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Poleward distribution of mesopelagic fishes is constrained by seasonality in light

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Abstract

Aim: Mesopelagic fishes have a near-global distribution in the upper 1,000 m from tropical to sub-Arctic oceans across temperature regimes. Yet, their abundance decreases poleward and viable populations seem excluded from high latitudes. Why?

Location: North Atlantic between 50–85°N, with implications for high-latitude oceans globally.

Time period: Present-day.

Major taxa studied: Diel vertically migrating (DVM) mesopelagic fishes.

Methods: We use a mechanistic, state-dependent life-history model to characterize DVM mesopelagic fishes. This model links light-dependent encounters and temperature-dependent physiology, allowing optimal DVM strategies to emerge. We run the model along a latitudinal gradient with increasing seasonality in light and track individual fitness-related measures, that is, survival and surplus energy, through the annual cycle to make predictions about population consequences.

Results: Mesopelagic fishes thrive in the oceans' twilight zone, and many are dependent on periods of darkness for safe foraging near the surface, before migrating back to depth during daytime. When daylight lasts for 24 hr during the Arctic summer, these fish are trapped in deep waters void of prey because it is never safe to forage in the shallow waters where zooplankton prey are found. Hence, they are left with two poor options, starvation at depth or depredation while foraging. Our model predicts surplus energy, vital for reproduction and growth, to halve from 50–85°N and annual survival to drop by two-thirds over a narrow range of 10° of latitude around the Arctic Circle. Thus, low recruitment and high predation mortality during summer make polar waters population sinks for mesopelagic fishes because of the extreme seasonality in light.

Main conclusions: At high latitudes, foraging mesopelagic fishes are exposed to sunlight in upper waters also at night. This makes them easy prey for visual predators, which limits their poleward distribution. Our findings highlight the importance to think beyond temperature to explain high-latitude range limits.

1 | INTRODUCTION

Mesopelagic fishes inhabit the ocean twilight zone, the 200–1,000 m depth interval (or mesopelagic zone) where the light intensity is between 10^{-9} and 10^{-1} μmol quanta m^2/s (Kaartvedt et al., 2019). Their global biomass is on the order of 1,000 to 10,000 million tonnes (Gjøsæter & Kawaguchi, 1980; Irigoien et al., 2014; Proud et al., 2019), maybe 10–20 times that of all other fishes combined. About half of all organisms forming the deep scattering layers (Klevjer et al., 2016), primarily fish, zooplankton, squid, and jellyfish, around 5,000 million tonnes globally, rise towards the surface at night and migrate down to depth during daytime. Diel vertically migrating (DVM) mesopelagic fishes therefore play an influential role in oceanic food webs (Cherel et al., 2010; Connan et al., 2007; Horning & Trillmich, 1999; Naito et al., 2013), carbon sequestration, and biogeochemical cycling (Aumont et al., 2018; Bianchi et al., 2013; Davison et al., 2013). Due to their estimated high global biomass, there is also renewed interest in the commercial exploitation of mesopelagic fishes (Prellezo, 2019; St. John et al., 2016). Mesopelagic fishes are found everywhere in the world's oceans, yet their abundance and acoustic backscatter strongly decrease in polar waters, both in the Southern (Escobar-Flores et al., 2018a, 2018b) and Northern Hemispheres (Gjøsæter et al., 2017; Knutsen et al., 2017; Kristoffersen & Salvanes, 1998; Norheim et al., 2016; Sameoto, 1989; Siegelman-Charbit & Planque, 2016). In Arctic waters north of Svalbard (> 79°N), myctophids (or lanternfish) only represent 2% or less of the biomass (Geoffroy et al., 2019), while in most other areas they are a dominant taxon in the mesopelagic zone (Jones & Checkley, 2019). Given their abundance and near-global distribution, the question is what limits their success at high latitudes?

The extensive diel vertical migrations of many mesopelagic fishes are commonly interpreted as a game of hide and seek (Bianchi & Mislan, 2016; Hays, 2003). Most mesopelagic fishes are small and slow planktivores, that in well-lit waters are easy prey for visual predators such as piscivorous fishes, and closer to the surface marine mammals (Naito et al., 2013; Stewart et al., 2018) and seabirds (Connan et al., 2007). Therefore, it is generally assumed that DVM mesopelagic fishes seek the best trade-off between visual feeding aided by their light-sensitive eyes (de Busserolles & Marshall, 2017; Musilova et al., 2019) and staying undetected by predators whose eyes work best under more light. The resulting behaviour is that DVM mesopelagic fishes are found in ambient light intensities typically spanning some orders of magnitude, and appear to track this light comfort zone (LCZ) during day as well as night (Aksnes et al., 2017; Klevjer, Melle, Knutsen, & Aksnes, 2020; Langbehn et al., 2019; Røstad et al., 2016a, 2016b). According to this interpretation, mesopelagic vertical migrators can feed more in upper waters during night, where zooplankton prey is more abundant, than at depth during daytime. Such behaviour ensures that their light exposure is low during both day and night, so that their mortality from visual predation is minimized.

While light penetration predominantly structures the vertical distribution of mesopelagic organisms (Aksnes et al., 2017; Kaartvedt et al., 2019), the environmental drivers and mechanisms that limit the poleward distribution of mesopelagic fishes remain unclear. Here, we investigate the untested hypothesis that the extreme photoperiod at polar latitudes constrains their distribution (Kaartvedt, 2008; Kaartvedt & Titelman, 2018; Sameoto, 1989).

We explore this hypothesis by dynamic state modelling (Houston & McNamara, 1999; Mangel & Clark, 1988) of optimal migratory behaviour in a seasonal environment along a latitudinal gradient (50–85°N, Figure 1a). This approach is rooted in evolutionary ecology, and we include explicit mechanisms of temperature-dependent physiology and light-dependent foraging interactions (Figure 1d). We have previously found high agreement between model predictions and acoustic observations along a latitudinal transect in the Norwegian Sea (Langbehn et al., 2019).

2 | MATERIAL AND METHODS

2.1 | A dynamic state-variable optimization model

We use a state-dependent life history model that integrates explicit mechanisms for physiology and visual encounters. The model uses stochastic dynamic programming (Clark & Levy, 1988; Houston & McNamara, 1999; Mangel & Clark, 1988) to predict optimal DVM behaviour in a mesopelagic fish, characterized as the myctophid *Benthosema glaciale*, through the shifting seasons, repeated for a range of positions along a latitudinal gradient from 50° to 85°N (Figure 1a). The case studied here is highly relevant for the distribution of DVM mesopelagic fishes at high latitudes. *Benthosema glaciale* is prominent among the diel vertical migrators and dominates the catches of mesopelagic fishes in the Norwegian Sea and Iceland Sea (Klevjer, Melle, Knutsen, Strand, et al., 2020). The Nordic Seas (the Greenland, Iceland, and Norwegian Seas) are the only deep ocean basins globally above the polar circles that remain largely ice-free year-round. Our model finds optimal risk-taking, energy allocation, and migration strategies from multiple trade-offs in a given ecological system. We refer readers to Supporting Information Appendix S1 for a copy of the original model description, including all equations, originally published as a supplement to Langbehn et al. (2019). Further, a list of model parameters (Supporting Information Table S2.1) and the Fortran source code (Supporting Information Appendix S4) can also be found in the Supporting Information.
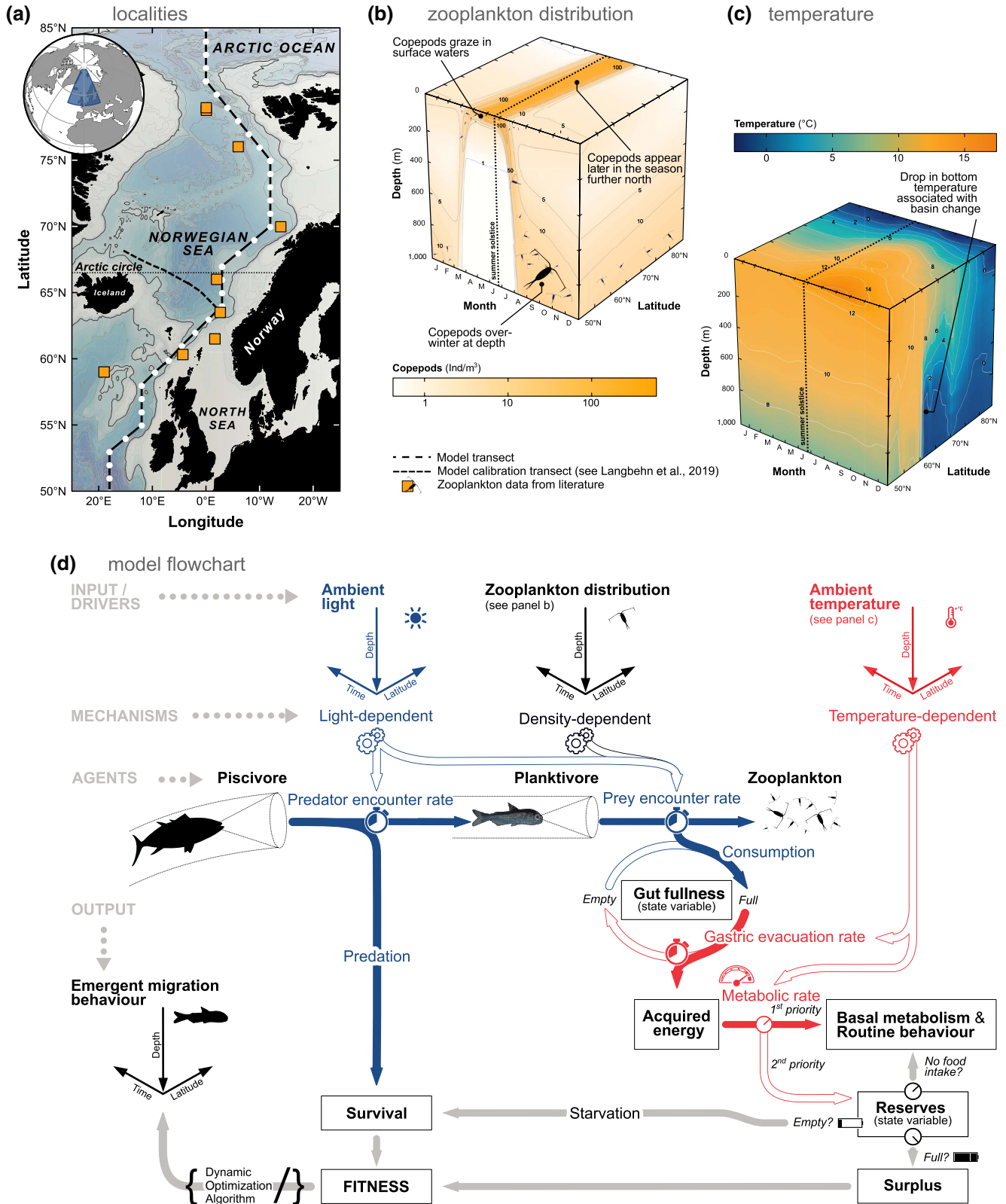
FIGURE 1 From data to predictions through mechanistic modelling. (a) Map of the study area shows the primary model transect (solid black line and white dots), a secondary transect used to validate the model with observations (Langbehn et al., 2019), and the zooplankton sampling sites (orange squares) used to inform the prey field. Data input to the model are (b) the zooplankton prey field based on literature values and (c) ocean temperatures along the model transect from the Greenland-Iceland-Norwegian Seas Regional Climatology (Seidov et al., 2018). Surface light intensities are modelled, see Supporting Information Appendix S1 for details. (d) Model flowchart of drivers, mechanisms, and agents

2.2 | Temperature environment

In the model, we use NOAA's Greenland-Iceland-Norwegian Seas Regional Climatology version 2 (Seidov et al., 2018) as the 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 1,500 m depth. We use cubic spline interpolation to convert these to the resolution of our model: daily temperature fields with a vertical resolution of 10 m, between the surface and 1,000 m depth (Figure 1c).

2.3 | Surface light and water clarity

In our model, light at the sea surface varies with latitude, the time of day, and season. Surface light calculations are adopted from the ESOP2 version of MICOM (Drange & Simonsen, 1996). Light calculations were modified to allow twilight to fade into starlight, assumed at 10^{-9} that of peak surface light at the time the sun sets below the horizon (Ryer & Olla, 1999). We do not account for lunar light since bright moonlight is about 3×10^{-6} that of sunlight, that is, on the order of 3×10^{-3} μmol quanta m^2/s (Cohen et al., 2020; Denton, 1990). Therefore, moonlight only becomes a relevant driver of vertical migration behaviour where and when it is the dominant source of light, that is, during nighttime at low latitudes, or during the darkest parts of the polar night at high latitudes (see e.g. fig. 3.4 in Cohen et al., 2020). While moon phase affects mesopelagic scattering layer depth (Prihartato et al., 2016), and in some cases generates cascading effects across trophic levels (Hernandez-Leon et al., 2010; Horning & Trillmich, 1999), the expected effect on our predictions is small (but see Section 4.6 on model limitations).

For simplicity we assume no effects of waves or overcast on reflection of surface light but acknowledge that both factors contribute to variation in light along the latitudinal gradient, particularly when the sun is low around dusk and dawn. Surface light calculations have been validated against observations from the southern Norwegian Sea (Langbehn et al., 2019). Light in water decays exponentially with depth at a rate that depends on water clarity. 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, .052 per m for the upper 100 m and .034 per m below (Norheim et al., 2016).

2.4 | Predator abundance and predation risk

Here, we neither model predator population dynamics nor predator foraging behaviour explicitly. Instead, we assume a constant predator abundance of 5.0×10^{-6} ind./m^3 throughout the water column. This value was chosen to be within the range of predator abundances in a nearby fjord system where densities of piscivorous fishes range between 2.5×10^{-6} and 1.2×10^{-5} ind./m^3 (Staby et al., 2013). The efficiency of visual foraging by piscivorous fishes is modelled using the same equations as for zooplankton encounters by mesopelagic fishes (see Supporting Information Appendix S1 for details) but with different parameter values. Predator foraging efficiency declines with depth as light from the surface fades – to a level where predator abundance does not affect predation risk. Prior sensitivity analyses have shown migration behaviours to be insensitive to variation in predator abundance within one order of magnitude (Langbehn et al., 2019). At the optimal predicted depth for myctophids (which have eyes uniquely adapted to vision in dim light), light intensities are just below the visual threshold of their epipelagic predators with less light sensitive eyes (Supporting Information Figure S3.1). Therefore, increasing the number of predators in the model but not their eye sensitivity will only increase predation pressure at light intensities already avoided by myctophids with little or no change in experienced predation risk. However, the eye sensitivities of mesopelagic fishes and their predators are hard to quantify. We used values that correspond to the upper and lower ambient light intensity observed for the mesopelagic scattering layer, dominated by *B. glaciale* (Klevjer, Melle, Knutsen, Strand, et al., 2020; Norheim et al., 2016) in the study area, 10^{-8} mW/m^2/nm at 486 nm for the mesopelagic fish and 4×10^{-4} mW/m^2/nm at 486 nm for the piscivores (Norheim et al., 2016, see fig. 4b therein).

2.5 | Zooplankton

We conceived idealized zooplankton prey fields, with explicit seasonal vertical migration but without diel vertical migrations (reasons discussed below), population dynamics, and a delayed phenology with increasing latitude (Figure 1b). We aim to reflect general characteristics of seasonal dynamics along the latitudinal gradient, rather than local realism. We base our prey field on data available from the literature (Espinasse et al., 2018; Gislason et al., 2007; Gislason & Silva, 2012; Gluchowska, Dalpadado, et al., 2017; Gluchowska, Trudnowska, et al., 2017; Heath et al., 2000; Irigoien, 2000; Melle et al., 2004, 2014; Nöthig et al., 2015; Østvedt, 1955) (for localities see Figure 1a). Here, we consider copepods of 2.7 mm length, that is, CV-CVI *Calanus finmarchicus*, CIV-CV *Calanus glaciale* or CIII-CV *Calanus hyperboreus*, as suitable prey for *B. glaciale* (Pepin, 2013). We parameterize the spatio-temporal distribution of these copepods from observations showing that they perform extensive seasonal vertical migration to diapause during parts of the year, 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 ind./m^3, leaving deep waters almost void with concentrations < 1 ind./m^3. In autumn, surface aggregations disperse and copepods descend into deeper waters between 600 and 1,200 m depth for hibernation (Espinasse et al., 2018; Gislason et al., 2007) where they spread out over a large vertical range, causing densities to be low but

homogenous across depth (Irigoien, 2000; Melle et al., 2004). In the model environment, the total number of copepods varied seasonally between 2,000 and 16,000 ind./m², declining continuously after the population peak in summer until next year when abundance sharply increased again due to reproduction (Heath et al., 2000; Østvedt, 1955). We assume a shift in annual phenology with increasing latitude, such that the ascent and descent of zooplankton occurred gradually later in the season (Melle et al., 2004). We parameterized this as a shift of 1.3 days for every 1° increase in latitude, while the length of the productive season remained constant across latitudes.

Zooplankton do not perform diel vertical migrations in the model. We acknowledge this is a simplification, but previous tests have shown little effect on the predicted behaviours in our model (Langbehn et al., 2019). This assumption is further warranted because zooplankton diel vertical migrations are confined to the epipelagic. At night near the surface, zooplankton will always be susceptible to predation from mesopelagic fishes (Kaartvedt et al., 2019). While regular diel vertical migration may help zooplankton avoid epipelagic planktivores, it probably does not provide them with efficient protection from mesopelagic predators from below. If zooplankton diel vertical migrations were to avoid predation by mesopelagic fishes, one would expect an inverse migration pattern (Ohman et al., 1983) where copepods evade surface waters at night. However, even then, twice a day copepods would have to pass through light intensities optimal for feeding by mesopelagic planktivores migrating in the opposite direction (Clark & Levy, 1988; Supporting Information Figure S3.1).

2.6 | Sensitivity analysis

We tested the sensitivity of our predictions to perturbations of the initial values for 37 abiotic and biotic parameters, resulting in 73 model runs. Most parameters were varied by ± 20%. For a few cases where uncertainty in the initial parameter values was high, a wider parameter range was adopted. Accordingly, we varied the initial parameter values for composite eye saturation and starlight by one order of magnitude and predator abundance by ±50%.

3 | RESULTS

Our model predicts that waters beyond the polar circle are a population sink for DVM mesopelagic fishes (Figure 2). In our simulations, annual survival drops to about one third when crossing from sub-Arctic to Arctic latitudes (Figures 2a and 3d), while surplus energy, that is, energy the individual potentially could channel towards reproduction or growth, was gradually more than halved (Figures 2b and 3b).

At high latitudes, only 20% of the 6-cm length class, representative of mature adults of the myctophid *B. glaciale* aged 4–6 years (Gjøsæter, 1981), survived to the end of the year according to our
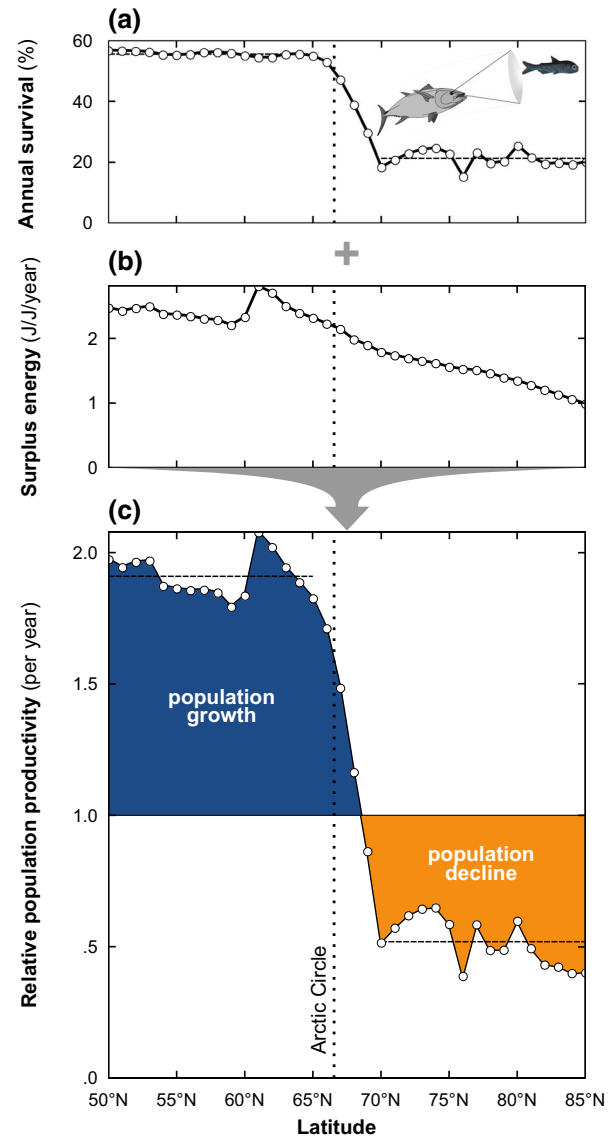

FIGURE 2 Arctic waters are population sinks for diel vertically migrating (DVM) mesopelagic fishes. (a) Our model predicts that annual survival and (b) surplus energy decrease poleward, (c) resulting in a negative population growth at latitudes above the Arctic Circle. Dashed lines indicate the mean across 50–65° and 70–85°N. The spike in surplus energy and population growth around 60°N is explained by cooler deep waters (see Figure 1c) and therefore lower metabolic demands in the Norwegian Sea basin (see Figure 1d)

model. A reduction in annual surplus energy together with high predation mortality during summer explain the predicted negative population growth (Figure 2c).

Towards the poles, daylight hours become increasingly seasonal, with winter darkness during the polar night, and similar periods with midnight sun during the summer months (Figure 3a). Our model predicts marked latitudinal gradients in scattering layer migration depth both during the summer and winter season (Figures 3b and 4). Little variation in optimal vertical migration depth and amplitude is predicted for latitudes below 60°N. The
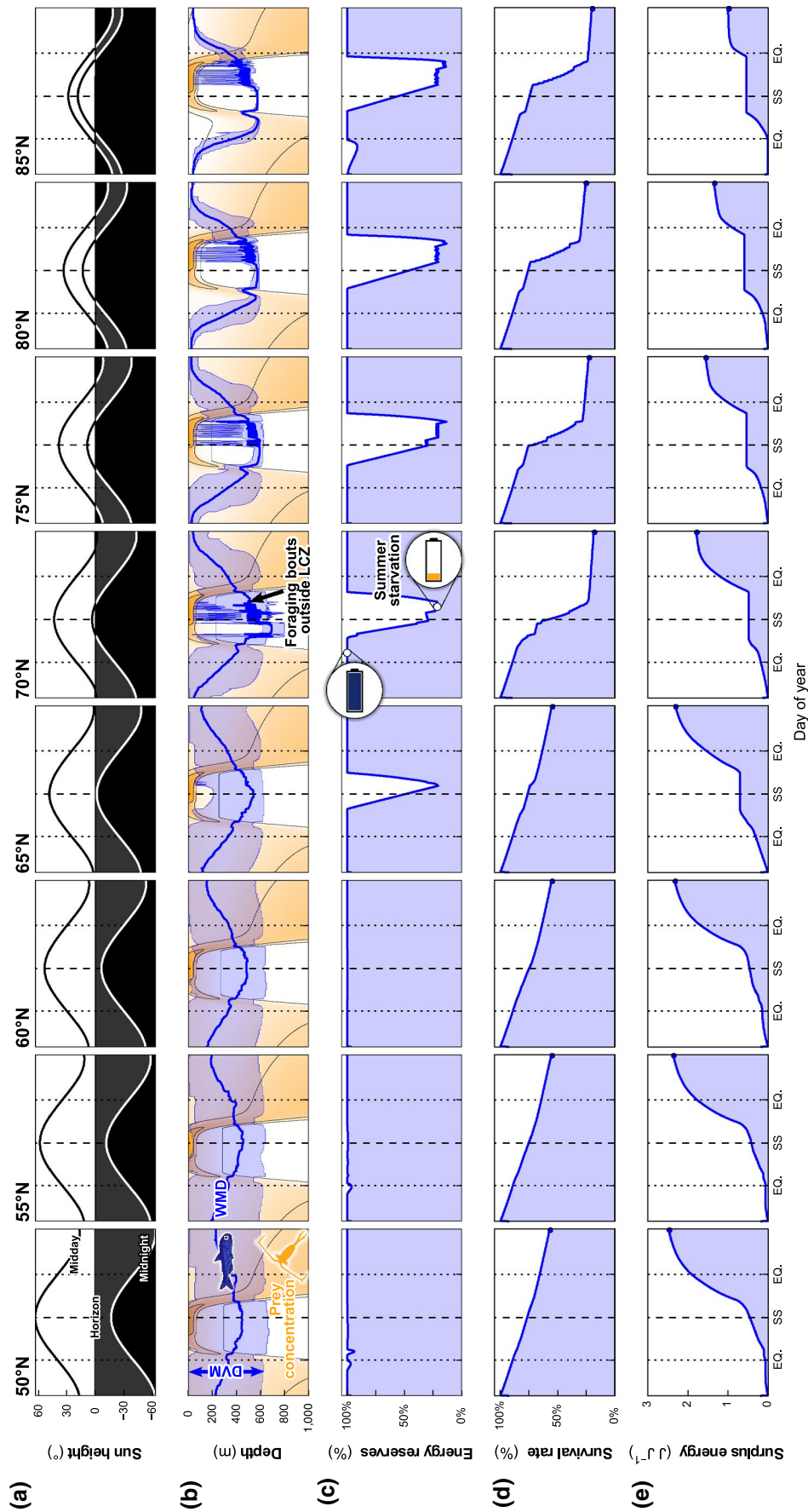
FIGURE 3 Model predictions of optimal migration behaviour, energy reserves, survival rate, and surplus energy alongside relevant drivers for selected latitudes along a transect from 50–85°N. (a) Sun height relative to the horizon, with lines marking the daily extreme points at midnight and midday. (b) Optimal vertical migration depth. The blue envelope shows the diel vertical migration amplitude over a 24-hr cycle and the thick blue line indicates the weighted mean depth (WMD). Intensity of orange background shading shows prey concentrations, with stronger colour indicating higher concentrations, for details see Figure 1b. (c) Individual energy reserves as percent of maximum. (d) Cumulative survival rate from the beginning of the year. Slope of the blue line reflects instantaneous mortality. (e) Cumulative surplus energy from the beginning of the year. Slope of the blue line indicates instantaneous surplus energy gain. In all panels, vertical dotted lines mark the vernal and autumnal equinox (EQ.) and the dashed line denotes midsummer, that is, summer solstice (SS). LCZ = light comfort zone

(a) Winter

(b) Summer
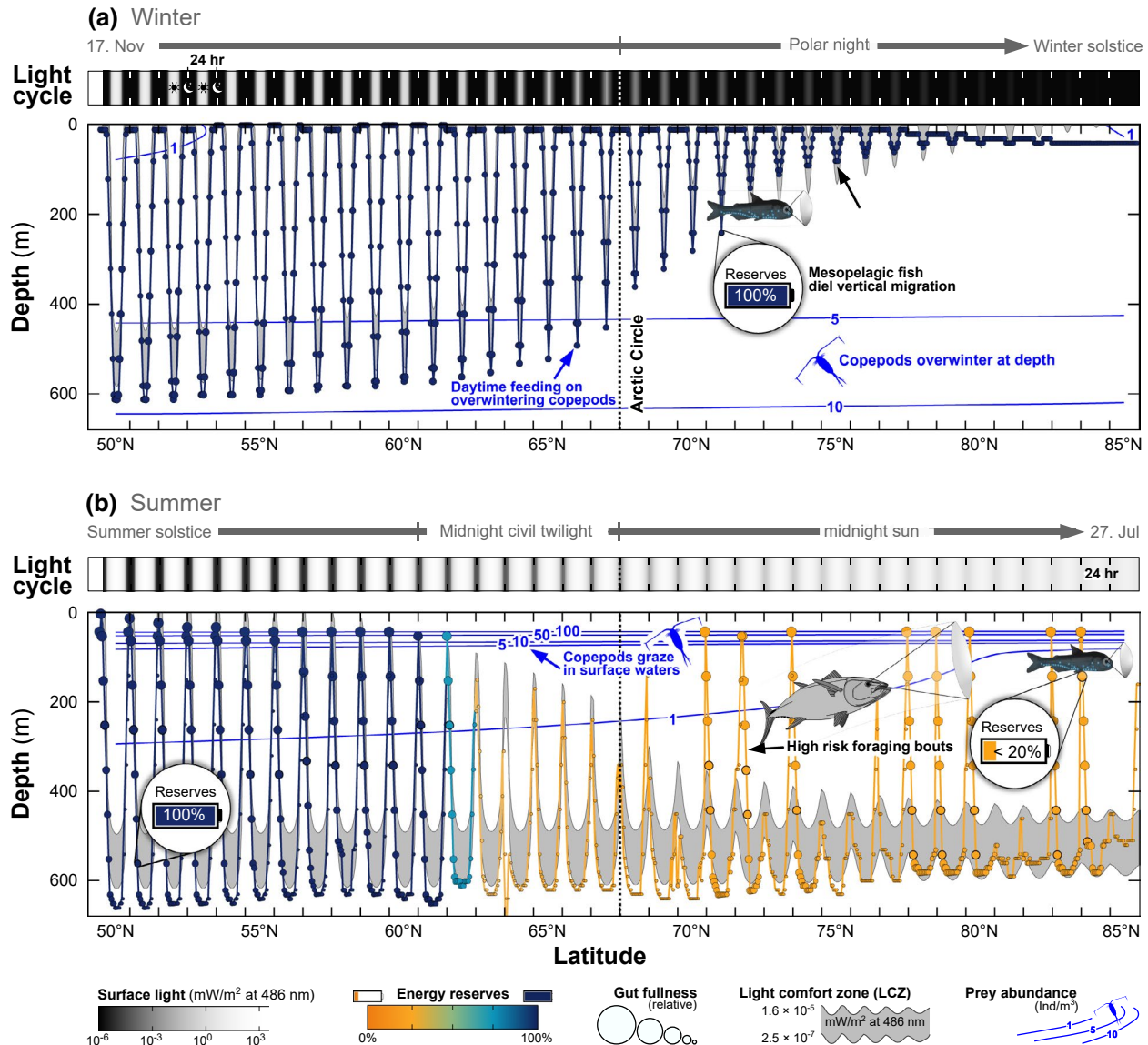
FIGURE 4 Predicted vertical migration behaviour in a mesopelagic fish along a south–north transect (50–85°N) in the Norwegian Sea shown in Figure 1. (a) In winter, daylight fades towards higher latitudes and optimal nighttime distributions (dark blue line and dots) shift closer to the surface where mesopelagic fishes with diel vertical migration find suitable light conditions (grey shading) at all times. At this time of year, their zooplankton prey (blue contour lines) is dispersed and mostly hibernates at great depth. Low temperatures, and consequently low metabolic demands, allow the mesopelagic fish to maintain high energy reserves (line and dot colour, with dark blue indicating high levels of reserves) throughout the polar night despite the low number of prey encounters. (b) In summer, when temperatures are higher, the nights are lighter further north, zooplankton remains near the surface, and the mesopelagic fish struggles with starvation (line and dot colour, orange indicating low levels of reserves) because it is never safe for it to forage near the surface. Individuals running short of energy accept higher risk and make foraging bouts outside the light comfort zone (grey shading) to fill their guts (larger dots indicate fuller stomachs) and thus avoid starvation but incurring greater risk of predation

optimal strategy is to follow the same light comfort zone as mesopelagic organisms in the Norwegian Sea, with light levels between 2.5×10^{-7} and 1.6×10^{-5} mW/m²/nm. However, with increasing latitude (> 60°N), optimal vertical migration depth and amplitude diverge seasonally.

At higher latitudes during winter (Figure 4a), the light comfort zone of DVM mesopelagic fishes is found closer to the surface. They track this light comfort zone through time, and their descent to depth at dawn is halted at successively shallower depths further

to the north. Whilst at < 60°N, individuals are predicted to migrate between surface waters and a daytime depth of around 600 m, just 15° to the north, the optimal migration depth is confined to the upper 100 m throughout the diel cycle (Figure 4a). In the model, the mesopelagic fish survives the winter and maintains high levels of energy reserves along the entire latitudinal gradient (Figures 3c and 4a, where dark blue indicates high energy reserves). Ample daylight at latitudes below the Arctic Circle allows mesopelagic fishes to feed on overwintering copepods at depth. With little to no daylight
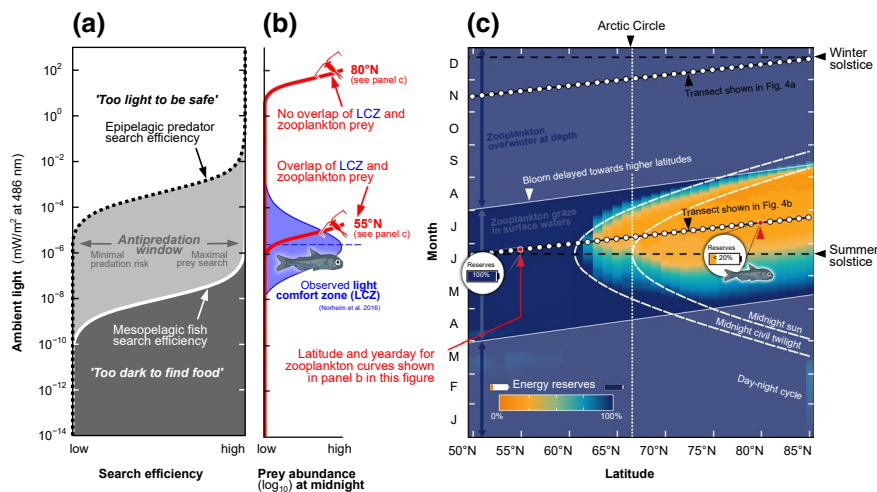
FIGURE 5 Little overlap between suitable light habitat and potential prey cause starvation at high latitudes in mesopelagic fishes with diel vertical migration. (a) The antipredation window (central light grey area) at ambient light levels where the ratio of predation risk (dotted black line) over feeding rate (solid white line) is minimal explains (b) the emergence of an apparent light comfort zone (blue shaded area) around 2×10^{-6} mW/m²/nm at 486 nm (blue dashed line), as predicted by observations (Norheim et al., 2016). In summer, at low latitudes (shown for 55°N) the light comfort zone at night overlaps with concentrations of potential prey (solid red lines), while at higher latitudes (here shown for 85°N) ambient light levels in prey-rich surface waters during summer are several orders of magnitude outside the light comfort zone. (c) In consequence, energy reserves of diel vertically migrating (DVM) mesopelagic fishes (colour coding, orange indicating low, dark blue high levels of reserves) run low when zooplankton is concentrated close to the surface (period outlined by thin solid white lines) at latitudes and times of the year with midnight twilight or midnight sun (dashed white curves). The summer and winter transects (see Figure 4a,b) are shown for reference (solid black line with white dots)

during the polar night, visual foraging at depth is limited at higher latitudes, even though mesopelagic fish have highly light-sensitive eyes. At these latitudes, cooler temperatures, and thus low metabolic demand, help sustain energy reserves despite the low number prey encounters during the polar night (Figures 3c and 4a). Yet, there is little possibility of accumulating much surplus energy (Figure 3e).

In contrast, during summer (Figure 4b) migration amplitude in the model gradually declines with increasing latitude as nighttime ascent towards the surface is halted at greater depths further north, where the days are longer and the nights lighter (Figure 3a). During the midnight sun period, even at night the light comfort zone of DVM mesopelagic fishes is confined to a depth layer of 450–600 m (indicated by the grey shaded area in Figure 4b). Consequently, DVM mesopelagic fishes are largely separated from their zooplankton prey, which at this time of year graze near the surface. As a result, the model predicts feeding rates to be insufficient to cover the energetic costs, leading mesopelagic fishes to starve (Figures 3c and 4b, where orange indicates low energy reserves). The predicted optimal strategy then becomes to intermittently abandon the relative safety of the light comfort zone and take high-risk foraging bouts to the surface (Figures 3b and 4b, where larger dots indicate fuller stomachs).

Nights during which light levels never fall below that of civil twilight emerge as a good predictor for where and when summer starvation occurs (Figure 5c). The longer the period with civil twilight (the centre of the Sun's disc is at most 6° below the horizon) or sun at night, the longer *B. glaciale* are trapped in barren deep-water, and the higher is the potential for starvation.

While the exact latitude of the predicted poleward range limit (Figure 2c) is sensitive to variation in abiotic and biotic parameters

(Supporting Information Figures S.3.2 and S.3.3), the overarching prediction that diel-vertically migrating mesopelagic fishes are excluded from high latitudes by seasonality in light holds, without exception, for all 73 model runs; our sensitivity analysis indicates a range of critical latitudes between 65° and 73°N. Previous sensitivity analyses have found the predicted behaviours similarly robust to parameter perturbations (Langbehn et al., 2019).

4 | DISCUSSION

Our simulations suggest that the extreme light regime is the main limitation for DVM mesopelagic fishes at high latitudes. We show that where daylight lasts 24 hr, time for safe foraging in the upper waters is limited. This leaves DVM mesopelagic fishes with two poor options: starvation or predation. Moreover, the other extreme, that is, continuous darkness during the polar night, renders efficient visual foraging on diapausing calanoid copepods in deep water impossible. Across the Arctic Circle, predation mortality therefore increases and energy available for reproduction decreases in our simulations. These model results support the untested 'photoperiod constraint hypothesis' (Kaartvedt, 2008).

4.1 | Changes in migration behaviour across latitudes

Our model predicts general migration patterns and depth distributions that match acoustic observations, which show a latitudinal

change in vertical migration behaviour of mesopelagic organisms across the Arctic Circle.

Observations show that during the summer months, when daylight lasts much longer at high latitudes, vertical migration amplitude decreases with increasing latitude (Klevjer, Melle, Knutsen, & Aksnes, 2020; Norheim et al., 2016; Sobolevsky et al., 1996) and the deep scattering layer community remains at mesopelagic depths day and night (Geoffroy et al., 2019; Gjøsæter et al., 2017; Knutsen et al., 2017; Norheim et al., 2016; Priou et al., 2021; Siegelman-Charbit & Planque, 2016). Moreover, at high latitudes in the Southern Hemisphere, near Antarctica, synchronized diel vertical migration patterns have on occasions been observed to disappear in response to long periods of daylight (Dietz, 1962). During winter, dim light compresses the twilight zone towards the surface in polar regions (Kaartvedt et al., 2019). Accordingly, 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 fishes (Bozman et al., 2017), suggest suitable light conditions at shallow depth during mid-winter. These large-scale patterns in migration behaviour are well reflected in the model.

4.2 | Changes in mesopelagic fish abundance and biomass across latitudes

In the North Atlantic, mesopelagic biomass, abundance, taxonomic composition, and the proportion of diel vertical migrators differ on a basin scale (Klevjer, Melle, Knutsen, Strand, et al., 2020). Clear differences exist between the basins of the Irminger and Labrador Seas in the south-west (below the Arctic Circle) and the Norwegian and Iceland Seas to the north-east (which in parts extend far above the above the Arctic Circle).

In the south-western basins, mesopelagic fish biomass and diversity are generally higher than in the north-east, and fishes account for more than half of the non-gelatinous micronekton scattering layer biomass (Klevjer, Melle, Knutsen, Strand, et al., 2020). Here, typical non-migratory species, that is, gonostomatids, contribute to the high biomass densities and a strong stationary scattering layer is present between 400 and 600 m in the Irminger Sea and a weaker one around 700 m in the Labrador Sea. It should be noted, however, that the model does not simulate fishes that feed and reside permanently in the mesopelagic and hence does not capture these stationary layers. Gonostomatids, bathylagids, barracudinas, and stomiids dominate the micronekton catches in the Irminger and Labrador Seas, and their combined weight exceeds that of myctophids (Klevjer, Melle, Knutsen, Strand, et al., 2020). In contrast, these groups appear absent (Klevjer, Melle, Knutsen, Strand, et al., 2020) or may only occur sporadically (e.g. Dalpadado et al., 1998) in the north-eastern basins of the Norwegian and Iceland Seas. An exception is Mueller's pearlside, *Maurolicus muelleri* (order: Stomiiformes), which is abundant in many fjords and near the coast of western Norway (e.g. Kaartvedt et al., 1998; Prihartato et al., 2015; Staby et al., 2013). Myctophids, exclusively represented by *B. glaciale*, are the dominant mesopelagic fish taxon in the Norwegian and Iceland Seas, but crustaceans make up about half of the non-gelatinous micronekton biomass (Klevjer, Melle, Knutsen, Strand, et al., 2020).

Across the two north-eastern basins (which are studied here), there is a strong and persistent decrease in mesopelagic acoustic backscatter (about one order of magnitude) from the south-east of the Norwegian Sea to the north-west of the Iceland Sea (Dale et al., 1999; Klevjer, Melle, Knutsen, Strand, et al., 2020; Norheim et al., 2016; Torgersen et al., 1997). This poleward decline in backscatter is consistent with observations along the Norwegian coast (Knutsen et al., 2017; Melle et al., 1993). These gradients are also reflected in the average biomass of mesopelagic catches. Across all four basins, the highest mesopelagic fish biomass estimated from catches is found in the Irminger Sea (24.5 g WW/m^2), followed by the Labrador Sea (15.4 g WW/m^2), the Norwegian Sea (0.8–1.0 g WW/m^2), and the lowest values are recorded in the northernmost basin, the Iceland Sea (0.8 g WW/m^2) (Klevjer, Melle, Knutsen, Strand, et al., 2020). Other studies have shown that catch per unit effort of *M. muelleri* decreased by at least five orders of magnitude along the Norwegian coast from 57°–80°N (Kristoffersen & Salvanes, 1998).

In the model, similar latitudinal gradients in abundance follow from the combined effects of elevated predation mortality and individuals that are unable to build up sufficient surplus energy for reproduction.

4.3 | Advection and high-latitude expatriate populations

Our model provides a unified explanation for the existence of high-latitude myctophid populations that appear unable to reproduce successfully (Saunders et al., 2017), and the steep poleward decline in mesopelagic acoustic backscatter (Escobar-Flores et al., 2018a, 2018b; Gjøsæter et al., 2017; Klevjer, Melle, Knutsen, Strand, et al., 2020; Knutsen et al., 2017; Norheim et al., 2016; Sameoto, 1989; Siegelman-Charbit & Planque, 2016). Both in the Southern Ocean and in the sub-Arctic Atlantic Ocean, observations suggest that myctophid (or lanternfish) populations at the poleward range margins are non-reproducing, and consist entirely of adult expatriates advected from lower latitudes (Sameoto, 1989; Saunders et al., 2017), with the largest individuals found closest to the poles (Saunders & Tarling, 2018). Similar latitudinal size gradients seem to also apply in the North Atlantic, with few small (< 3 cm) individuals of *B. glaciale* occurring in the Iceland Sea (Klevjer, Melle, Knutsen, Strand, et al., 2020). Our model provides a mechanistic explanation for both the latitudinal size gradient and low reproductive success. The model simulations suggest that at higher latitudes, myctophids are unable to accumulate enough surplus energy to reproduce. Moreover, lack of reproduction implies that the size distribution will be skewed towards larger adult sizes.

Constant passive advection from temperate or sub-polar waters may support populations at higher latitudes through source–sink dynamics (Gjøsæter et al., 2017; Knutsen et al., 2017) and thus

subsidizes high-latitude food webs (Saunders et al., 2017). This is supported by the observations of advected adult expatriates at poleward range margins (Sameoto, 1989; Saunders et al., 2017). In the Southern Ocean, many top predators feed frequently on meso-pelagic fishes (Cherel et al., 2010; Connan et al., 2007). Particularly, the abundant endotherm predators such as birds and marine mam-mals benefit from advection of cold, sluggish, and distressed prey into polar waters (Grady et al., 2019). In the Norwegian Sea, meso-pelagic organisms that are advected northward with Atlantic Water masses may reach the Arctic–Atlantic gateway around 1,500 km further upstream in 6–12 months (Gjøsæter et al., 2017). Our model predicts that mesopelagic fishes are forced to take foraging bouts to the surface during the midnight sun period, where predation risk is high. Smaller individuals have smaller stores and a higher specific metabolic rate than large individuals, forcing them to take the risk associated with feeding near the surface more often. Consequently, one would expect large individuals to be more likely to survive the drift further into higher latitudes.

It seems unlikely that myctophids can escape advection and thus starvation or increased risk of predation through horizontal migra-tion. Acoustic target tracking of individual *B. glaciale* has shown that this species essentially acts as a plankton, passively drifting with weak tidal currents back and forth (Kaartvedt et al., 2009). Gjøsæter et al. (2017) estimated an advection velocity of 5–10 cm/s in the eastern part of the Norwegian Sea and up to 30 cm/s in the core of the swift West Spitsbergen Current. Consequently, ocean current velocities in the Norwegian Sea are about 2–5 times higher than the generally assumed swimming velocities of *c.* 1 body length/s (here assuming adults of 6 cm), making it unlikely for *B. glaciale* to be able to swim against the strong northward Atlantic water flow.

4.4 | Photic barriers arise due to little overlap between suitable light habitat and potential prey

Our model predicts the main constraint for the distribution of DVM mesopelagic fishes at high latitudes is little overlap between their light comfort zone and the location of potential prey. A theoretical explanation for the emergence of a light comfort zone (Langbehn et al., 2019) is provided by the antipredation window hypothesis (Clark & Levy, 1988). The antipredation window is the time and space where the ratio of predation risk over feeding rate is mini-mal. For mesopelagic fishes like *B. glaciale* this is where light permits feeding on zooplankton but constrains visual detection by piscivores (Figure 5a). This partly arises from differences in eye sensitivity be-tween species, but also because small mesopelagic fishes detect more numerous small prey at short distances and are less sensitive to light scattering than piscivores that search for larger visual objects at longer distances (De Robertis et al., 2003; Fiksen et al., 2002; Giske et al., 1994; Utne-Palm, 2002).

The antipredation window only exists if concentrations of prey overlap with the light comfort zone. For latitudes with a clear diel light-cycle, there is at least one window of opportunity per day

where conditions are right and allow mesopelagic fishes to feed. In winter, this occurs when daylight hours allow foraging on overwin-tering copepods at depth and during summer close to the surface at night when it is safe (Figures 4 and 5, Supporting Information Figure S3.1). For latitudes with a more seasonal light cycle and little diel variation in light, our results reveal an increasing ver-tical mismatch between the light comfort zone of our mesope-lagic fish and the distribution of suitable prey (Figures 4 and 5). Even though recent studies have shown ongoing biological activ-ity in the upper waters during the polar night (Berge et al., 2015; Hobbs et al., 2018) and discussed diapause as a facultative strat-egy (Kvile et al., 2019), the majority of calanoid copepods, which are prominent prey of *B. glaciale*, will already have left the surface waters and descended for hibernation. At depths of 600–1,200 m (Edvardsen et al., 2006; Melle et al., 2004) they are dispersed and diluted where it is too dark for visual predators, even mesopelagic fishes, to feed efficiently (Figure 3b).

South of the Arctic Circle, where there is sufficient daylight during winter, daytime predation at depth by mesopelagic fishes is a major contributor to the mortality of overwintering copepods (Bagøien et al., 2001; Espinasse et al., 2018; Gislason et al., 2007) and this is also well predicted by the model (Figure 4a).

In our model, the starvation–predation trade-off is state-dependent. Mesopelagic fishes are small and their energy reserves insufficient to last through the entire midnight sun period, so waiting within the safety of their light comfort zone throughout the sum-mer is not an option. Cutting back on metabolic expenditures by migrating to cooler waters at greater depths could help stretch the reserves and is predicted by the model as a strategy near the Arctic Circle, where the period without dark nights is short. At higher lat-itudes, this strategy is futile as seasonality in light becomes even more extreme and the energy reserves run low before the end of the midnight sun period.

4.5 | The role of mesopelagic fishes in the structure and function of Arctic marine ecosystems

The absence of mesopelagic planktivores may also contribute to the larger body size (Brooks & Dodson, 1965) and the multi-year life cycles of high-latitude copepods such as *C. 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 unvi-able where mesopelagic fishes forage on overwintering stages at the rate they do in more southerly waters (Bagøien et al., 2001; Espinasse et al., 2018; Gislason et al., 2007). During their active period in summer, these copepods are large visual targets and profitable food for seasonally migrating epipelagic planktivores with long feeding migrations.

The predicted and observed decline in the abundance of verti-cally migrating mesopelagic fishes beyond the Arctic Circle leaves a niche vacant for horizontally migrating planktivores like herring,

capelin, and mackerel at high latitudes. Interestingly, in Klevjer, Melle, Knutsen, Strand, et al. (2020), pelagic fishes, that is, herring, were only observed in the north-eastern basins (Norwegian and Iceland Seas). In the south-western basin (Irminger and Labrador Seas), they contributed nil to the acoustic backscatter where trawl catches indicated *c.* 15 to *c.* 20 times higher mesopelagic fish biomass. In contrast to DVM mesopelagic fishes, epipelagic planktivores profit from longer feeding days during summer (Ljungström et al., 2021), a strategy that is predicted to receive a boost by the retreat of sea-ice in the near future (Langbehn & Varpe, 2017; Varpe et al., 2015).

4.6 | Model limitations

While the model aligns well with observations, it has several limitations. The eyes of mesopelagic fishes are uniquely adapted to dim-light (scotopic) vision (de Busserolles & Marshall, 2017; Musilova et al., 2019), and they may be unable to utilize the strong daylight in upper waters. Daytime surface light can be 9–12 orders of magnitude higher than that of their normal daytime habitat (Kaartvedt et al., 2019) and might cause light-induced photoreceptor damage. Our model does not account for such a mechanism. However, our predictions of daytime foraging bouts into surface waters match observations where regular diel vertical migration patterns break up when daylight lasts for most of the day (Dietz, 1962). The model also does not allow for the emergence of alternative predator-avoidance behaviours, such as schooling, which has been observed for *M. muelleri* in light summer nights (Prihartato et al., 2015). Such behavioural adaptations could help extend distributions into more seasonal light environments.

The lanternfish *B. glaciale* (which we model here) is abundant in waters between 4 and 16 °C and occurs from cold Nordic seas (with temperatures < 1 °C) to the Mediterranean Sea (Halliday, 1970). Globally, myctophids occur in high numbers in a much wider range of thermal habitats, from −1 °C (Gjøsæter et al., 2017; Saunders & Tarling, 2018) at high latitudes to the sub-tropical Red Sea where even bottom waters reach 21 °C (Klevjer et al., 2012). In many locations, a regular vertical migration cycle may expose individuals to a daily temperature variation of up to 20 °C (Klevjer et al., 2016; Wang et al., 2019), and their planktonic life style transports them with ocean currents across ocean habitats that vary substantially in vertical temperature profiles. The latitudinal decline in abundance in the North Atlantic is observed also within the northward-directed outflow of the Gulf Stream that transports relatively warm Atlantic water far beyond the Arctic Circle, where mesopelagic biomass is lower even though mesopelagic fishes are found in abundance in colder water at lower latitudes. It is therefore not obvious that temperature alone poses a strong constraint on the spatial distribution of many mesopelagic species. Unfortunately, fossil otolith data from the Arctic Ocean deposited during the late Miocene or Pliocene, an analogue of a warmer future climate, are unknown but could help

resolve whether mesopelagic fish distribution extended further north during earlier periods of warming.

Our model is parameterized with, and validated against, observations from the Norwegian and Iceland Seas, which may not fully capture the southern and northern extremes of the transect, which therefore should be interpreted more carefully. Specifically, our zooplankton parameterization is representative of a boreal or Arctic community dominated by large calanoid copepods with a diapausing life history strategy, an assumption that is justified for these high-latitude ecosystems (Melle et al., 2004, 2014). However, the prevalence of diapausing copepods decreases towards the southern end of our model transect. Here, smaller temperate species that remain active throughout the winter become numerically more important. This is not captured in our prey field. In the Rockall Trough west of Ireland, towards the southern end of our transect, adult individuals of *B. glaciale* are nevertheless predominantly feeding on calanoid copepods, with *Pleuromamma robusta* being the dominant species in their diet (Kawaguchi & Mauchline, 1982). Their minimum adult female size is 2.7 mm (Ferrari & Saltzman, 1998). This coincides with the copepod size in our model. We assume lower prey abundances in surface waters during the wintertime along the entire transect as copepods in the model hibernate at depth. If, however, at low latitudes copepods were to remain active in the upper water column throughout the year, the model would still predict DVM behaviour as the optimal strategy, but with higher food intake rates at night near the surface rather than during daylight hours at depth.

In some years, seasonal ice-cover may influence the underwater light regime at the northern end of the transect, adding to the pronounced winter darkness but also shading the water column far into the midnight sun period. In situ irradiance below sea-ice may be reduced by several orders of magnitude, creating near surface light environments similar to that found during daytime at depths of several hundred metres in the mesopelagic zone elsewhere (Kaartvedt et al., 2019). Thus, mesopelagic organisms that migrate to maintain position within a light comfort zone (Aksnes et al., 2017; Klevjer, Melle, Knutsen, & Aksnes, 2020; Langbehn et al., 2019; Røstad et al., 2016a, 2016b) would be expected to show shallower distribution in ice-covered waters, which indeed has been found in the ice-covered Southern Ocean (Ainley et al., 1986). But, acoustic observations from ice-covered waters north of Svalbard found stationary mesopelagic scattering layers at depths between 280 and 600 m, with highest densities just below 400 m (Priou et al., 2021). These depths are similar to those predicted by our model, although shading by sea-ice was not considered since we expect (and show) photoperiodic constraints to emerge at latitudes far below where sea-ice can reasonably be expected to occur in the Norwegian Sea west of Svalbard. Differences in species composition of the mesopelagic assemblage may explain differences in scattering layer depth. Instead of myctophids, scattering layers north of Svalbard were mainly composed of juveniles of beaked redfish, polar cod, and demersal species such as Atlantic cod and haddock (Geoffroy et al., 2019; Knutsen et al., 2017; Priou et al., 2021).

Lunar light is not captured in the model but is unlikely to change the overall predictions. During the polar night, the model predicts daytime vertical distributions in the upper 200 m at high latitudes (Figure 4a). Because the sun remains below the horizon for the full 24-hr cycle, bright light from a full moon may cause a deepening of mesopelagic scattering layers during the full moon period relative to what we predict here. However, this is unlikely to significantly alter foraging rates as most copepods overwinter at much greater depth (Melle et al., 2004). At latitudes below the Arctic Circle, the model predicts that DVM mesopelagic fishes can forage on overwintering copepods during daytime at depths below 400 m (Figure 4a). Here moonlight only becomes the dominant source of light at night, and hence has little consequence for daytime foraging. The same is true for the midnight sun period at high latitudes, where sunlight prevails throughout the 24-hr cycle (Figure 4b). Consequently, moonlight would only affect foraging rates of DVM mesopelagic fishes at latitudes below the Arctic Circle during summer when copepods graze near the surface (Figure 4b). Then, during moonlit nights, vertically migrating organisms may halt their upward migration at greater depth. However, since the model predicts that DVM mesopelagic fishes maintain high levels of energy reserves at low latitudes during the summer, periodic short-term starvations during the full moon period are unlikely to cause changes to the poleward range limits predicted here. Such variation falls within the range covered by the sensitivity analysis.

Furthermore, our findings do not apply to permanently deep-living species, for which variations in downwelling sunlight are of little or no relevance for vital processes, as might be the case for, for example, *Cyclothone* spp. Non-migratory mesopelagic fishes may feed on cyclopoid copepods such as *Oithona* spp. and *Oncaea* spp., which are considered important in fragmentation of detritus/particulate organic matter (POM) (Mayor et al., 2020). Potentially, POM and the associated microbial biota are an important food source for these copepods, and thereby for resident mesopelagic fishes and invertebrates. This trophic pathway, which is not realized in our model parameterization, should be explored in future field and model studies.

4.7 | Conclusion

In Ljungström et al. (2021), we tested the persistence of a photic barrier under a representative 2 °C warming of surface waters and found that poleward range shifts of DVM mesopelagic fishes into the Arctic Ocean are not likely to follow from global warming (Kaartvedt, 2008; Kaartvedt & Titelman, 2018). Taken together, this reasoning and our extensive sensitivity analysis (Supporting Information Figures S3.2 and S3.3, but see also supplement to Langbehn et al., 2019) suggest that the changing light regime at high latitudes is a first-order driver of DVM mesopelagic fish distribution and population patterns at these latitudes, which are only slightly modulated by temperature.

Recent reviews have highlighted the need for mechanistic models and a better understanding of the interaction between physiology, ecology, and the photic environment as key to reliable predictions for climate-driven species re-distributions in high-latitude environments (Huffeldt, 2020; Spence & Tingley, 2020; Twiname et al., 2020). Photoperiod limits poleward distributions in higher plants (Bjorkman et al., 2017), diapausing insects (Lehmann et al., 2014), and corals (Muir et al., 2015). Here, using predictions from a mechanistic model, we add fish as a prominent vertebrate group to the list. Many mesopelagic fishes have found a niche in twilight conditions where their predators have difficulties finding them, while they are still able to find their prey. A similar mechanistic loophole of light and vision may also apply to other vertebrate groups foraging in dim light, such as bats, owls, and nightjars. The seasonal cycle of continuous light and darkness is a powerful environmental factor for numerous animals depending on vision, and the challenges that follow can be important for their range limits.

AUTHOR CONTRIBUTIONS

TJL and CJ conceived the study and developed the model. DLA, SK, and ØF helped with model input and parameterization. TJL, CJ, and GL analysed the output. TJL wrote the paper. All co-authors interpreted results, commented, and edited.

DATA AVAILABILITY STATEMENT

All data and code are contained in the main text, the Supporting Information or public repositories (Seidov et al., 2018).

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