



## Food for Thought

### A fish-eye view on the new Arctic lightscape

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A gigantic light experiment is taking place in the Arctic. Climate change has led to substantial reductions in sea ice extent and thickness in the Arctic Ocean. Sea ice, particularly when snow covered, acts as a lid hindering light to reach the waters underneath. Less ice will therefore mean more light entering the water column, with profound effects on pelagic and benthic ecosystems. Responses through primary production are so far well acknowledged. Here we argue that there is a need to broaden the view to include light-driven effects on fish, as they depend on light to locate prey. We used the Norwegian Earth System Model estimates of past and future sea ice area and thickness in the Arctic and applied attenuation coefficients for ice and snow to estimate light intensity. The results show a dramatic increase in the amount of light predicted to reach the future Arctic Ocean. We combined this insight with mechanistic understanding of how light modulates visual prey-detection and predict that fish will forage more efficiently as sea ice diminishes and that their populations will expand to higher latitudes, at least seasonally. Poleward shifts of boreal fish species have been predicted by many and to some extent observed, but a changing light environment has so far not been considered a driver. Expanding distributions and greater visual predation may restructure ecological relationships throughout the Arctic foodweb and lead to regime shifts. Research efforts should focus on the dynamics of how less sea ice will affect the feeding ecology and habitat usage of fish, particularly the northern limits of distributions. Mechanistic approaches to these topics offer insights beyond statistical correlations and extrapolations, and will help us understand how changing biophysical dynamics in the Arctic influence complex processes including production, predator–prey interactions, trait-evolution, and fisheries.

**Keywords:** ecology, fish vision, light, sea ice, spatial distributions, visual ecology, zooplankton size.

#### Introduction

Substantial reductions in Arctic sea ice extent and thickness have been observed during the recent decades, and further reductions are predicted (Stroeve *et al.*, 2012). Less ice means more light reaching the waters of high-latitude oceans because sea ice, particularly when snow covered, acts as a lid hindering light to reach the water column (Grenfell and Maykut, 1977; Sturm and Massom, 2010). The current sea ice changes therefore also correspond to a massive and large-scale change in the light regime—most likely with profound effects on both pelagic and benthic ecosystems. Light is the core driver of photosynthesis, and we know that less sea ice, and thereby more light entering the water column, can increase the primary production in the pelagic zone (Arrigo *et al.*, 2008) and alter its seasonal timing (Ji *et al.*, 2013). Benthic primary producers

are similarly impacted (Clark *et al.*, 2013). Sea ice reductions have been suggested to cause regime shifts in the community structure as benthic algae receive sufficient light to become abundant (Kortsch *et al.*, 2012) and to dominate the seabed community (Clark *et al.*, 2013). These are influential findings that also suggest tipping points, trophic cascades, and subsequent ecosystem changes.

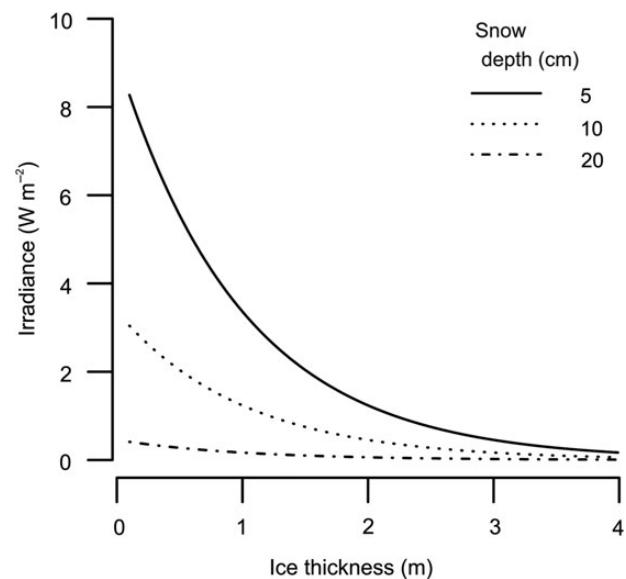
Algal responses to a changing light regime are well-acknowledged and studied *in situ* (Sigler *et al.*, 2014), by remote sensing (Arrigo *et al.*, 2008; Ji *et al.*, 2013; Ardyna *et al.*, 2014) and through biophysical modelling (Slagstad *et al.*, 2011; Jin *et al.*, 2012). Here we argue that the dramatic sea ice changes calls for a broader view on how the changing light regime influences the ecology of the water column. Particularly, we must extend our perspective to visual interactions

(Nilsson *et al.*, 2014) and, as we focus on here, on how visually searching predators, organisms relying on light for efficient feeding, are impacted by the new Arctic lightscape. Below we elaborate on this perspective and (i) illustrate how ice works as a lid on the oceans by attenuating or blocking light; (ii) present modelled time-series of past and future sea ice area, thickness, and age and quantify the cumulative light consequences these changes have on a Pan-Arctic scale; (iii) use mechanistic reasoning to predict how the feeding efficiency and distributions of fish may change with less sea ice; and (iv) use knowledge of the size distributions of plankton combined with theory for predator–prey interactions and life history theory to discuss how top-down effects through fish responses may impact zooplankton communities in ice-associated ecosystems. We focus on the Arctic ecosystem and the ongoing sea ice changes, but our reasoning and opinions are relevant to other aquatic systems, such as the Southern Ocean and high-latitude or alpine lakes, where changes in the ice and/or snow cover impact visually searching predators. The complexity of the many ecological interactions involved and the importance of the visual biology and ecology of fish are also discussed.

### Modelling light through ice and snow

Over the course of the last few decades, climate models have improved tremendously in their ability to simulate the Earth's climate system and complex interactions between its components such as oceans, atmosphere, cryosphere, land surface, and humans. Today's climate models, the earth system models (ESMs), have shown improved skills in predictions compared with previous modelling efforts (Reichler and Kim, 2008). Here we use predictions of sea ice conditions across the Arctic Ocean from the Norwegian Earth System Model (NORESM AR5; <http://cmip-pcmdi.llnl.gov/cmip5/>) as input to calculate how changes in sea ice will affect the amount of light reaching the water column. We used NORESM predictions based on the greenhouse gas scenario Representative Concentration Pathway 8.5. For this scenario, emissions are expected to rise throughout the 21st century and on average lead to an increase of  $8.5 \text{ W m}^{-2}$  relative to pre-industrial values. Compared with satellite data, and some of the other ESMs, the NORESM overestimates sea ice cover for parts of the year (Langehaug *et al.*, 2013), hence our estimates are on the conservative side. We modelled surface light (on top of snow and ice) at noon as a function of day of the year and latitude, assuming zero clouds and accounting for modelled albedo, following Jin *et al.* (2008). Using information for snow and ice from the ESM model, light below snow and ice (at the ice–water or air–water interface) was estimated assuming light intensity at the top of snow and ice according to Skartveit *et al.* (1998), and attenuated through snow using attenuation coefficients of  $20 \text{ m}^{-1}$ ,  $5 \text{ m}^{-1}$  for the top 10 cm of ice and  $1 \text{ m}^{-1}$  for ice below the top 10 cm (Grenfell and Maykut, 1977; Perovich, 1996). See Figure 1 for an example that illustrates the effects of sea ice and snow on the amount of light entering the water column for a specific geographic location and time. We acknowledge that our approach is a simplification of the very complex optical properties of snow and sea ice (Perovich *et al.*, 1998; Ehn *et al.*, 2011). Our motivation is to provide a simplified illustration of the scale on which the future Arctic lightscape may change and to highlight the rapid changes in light regimes resulting from changes in ocean snow and sea ice cover.

NORESM data for our Pan-Arctic analyses included sea ice thickness (Figure 2a), snow thickness, and albedo, available for

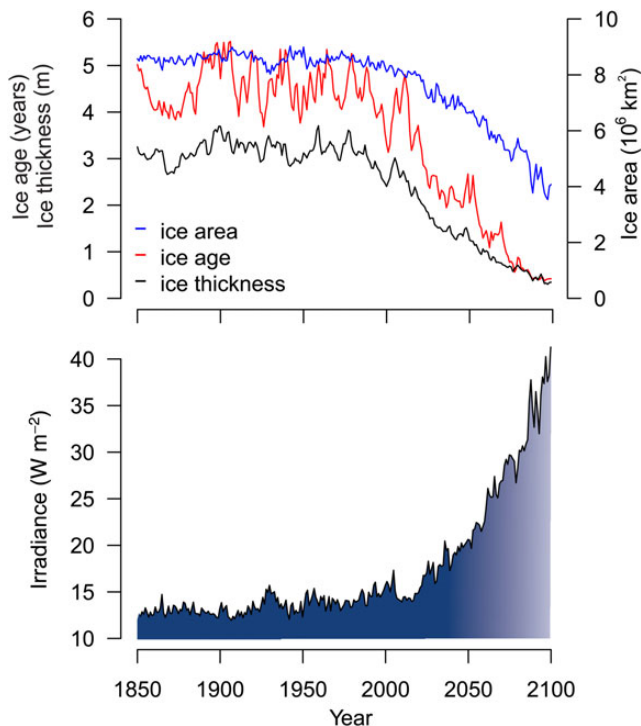


**Figure 1.** Less sea ice leads to more light in the water column as illustrated by a simplified model of the effects of sea ice and snow on the irradiance reaching the water column. Calculations are from a clear sky scenario, at  $80^\circ\text{N}$  and  $15^\circ\text{E}$ , at noon at summer solstice (23 June) with irradiance summed over wavelengths ranging from 300 to 3000 nm. The albedo was set to 0.9 for the snow and ice-covered waters illustrated here. We display light reaching the water column with increasing ice thickness and for snow cover of 5, 10, or 20 cm. For simplicity, because snow on no ice is unrealistic, we plot values for ice thickness of 10 cm onwards. For alternative units of irradiance:  $1 \text{ W m}^{-2} = 0.217 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

each  $1 \times 1$  degree longitude and latitude grid points. We considered all data-points north of  $60^\circ\text{N}$  ( $0\text{--}360^\circ\text{E}$  longitude). Light was calculated at each grid cell for every monthly time-step between years 1850–2100. If there was no snow and ice present in the grid cell, the amount of light reaching the water surface equalled the maximum amount of light available. The Python and Fortran programmes used to do the calculations are available online at <https://github.com/trondkr/OceanLight>.

### Less ice opens up for increased light

Our model predictions provide a quantification of the below-surface light changes we expect, at a Pan-Arctic scale, under continued climate change. When we quantified changes in light intensity [irradiance ( $\text{W m}^{-2}$ )] as an annual average over the Pan-Arctic region, we found that light reaching the water column will on average significantly increase relative to historical values (Figure 2b). If projected changes in the physical conditions of ice, ocean, and atmosphere take place, light intensity in the water will increase dramatically after 2040 (Figure 2b). These changes are substantial and the outcome of a process where light levels increase rapidly as the lid, the sea ice, becomes less efficient. Importantly, Arctic regions are often ice-covered far into the well-lit spring and summer. With sea ice changes at this time of year, the light regime in the ocean will see highly non-linear changes (Clark *et al.*, 2013). This non-linearity will increase with latitude and provides a mechanism for abrupt ecosystem transformations also referred to as tipping points (Clark *et al.*, 2013).



**Figure 2.** Sea ice properties of the past and future Arctic and its consequences for the light regime of the water column. Presented values are model output from the NorESM. (a) Ice thickness, ice age, and ice-covered area in the region north of 60°N. (b) Estimated annual average irradiance ( $\text{W m}^{-2}$ ) that reaches the surface layer of the water column (the ice–water or air–water interface) based on monthly predicted changes in snow thickness, ice thickness, and albedo for the same region.

### Beyond phytoplankton: light consequences for fish

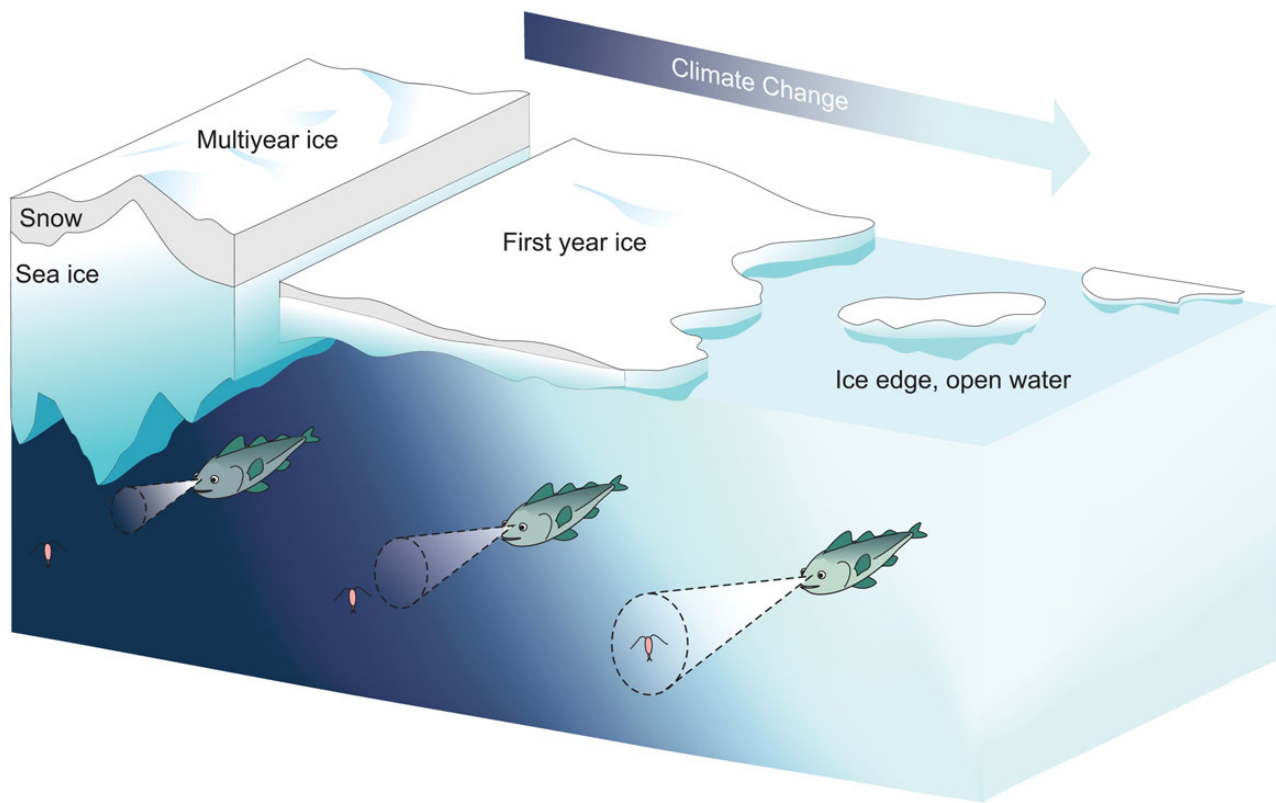
Fish depend to a large extent on light to locate prey (Vinyard and O'Brien, 1976; Aksnes and Giske, 1993; Utne-Palm, 1999; Evans, 2004), and light limitations on prey encounter may determine both spatial (Aksnes et al., 2004; Kaartvedt, 2008) and seasonal (Varpe and Fiksen, 2010) patterns of fish distributions. Similar considerations are valid for other visual predators, such as diving seabirds (Johansen et al., 2001; Regular et al., 2011). Furthermore, fish have long been known as drivers of interactions in pelagic ecosystems (e.g. Clark and Levy, 1988), with particularly convincing examples from studies of lakes with and without fish, such as small-sized planktonic prey resulting from the presence of planktivorous fish (Brooks and Dodson, 1965). The sub-Arctic oceans are home to some of the world's largest fish populations and fisheries (Hollowed and Sundby, 2014), and the future may see these populations shifted northwards (Hollowed et al., 2013; Fosheim et al., 2015). With the predicted sea ice changes and resulting changes to the light regime, we must now try to understand how a widening of the euphotic zone at high latitudes may impact fish habitats. For example, will behavioural responses in fish have cascading consequences through the marine foodweb? Here, we argue that a mechanistic view of how light modulates the visual search (cf. Aksnes and Giske, 1993) allows improved understanding of the potential future ecosystem dynamics of the Arctic. In fact, we can predict that (i) fish already inhabiting ice-associated waters will be less constrained by light and therefore achieve a more efficient

prey search for a longer duration of the year (Figure 3); (ii) as a consequence of the increased opportunities for visual search, fish species at lower latitudes will expand towards the poles; and (iii) seasonal migrants will be more common as migrating species able to move into the Arctic during summer, and back south during the polar night, will benefit from exploiting this new light regime.

### Foodweb consequences of improved visual search

Both competition and predator–prey interactions in the ocean may change because fish experience improved feeding conditions and their distributions are shifted towards the poles. The fish species already inhabiting the Arctic (Mecklenburg et al., 2011), such as polar cod *Boreogadus saida*, may experience stronger competition from sub-Arctic species expanding north (although there is little evidence of competition in a recent study of juvenile gadoids during autumn, Renaud et al., 2012). Furthermore, because visually searching predators detect larger prey more easily, the zooplankton community of the Arctic will suffer increased and stronger size-dependent predation with selection pressures shifting to favour smaller plankton individuals. Changes in zooplankton body size with increased predation pressure are well documented in freshwater environments (Brooks, 1968; Svensson, 1997). Interestingly, for some taxa such as *Calanus* spp. the high-latitude zooplankton species are larger than at lower latitudes (Falk-Petersen et al., 2009b; Sainmont et al., 2014), a size pattern that may in fact have evolved due to lower predation by fish in high-latitude ice-covered waters (cf. Kaartvedt, 2008). We predict that the selection pressure on zooplankton size will change as conditions for planktivorous fish improve, and that large prey species will be most impacted by increased fish predation (cf. Brooks and Dodson, 1965). The large and lipid-rich zooplankton species of the Arctic are central in the energy transfer of the marine ecosystem (Bradstreet and Cross, 1982; Falk-Petersen et al., 2009a). Small-sized zooplankton will likely have knock-on effects at the higher trophic levels including birds and marine mammals (Kwasniewski et al., 2010). To summarize, the future Arctic may see light-driven tipping points, caused not only by the impact of light on photosynthesis (Kortsch et al., 2012; Clark et al., 2013) but also by the impact of light on visually searching predators.

The above argument is for an all-else-equal scenario. Increased light entering the water column is also likely to alter other aspects of the ecosystem that in turn could impact both fish and zooplankton in complex ways. For instance, higher algal growth and photosynthesis in the surface layer could lead to decreased attenuation and reduce the amount of light actually available to fish at greater depths (a shadow effect). Changes in primary production levels could also change the zooplankton community through bottom-up processes. Furthermore, zooplankton may respond behaviourally to visual predation through increased diel vertical migration and hence avoidance of well-lit surface layers, or through changes in morphology such as reduced pigmentation—which in turn reduces contrast and detectability. The food search behaviour of fish is also highly dynamic and dependent on prey density, prey size, and the visual conditions (O'Brien et al., 1989), and the sensory system of fish also changes with a changing light regime (Evans, 2004). Furthermore, some fish species filter feed, particularly on high prey concentrations, which would complicate our predictions above, which are based on particulate feeding and a visual search (Batty et al., 1990; Macy et al., 1998). Fish can act as both predator and prey depending on species and life stage. Consequently, an increase in light will not only make feeding conditions better for



**Figure 3.** Schematic representation of the impact of sea ice changes on the prey-detection performance of a visually searching fish predator. Sea ice conditions are here represented by a gradient from multiyear ice with substantial snow cover, to the thinner and more homogenous annual ice with less snow, to the ice edge and open waters. Less sea ice means more light entering the ocean, and more light means better visual conditions for fish. The copepod illustrated here (of the same size and at a given distance from the fish) becomes more and more likely to be encountered as the snow and sea ice gets thinner.

small planktivores but also make them more vulnerable to larger and visually searching piscivores (Vogel and Beauchamp, 1999). This will complicate the trophic interactions and our predator–prey argument. At high latitudes, light conditions during winter and the dark polar night must also be considered. Light available for visual search is very modest during the polar night, also without sea ice (Cohen *et al.*, 2015) and moon light would be the strongest light source, except the bioluminescence produced by organisms in the water column. The extreme light regime of polar seas, including the polar night conditions, has been suggested to constrain fish distributions (Kaartvedt, 2008). Fish, including polar cod *Boreogadus saida* and Atlantic cod *Gadus morhua*, from Svalbard fjords are however observed with pelagic prey in their stomachs also during the polar night (own observations). To what extent they then rely on other senses than vision is so far unknown.

### Northern fish distributions: what is the role of light?

Changing fish distributions caused by less ice and therefore increased light in the water column is a prediction so far absent from reviews on climate change effects on Arctic ecosystems (e.g. Smetacek and Nicol, 2005; Schofield *et al.*, 2010; Wassmann *et al.*, 2011; Post *et al.*, 2013). Current observations and predictions for range expansions in fish are rather based on changes in food availability and particularly temperature (Perry *et al.*, 2005; Hollowed *et al.*, 2013; Fossheim *et al.*, 2015; Wisz *et al.*, 2015). We propose

light limitations caused by ice cover, and the long dark winter, as an additional explanation for the northern limits of fish distributions. With sea ice reductions we would consequently expect visually searching fish to expand northwards. For species with migration capacity, these shifts may take a seasonal nature because the dark polar night makes visual search difficult also in the absence of sea ice, leading to seasonal migrations to higher latitudes during the well-lit summer and to lower latitudes during the dark winter.

### Recommendations for progress and concluding remarks

We hope our perspectives will provide food for thought and inspire future studies designed to quantify and understand the processes and interactions involved. Here we provide five areas of research that we believe are of the highest importance if we are to improve our understanding of the light-driven consequences of diminishing sea ice for Arctic biota:

- (i) *Mechanistic models and reasoning.* Biological systems are inherently difficult to predict. However, mechanistic models that include both biology and physics can provide qualitative predictions that add realism to a field often dominated by statistical correlations and extrapolations from these. Our reasoning here provides such an example. We urge for further development of models in visual ecology (Aksnes and Utne,



1997; Nilsson *et al.*, 2014) and particularly for prey-detection models for fish in ice-covered waters. This perspective should also include the potential role of bioluminescence as well as the role of vision in predator detection and avoidance (Nilsson *et al.*, 2014), topics we have not covered here.

- (ii) *Prey-detection experiments on Arctic fish species.* To develop realistic biological models, we need parameters on the visual capacity of fish. For questions related to Arctic sea ice, we are in dire need of parameters obtained for Arctic fish species. Prey-detection experiments under different light conditions and seasons would be particularly useful. There is to our knowledge no such information available, and models, also for lower latitude fish, often rely on parameters obtained for one or a few species (e.g. Varpe and Fiksen, 2010), and for environmental conditions that are no longer representative. Polar cod *Boreogadus saida*, a key Arctic fish species (Welch *et al.*, 1992; Hop and Gjøsaeter, 2013), would be a prime candidate for the suggested experiments.
- (iii) *Eye physiology and comparative studies.* We also need a better understanding of eye physiology and morphology of high-latitude fish species. Comparisons of Arctic species with the potential newcomers to the Arctic would be instructive. Jönsson *et al.* (2014) recently compared the eye physiology of polar cod and Atlantic cod *Gadus morhua* detecting differences in short-term plasticity in lens optical properties during the polar night. Pan-Arctic comparisons of the visual physiology of selected key species are also interesting because of the vast span of latitudes and ice conditions of Arctic waters, and hence large variability in light conditions that some of these species occupy.
- (iv) *Zooplankton size.* Prey size is key in the interaction between visual predators and their food. Our prediction suggests that body size will decrease with increases in light and predation pressure, either at species or community levels (shift to smaller species). Similar predictions have been made with regard to increasing temperatures (Daufresne *et al.*, 2009). If we are to understand the consequences of diminishing sea ice on Arctic zooplankton species and communities, we therefore strongly recommend that field studies monitor body size variability within species. Furthermore, re-analysis of existing datasets that already include zooplankton body size should provide valuable insights. We also believe novel observation methods such as the Laser Optical Plankton Recorder and the Video Plankton Recorder will be instrumental in studies combining information on body size with large spatial coverage.
- (v) *Fish distributions and detection of shifts and expansions.* We need spatial data on fish that allow changes in fish distributions to be detected. Importantly, sufficient resources must also be allocated to analyses of the substantial data collections that indeed take place in some high-latitude marine ecosystems. Time series with high spatial coverage do exist for some regions, allowing for solid investigations of fish distributions such as in the recent analyses of Barents Sea data by Fosshiem *et al.* (2015). We suggest that the light regime should be considered when evaluating the drivers causing observed borealization of the Arctic. Finally, we also encourage development of technology that can be used for studies of fish distributions under ice, as our current view of the far north is

heavily biased towards ice-edge studies, with trawling and acoustical measurements performed next to or in the marginal ice zone.

Acknowledging light regulated prey-encounters allow basic prediction on species distributions as well as interactions including top-down influences on plankton. The *less sea ice—increased light—more efficient visual search* perspective (Figure 3) offers mechanistic insights, allows predictions, and has far reaching implications for ecological interactions that influence biological production and trait-evolution as well as fisheries, management, and conservation in a future Arctic.

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