesopelagic fish starve when zooplankton is concentrated close to the surface during midnight twilight or midnight sun periods **(A)**. Our model prediction of an antipredation window (Clark & Levy, 1988) outlining where foraging is safe, explains the emergence of an apparent light comfort zone as observed in the Norwegian Sea **(B)**. At low latitudes, the antipredation window shifts at night (here shown for midnight) into prey-rich surface waters **(C)**, while the antipredation window at higher latitudes with midnight twilight or midnight sun is constraint to greater depth and never reaches where the prey is, causing mesopelagic fish to starve **(A)**.

During summer, lighter nights towards higher latitudes push the antipredation window downwards while the zooplankton prey remains in the productive surface waters. At latitudes with a clear day-night cycle, where the sun is more than 10 below the horizon at night, the apparent light comfort zone of mesopelagic fish overlaps with the zooplankton rich near-surface waters at night, allowing mesopelagic fishes to forage at low risk of predation from visually hunting piscivores (Fig. 4C). Towards latitudes with midnight twilight or midnight sun, the light comfort zone will not reach the surface, and thus the prey field, for extended parts of the season, preventing mesopelagic fishes from foraging unless they take excessive risks (Fig. 4D).

Analyzing the joint dynamics of energy reserves and vertical migration across latitude and season reveals the environmental bottlenecks more clearly. During winter, normal vertical behaviour is seen across all latitudes, with mesopelagic fishes close to the surface during night and staying deeper during daytime, although less so at higher latitudes because of the polar night (Fig. 3A). It is during summer the differences become dramatic. At lower latitudes, up to 60°N, normal diel vertical migration is seen; the fish forage in productive waters during daytime and are in good energetic state (Fig. 4A). Right below the Arctic Circle, where there is midnight twilight, our model suggests that mesopelagic fish have sufficient internal reserves to wait out the relatively short period without darkness at night (Fig. 4A). However, without foraging, there is also no surplus energy to be gained during this period, and fish deprive energy reserves. Beyond the Arctic Circle, where the period of midnight twilight and midnight sun becomes progressively longer, reserves do not last through the starvation period and the energy reserves of mesopelagic fishes reach critically low levels. The model then predicts two different strategies. First, for latitudes around 70°N, the model suggests that fish may cut back on metabolic expenditures by migrating to cooler waters at greater depth (Fig. 3, Fig. 5 - summer). This can help stretch the reserves until darker nights once again permit foraging close to the surface. Second, where the period of midnight twilight and midnight sun lasts longer, mesopelagic fishes are eventually forced to the surface to feed to avoid death by starvation. In the model, individuals with empty guts and energy reserves $<25\,\%$ abandon the safety of the light comfort zone and perform sporadic foraging bouts into near-surface waters (Fig. 5) where encounter rates both with prey an predators are high. Individuals with high body condition remained close to the observed light comfort zone, most likely these were individuals who had recently performed a bout of high-risk feeding.

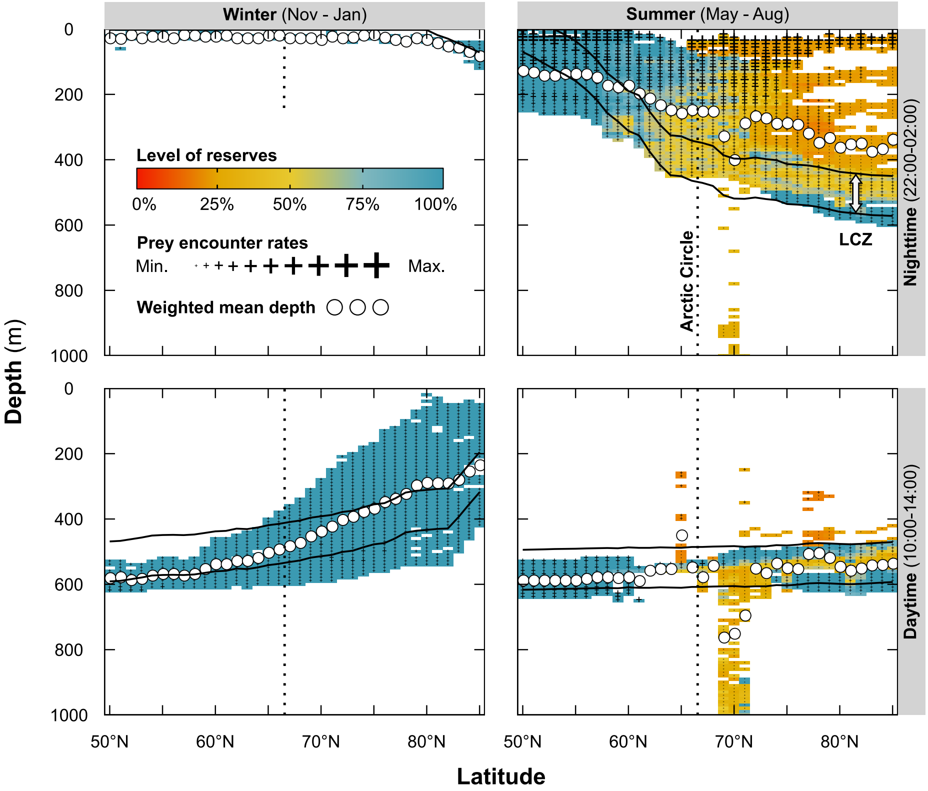

**Figure 5: Mesopelagic fish at high latitudes face a tough choice during summer: starve at depth, or risk predation while feeding close to the surface.** Our model predictions suggest that mesopelagic fish face starvation (i.e. low energy reserves) at high latitudes during summer Fig. 4A, when the nights are light (Fig. 1B) and zooplankton aggregates near the surface (Fig. 1D). Fish with low energetic reserves accept higher risk and take foraging bouts outside the light comfort zone (LCZ), around $2 \times 10^{-6}\,\mathrm{mW{\cdot}m^{-2}{\cdot}nm^{-1}}$ at 486 nm (Norheim *et al.*, 2016), to avoid starvation. During winter, foraging near the surface is safe but encounter rates are reduced compared to the summer situation because there is no overlap of appropriate light habitat with the depth at which zooplankton overwinters. See Figure S1 in the supplementary for vertical distributions as a function of ambient light.

# General discussion

Our model suggest that light is a main driver for the broad biogeographical pattern of mesopelagic fishes, and that the extreme seasonality in light towards high latitudes poses a critical challenge for such a small and slow planktivore. Although the model aligns well with observations, there are a couple of known limitations where model predictions likely are more inaccurate. The eyes of mesopelagic fishes are adapted to twilight (scotopic) vision, and it is likely that they are unable to utilize the strong daylight in upper waters. Surface light can be 9-12 orders of magnitude higher than that of their normal habitat, and beyond light saturation and reduced efficiency, photodegradation of visual pigments may lead to lasting damage. Our model does not account for such mechanisms. However, our predictions of daytime foraging bouts into surface waters match observations that regular diel vertical migration patterns break up where the daylight hours last for most of the day (Dietz, 1962, Siegelman-Charbit & Planque, 2016, Proud *et al.*, 2018a). In the pacific Arctic, reports of mesopelagic fish are restricted to a few dead or dying individuals washed ashore in the Bering Sea (Mecklenburg & Steinke, 2015). Similar sightings exist from the Labrador Sea, where dead or dying lanternfish are often observed at the surface. In this case, temperature can, however, not be excluded as a cause (Dunbar & Hildebrand, 1952).

While we do not find direct evidence of winter starvation (Fig. 5), the model shows that feeding rates are reduced during the winter months and allows only a very limited energetic surplus. Hence, low surface productivity and copepods hibernating at depth make it difficult for starved fish to refill their reserves and build up energy for growth or reproduction in the next season. Reproduction and growth govern species distribution and abundance, which requires that surplus energy exceed the running costs of the organism. According to the model, myctophids at higher latitudes are unable to build up the same reproductive capital during winter as their congenerics at lower latitudes can do over the entire year. Where the seasonality in light is extreme, low recruitment does not compensate for the high predation mortality during summer, and we thus predict negative population growth beyond the Arctic Circle (Fig. 2).

The predicted negative population growth at high latitudes matches well with observations. Both in the Southern Ocean and in the sub-Arctic Atlantic Ocean, observations suggest that myctophid populations at the poleward range margins are non-reproducing, and it has been concluded that these populations consist entirely of adults that are likely expatriates from lower latitudes (Sameoto, 1989, Saunders *et al.*, 2017). Constant passive advection from sub-Arctic waters may sustain populations at high-latitudes through source-sink dynamics (Dunbar & Hildebrand, 1952, Gjøsæter *et al.*, 2017, Knutsen *et al.*, 2017). The constant advection of mesopelagic organisms from lower latitudes might be substantial, while not fully acknowledged. Such an energy pathway may potentially sustain high-latitude food webs (Saunders *et al.*, 2017) and warrants further investigation. In the Southern Ocean, many top predators feed frequently on mesopelagic fish (Connan *et al.*, 2007, Cherel *et al.*, 2010).

The mesopelagic fauna in polar oceans is poorly developed when compared to adjacent seas (Sutton *et al.*, 2017) and deep scattering layer biomass declines by orders of magnitude with increasing latitude (Kristoffersen & Salvanes, 1998, Norheim *et al.*, 2016, Siegelman-Charbit & Planque, 2016, Escobar-Flores *et al.*, 2018b,a). Although decreasing temperatures correlate with the poleward decline in biomass and have been suggested to govern mesopelagic biogeography (Proud *et al.*, 2017, Escobar-Flores *et al.*, 2018a), temperature provides an unsatisfactory explanation for the observed patterns in the North Atlantic since thermal conditions in the northward-directed outflow of the Gulf stream remain relatively constant well beyond the Arctic Circle. Globally, closely related species of mesopelagic fish occur in a wide range of thermal habitats from polar waters close to 0 °C (Gjøsæter *et al.*, 2017, Saunders & Tarling, 2017) to the Red Sea where even bottom waters reach 21 °C (Klevjer *et al.*, 2012). Further, large temperature variation of  during a diel vertical migration cycle may be rather the rule than the exception, considering the size of tropical oceans versus high-latitude systems. A light-driven mechanism as modelled here provides a more parsimonious answer to the poleward decline in biomass, pointing to recruitment limitation and increased predation mortality in seasonal light environments as proximate causes. If light is the main constraint on mesopelagic biogeography towards high latitudes, then poleward range shifts of mesopelagic fish into the Arctic Ocean are not likely to follow from global warming (Kaartvedt, 2008, Kaartvedt & Titelman, 2018), because the present-day cold water might be exactly what enables them to survive at the latitude they currently do.

The model predicts reduced abundance of mesopelagic fish beyond the Arctic Circle. This is of significance because what is elsewhere a major predator on zooplankton from below leaves a planktivore niche vacant at high latitudes for horizontally migrating planktivores like herring, capelin, and mackerel. Together with the low temperature and slow development, the predicted absence of mesopelagic planktivores may account for the larger body size (Brooks  Dodson, 1965) and the multiyear life cycles of high-latitude copepods such as *Calanus glacialis* and *C. hyperboreus* (Kaartvedt, 2008). These copepod species require several feeding summers to reach sexual maturity (Falk-Pedersen *et al.*, 2009); a life history strategy that would likely be unviable where mesopelagic fish forage on overwintering stages at the rate they do in more southerly waters (Bagøien *et al.*, 2001, Gislason *et al.*, 2007, Espinasse *et al.*, 2018). During their active period in summer, these copepods are large visual targets and profitable food for the large stocks of horizontal migrating planktivorous fish. Because long migrations are linked to large body size (Roff, 1988), the large zooplankton at high latitudes may be exactly what enables the Norwegian spring-spawning herring to have the large body size needed to migrate there. Absence of mesopelagic fishes may thus enable a profitable food source that attracts and makes possible migrating planktivores such as herring at high latitudes, a strategy that is predicted to further benefit from the retreat of sea-ice in the near future (Varpe *et al.*, 2015, Langbehn & Varpe, 2017).

While photoperiod has been shown to potentially limit poleward distributions in higher plants (Bjorkman *et al.*, 2017), diapausing insects (Lehmann *et al.*, 2014) and corals (Muir *et al.*, 2015), to our knowledge, we present the first quantitative analysis of a proximate light mechanism that constrains poleward species distribution in vertebrates. However, a similar reasoning might be also applicable to other vertebrate groups, such as bats or nightjars (Aves:*Caprimulgidae*) that have found a niche in twilight conditions where they have the competitive advantage because their predators or competitors rely on vision to hunt.

# Material & Methods

## A dynamic state-variable optimization model

We use a state-dependent life history model implemented via stochastic dynamic programming (Mangel & Clark, 1988, Clark & Levy, 1988, Houston & McNamara, 1999) that integrates explicit mechanisms for physiology and visual encounters, to predict optimal vertical migration behaviour in mesopelagic fish through the shifting season, along a latitudinal gradient from 50°- 85°N. Our model can find optimal risk-taking, energy allocation, and migrations strategies from multiple trade-offs in given ecological systems. Here, we test if extreme seasonality in light explains latitudinal patterns in distribution of mesopelagic fish. For a full model description, including relevant equations and the complete Fortran source code, we refer to Langbehn *et al.* (in review) and their supplementary.

## Temperature environment

In the model we use NOAA's Greenland-Iceland-Norwegian Seas Regional Climatology version 2 (Seidov *et al.*, 2018), based on the World Ocean Database archive as a temperature environment. The climatology consists of monthly, $1/10° \times 1/10°$ gridded temperatures fields, averaging six decades of observation from 1955 to 2012, from the sea surface to 1500 m depth. To match the models temporal and spatial resolution, we use cubic spline interpolation to create daily temperatures fields with a vertical resolution of 10 m, between the surface and 1000 m depth. Temperatures gradually decline towards the pole and a basin shift associated with cooler deep water around 60°N is evident (Fig. 1C)

## Surface light and water clarity

In the model, light reaching the sea surface varies with latitude, the time of day and season. Light hitting the sea surface is partly reflected, in particular when the sun is low around dusk and dawn or at high latitudes during summer. We consider the case of glassy seas, and no overcast, but acknowledge that both factors contribute to variation in light along the latitudinal gradient. We do not account for lunar light either. The surface light calculations are adopted from the HYbrid Coordinate Ocean model HYCOM (www.hycom.org). However, we modified light calculations to allow twilight to fade into starlight, assumed $10^{-9}$ times that of peak surface light, when the sun sets below the horizon (Ryer & Olla, 1999, Kaartvedt *et al.*, 2019). Surface light calculations have been validated against observation from the southern Norwegian Sea (Langbehn *et al.*, in review, see supplementary methods). Dependent on water clarity, light in water decays exponentially with depth. Because the transect is located off-shelf, we assume clear oceanic conditions and adopt light attenuation coefficients from the central Norwegian Sea along the full latitudinal gradient, $0.052\,\mathrm{m}^{-1}$ for the upper 100 m and $0.034\,\mathrm{m}^{-1}$ for all depth below (Norheim *et al.*, 2016).

## Zooplankton prey fields

We conceived idealized zooplankton prey-fields, with explicit seasonal vertical migration, population dynamics, and a shifting phenology with increasing latitude (Fig. 1D). We aim to reflect general characteristic of the seasonal dynamics along the latitudinal gradient, rather than local realism. We base our prey-field on the most comprehensive data from literature, among others long-term studies conducted at weather ship station Mike and India, or seasonal studies form the Icelandic Sea and the Fram Strait (Fig. 1A, yellow squares). Here, we consider copepods of 2.7 mm length, e.g. CV-CVI *Calanus finmarchicus*, CIV-CV *C. glaciale* or CIII-CV *C. hyperboreus* as suitable prey (Pepin, 2013). We assume that the majority of the copepods perform extensive seasonal vertical migration to diapause during parts of the years, with only a small fraction remaining active in surface waters year round (Melle *et al.*, 2004). Because the polar night at high latitudes limits primary production, we assume this active fraction to be smaller at higher latitudes. In the scenario considered here, copepods ascend into the upper 100 m to forage and reproduce during the productive part of the season, with near surface densities peaking around $500\,\mathrm{Ind{\cdot}m}^{-3}$, leaving deep waters almost void with concentrations $<1\,\mathrm{Ind{\cdot}m}^{-3}$ (e.g. Gislason, 2018). In fall, surface aggregations disperse and copepods sink into deeper waters between  depth for hibernation, where they spread out over a large vertical range, causing densities to be more homogeneous across depth (Irigoien, 2000, Melle *et al.*, 2004). In the model environment, the total numbers of copepods varied seasonally between 3200 - 16 000 Ind$\cdot$m$^{-2}$, declining continuously after the population peak in summer until the next year when abundance sharply increases again due to reproduction (Østvedt, 1955, Heath, 2000). With increasing latitude, we assume a shift in phenology of annual events, such as the ascent and descent of zooplankton, occurred later in the season (Melle *et al.*, 2014). Here we assume a shift of 3 days for a 1° increase in latitude, while the length of the productive season remained constant across latitudes.

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# Supplementary figures

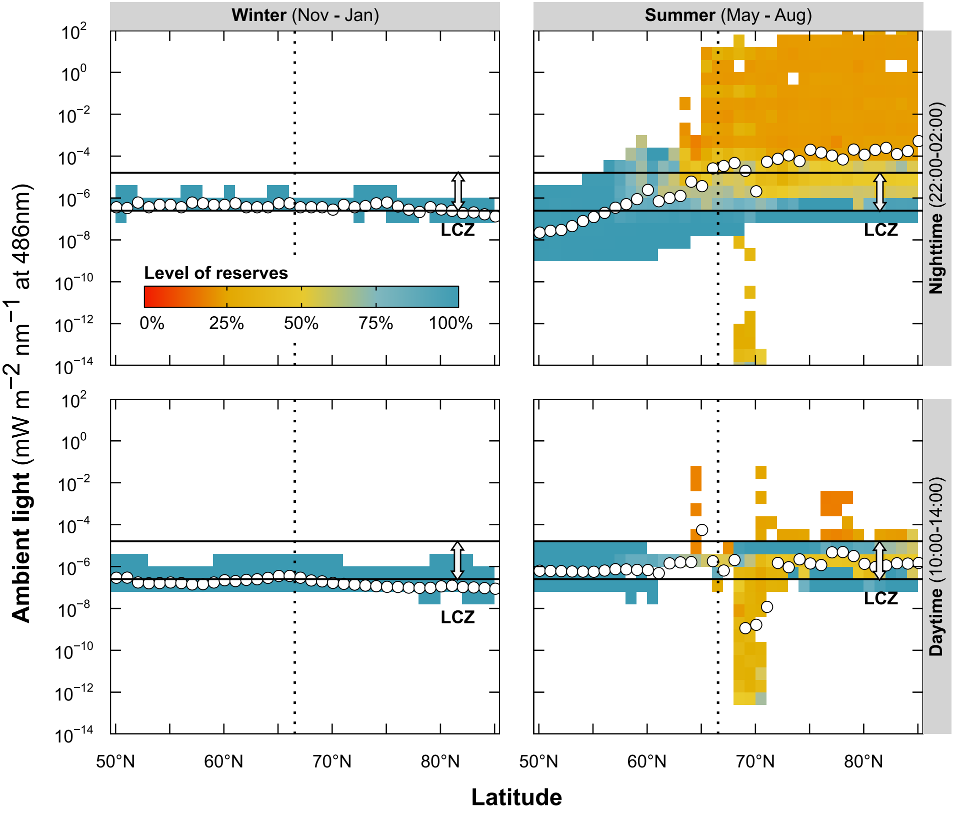

**Figure S1:** Modelled distribution of mesopelagic fish as a function of ambient light and levels of internal energy reserves

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