WILEY **Global Change Biology**

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

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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
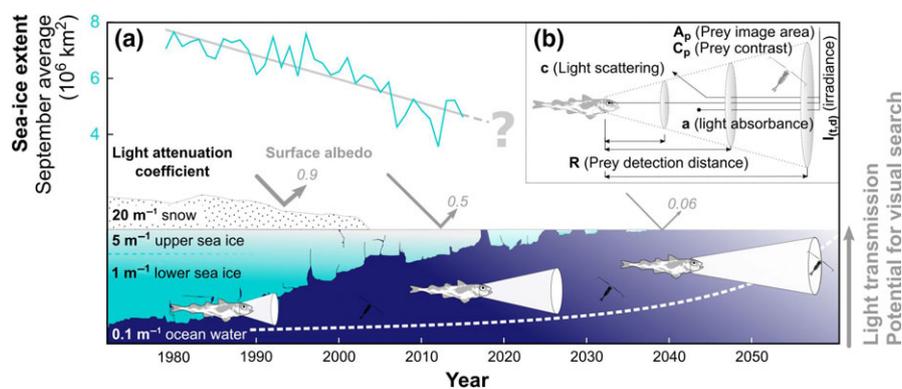
FIGURE 1 Visual search in a changing Arctic Ocean: (a) Less sea ice means increased light, which results in more efficient visual search. Sea-ice extent has retreated in the past (turquoise line) and is projected to continue in the future (extended linear trend line, grey) with consequences for the pelagic 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 [Colour figure can be viewed at wileyonlinelibrary.com]

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
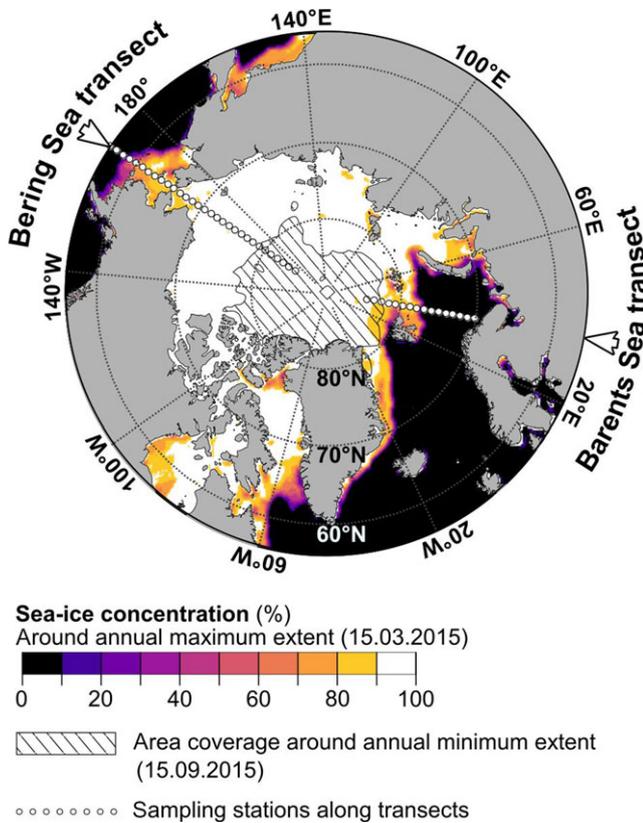
#	Explanation (units)	Equations	Parameter description
1	Visual range (m)[a]	$R_{(t,d)}^2 \exp^{(cR_{(t,d)})} = {\sim} C_p A_p E' \frac{I_{(t,d)}}{K_e + I_{(t,d)}}$ or if R <∼ 0.05 m $R_{t,d} = \sqrt{C_p A_p E' {\sim} \frac{I_{(t,d)}}{K_e + I_{(t,d)}}}$	c = beam attenuation coefficient = 0.3[b] C_p = prey contrast = 0.3[b] A_p = prey image area (m^2) = 3×10^{-6} [b] t, d = time (h) and Julian day I = ambient irradiance (Eq. 3) E' = visual capacity K_e (µE m^{-2} s^{-1}) = composite saturation parameter 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 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]. z = light path length in medium

[a]Aksnes and Utne (1997).
[b]Varpe and Fiksen (2010).
[c]Perovich (1996).
[d]Grenfell and Maykut (1977).

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.
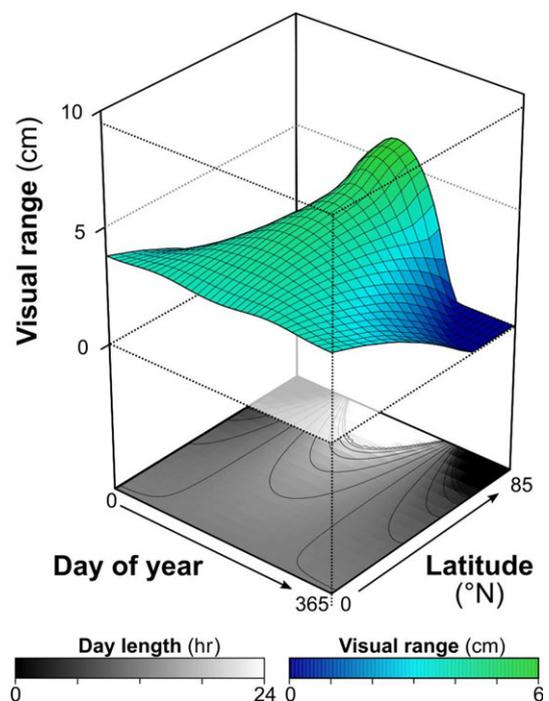
3 | RESULTS

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 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) [Colour figure can be viewed at wileyonlinelibrary.com]

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,

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 [Colour figure can be viewed at wileyonlinelibrary.com]

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. [Colour figure can be viewed at wileyonlinelibrary.com]

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 ($\pm$7 SD) and -110 ($\pm$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
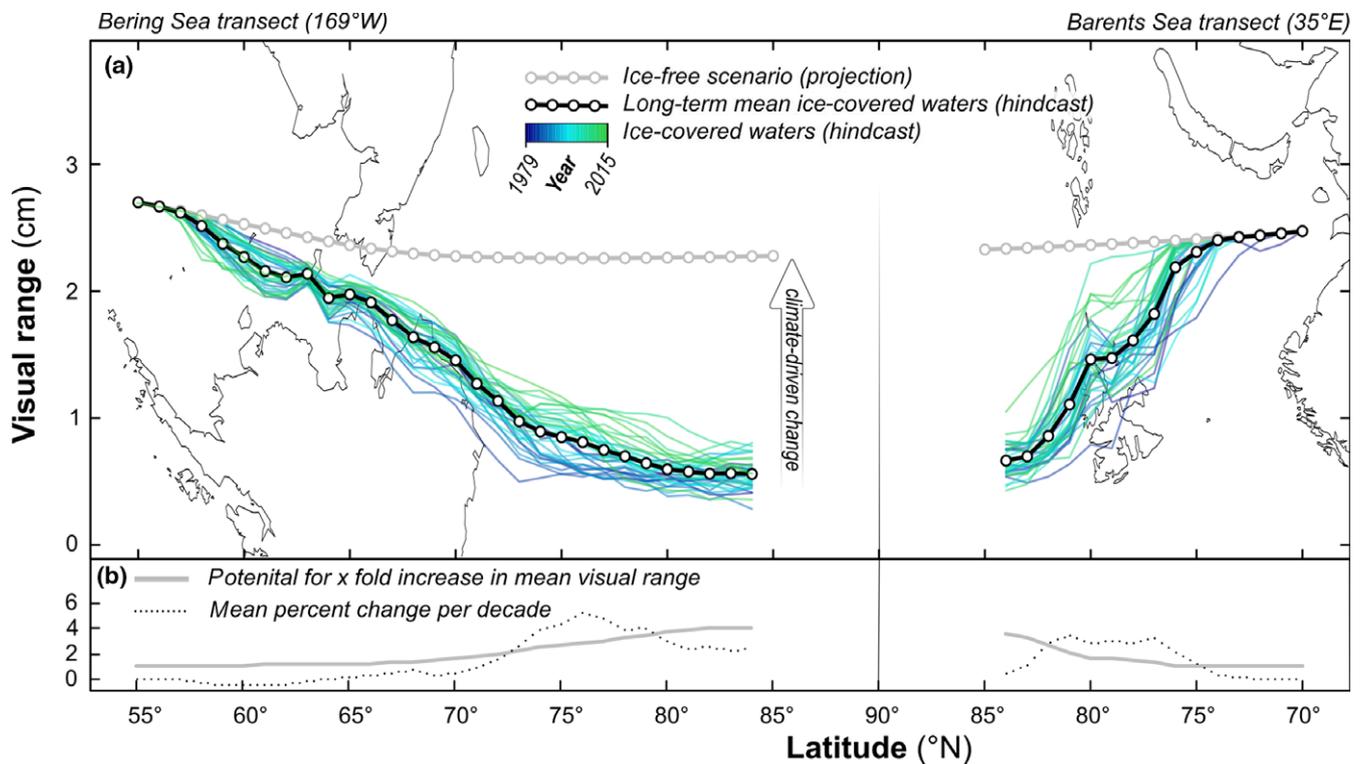
FIGURE 5 Climate-driven sea-ice decline unlocks potential for visual predation at high latitudes. (a) Hindcast visual range, given as yearly averages by increments of 1° latitude, for the years 1979–2015 are depicted by coloured lines, in comparison to projected estimates of visual range made for a future 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 [Colour figure can be viewed at wileyonlinelibrary.com]

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
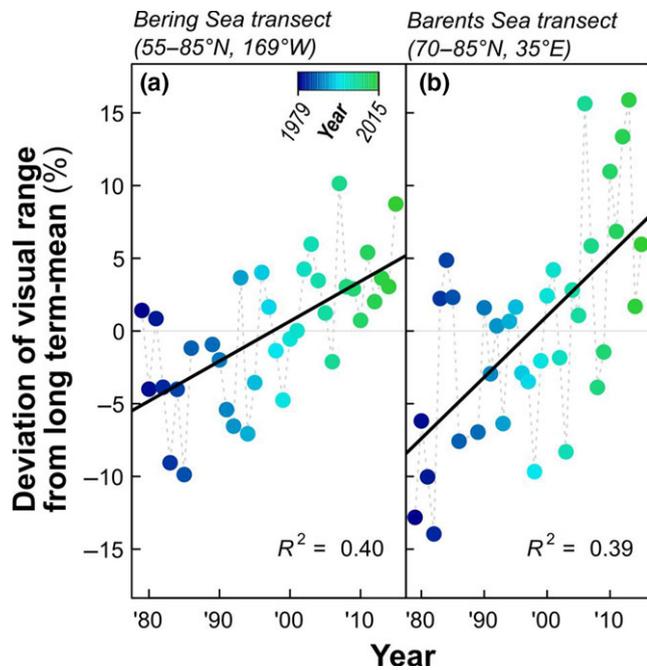
FIGURE 6 Modelling results predict a significant change in visual range of fish in the period 1979–2015, with a similar rate of change in the Pacific and Atlantic Arctic. Yearly averages of visual range (coloured dots) are shown as deviation from the long-term mean across all study years (grey horizontal 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. [Colour figure can be viewed at wileyonlinelibrary.com]

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
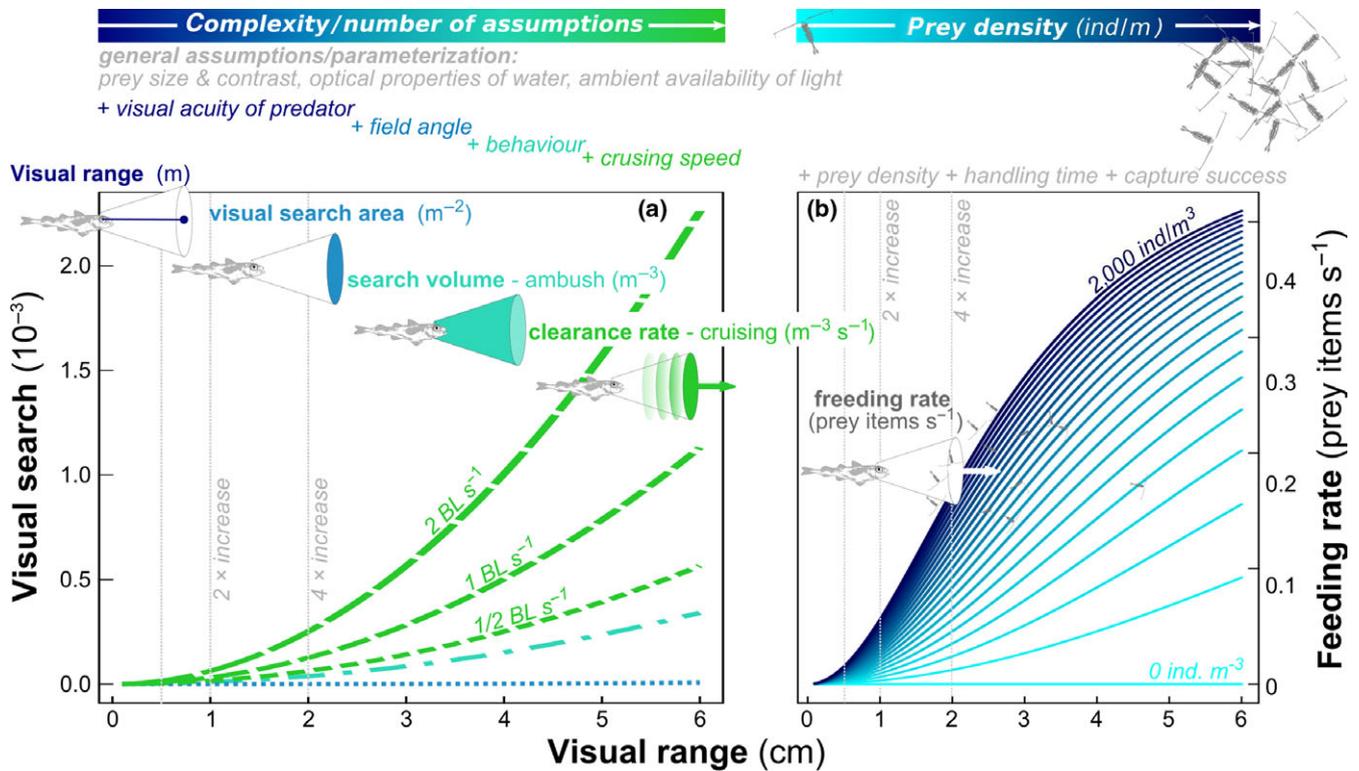
FIGURE 7 Visual range is the fundamental metric of visual search. Moving from visual range to more complex descriptors of visual search (visual search area [m^{-2}] ➝ search volume [m^{-3}] ➝ clearance rate [m^{-3} s^{-1}] ➝ feeding rate [prey items s^{-1}]), ecological relevance and interpretability 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 [Colour figure can be viewed at wileyonlinelibrary.com]

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) Sundby et al. (2016) 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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