Food for Thought

A fish-eye view on the new Arctic lightscape

Øystein Varpe¹,²*, Malin Daase³, and Trond Kristiansen⁴

¹The University Centre in Svalbard (UNIS), 9171 Longyearbyen, Norway
²Akvaplan-niva, Fram Centre, 9296 Tromsø, Norway
³UiT, The Arctic University of Norway, 9037 Tromsø, Norway
⁴Institute of Marine Research, 5817 Bergen, Norway

*Corresponding author: tel: +47 79026463; e-mail: oystein.varpe@unis.no


Received 14 February 2015; revised 29 June 2015; accepted 30 June 2015; advance access publication 17 August 2015.

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...
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 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 m\(^{-1}\), 5 m\(^{-1}\) for the top 10 cm of ice and 1 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 complexity of the many ecological interactions involved and the importance of the visual biology and ecology of fish as they search for prey in the water column.

NORESM data for our Pan-Arctic analyses included sea ice thickness (Figure 2a), snow thickness, and albedo, available for each 1 × 1 degree longitude and latitude grid points. We considered all data-points north of 60°N (0–360°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 (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).
Both spatial (Aksnes, 2004), and light limitations on prey encounter may determine O’Brien, 1976; Aksnes and Giske, 1993; Utne-Palm, 1999; Evans, Fish depend to a large extent on light to locate prey (Vinyard and Beyond phytoplankton: light consequences for fish (Varpe and Fiksen, 2010) 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 lightscape.

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 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 (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.
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,
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. Jónsson 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 Fossheim 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.

Acknowledgements

This work was supported by the Research Council of Norway, for ØV through grant 227046 and for ØV and MD through grant 226417. We thank Tom Langbehn and two anonymous reviewers for valuable comments on a previous version. ØV and TK also thank the Theoretical Ecology Group at Department of Biology, University of Bergen, for the stimulating learning environment we were exposed to there during our PhDs and for seeding reflections and research on how visual predators operate and impact their environment. ØV designed the paper, outlined the figures, and lead the writing, MD made the figures, TK did the calculations and model simulations, MD and TK contributed to the writing and to discussions.

References

A fish-eye view on the new Arctic lightscape


Fossheim, M., Primicerio, R., Johannessen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. 2015. Recent warming leads to a rapid bor- 


Handling editor: Francis Juanes