



Contribution to the Symposium: 'Ecosystem Studies of Subarctic and Arctic Seas' Food for Thought

Planktivorous fish in a future Arctic Ocean of changing ice and unchanged photoperiod

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Climate change drives fish and plankton species ranges toward the poles, often related to warmer waters mediating geographic distributions via changes in vital rates. Yet, the distribution of fish may also be governed by less acknowledged mechanisms. Ice limits access to air for physostomous fish filling their swimbladders at the surface. We hypothesize that release of ice constraints may facilitate northward expansion of physostomes, with implied impact on their zooplankton prey. On the other hand, even in a changing Arctic, the extreme high-latitude photoperiod will persist. The abundance of mesopelagic fish is low in the Arctic Ocean. Feeding conditions may be inferior during the darkness of winter and in light summer nights. If the photoperiod is constraining distributions, biogeographic boundaries of mesopelagic fish may be relatively unaffected by climate change. Alternatively, if low temperatures are their main constraint, we hypothesize that northward extensions in a warmer ocean may be detrimental to key Arctic copepods as we argue that their current success relates to low mortality during overwintering in the absence of mesopelagic fish. It is therefore essential to discriminate the role of the light climate at high latitudes from those related to temperatures for assessing future biogeographic boundaries.

Keywords: *Calanus*, ice, mesopelagic fish, midnight sun, physostomous fish, polar night

Introduction

It has been predicted that fishes like mackerel, herring, capelin, and salmon might migrate into a future warmer Arctic Ocean (Huse and Ellingsen, 2008; Christiansen, 2017). Poleward expansion of plankton, fish, and mammals (Beaugrand, 2009; Haug *et al.*, 2017) may relate to more hospitable temperatures, but also to habitat changes like reduction in ice. While reduced ice cover can disfavour ice-associated species (e.g. polar cod, Wyllie-Echeverria and Wooster, 1998; Christiansen, 2017), it may be advantageous for others. For example, as warming reduces sea ice extent and thickness in the Arctic Ocean (Comiso, 2012; Stroeve *et al.*, 2012), horizontally migrating fish may track the receding ice edge, benefitting from enhanced light levels during foraging forays into high-latitude oceans (Varpe *et al.*, 2015; Langbehn and Varpe, 2017). So-called physostomous fishes have an open swimbladder that they normally fill by gulping air at the surface (Harden Jones and Marshall, 1953), and might benefit from the

release of a constraining ice cover. However, this issue remains to be assessed in evaluations of a future Arctic Ocean.

While the Arctic Ocean is characterized by low temperatures and partly ice-covered waters that are sensitive to warming, it is also defined by an extreme photoperiod that will obviously not respond to climate change (Sundby *et al.*, 2016). Most pelagic organisms depend on the light regime for either food search, predator avoidance, or both. The life of mesopelagic fishes—i.e. fish spending daytime at several hundred metres depth and to a varying degree migrating to the surface at night—is strongly related to the ambient light conditions on temporal and geographic scales (Røstad *et al.*, 2016a, b; Aksnes *et al.*, 2017) and may be particularly affected by the extreme photoperiod at high latitudes (Kaartvedt, 2008).

Here, we discuss how ice cover and the photic environment may interact with the effect of warmer waters in mediating future distribution ranges of planktivorous fish. The physostomous fishes herring and capelin are major predators on the key copepod

Calanus in upper waters during summer (Hassel *et al.*, 1991; Varpe and Fiksen, 2010), while mesopelagic fish may impose heavy mortality on *Calanus* during their overwintering at mesopelagic depths (Bagoien *et al.*, 2001). Therefore, a main consequence of any altered habitats of these planktivores may be increased top down forces on the *Calanus*, and thus the Arctic pelagic food web at large. We do not strive toward an exhaustive review, but rather aim to raise examples and hypotheses (Table 1) regarding the importance of ice and light for future pelagic ecosystems at high latitudes.

Ice as a physical boundary

The ice lid blocks access to the surface. Common physostomes at high latitudes like salmonids (e.g. salmon), clupeids (e.g. herring), and osmerids (e.g. capelin) are unable to secrete gas into the swimbladder from the blood and instead fill their swimbladder by gulping air at the surface (Harden Jones and Marshall, 1953; Fahlén, 1968; Blaxter *et al.*, 1979). (Re)filling of the swimbladder would accordingly be restricted in ice-covered waters. The swimbladder wall of herring has a barrier of guanine crystals hampering diffusion rates and allowing for prolonged retention of gas (Blaxter *et al.*, 1979). For salmon, there is some gas leakage through time, resulting in smaller swimbladder volume and altered swimming behaviour (Korsøen *et al.*, 2009). Yet, clupeids, salmonids, and osmerids may release gas, but for uncertain, and debatable, reasons (Thorne and Thomas, 1990; Nøttestad, 1998; Rudstam *et al.*, 2003; Solberg and Kaartvedt, 2014).

Studies from ice-covered fjords and lakes as well as from aquaculture indicate decreased swimbladder volume, behavioural changes, well-fare issues, and even death when access to air is constrained by ice or other physical structures (Table 2, references therein). Because harsh winter weather and ice curb access to high latitude waters, knowledge of marine fish populations under ice is minimal. Yet, based on the limited current data (Table 2) we hypothesize that *Ice constrains the geographic distribution of physostomous fish by preventing filling of the swimbladder*, and that *the release of ice constraints to the future warmer ocean may facilitate northward expansion of physostomous fish*.

The largest stock of clupeids in northern waters is the Norwegian spring-spawning herring (*Clupea harengus*), but their population limit does not seem to intercept with the ice. However, the Pacific herring, *Clupea pallasii* abounds in ice affected areas, like the Bering Sea and the White Sea (Tojo *et al.*, 2007; Lajus *et al.*, 2007). The Bering Sea holds overwintering habitats of the Pacific herring that appear to be just at the ice edge (Tojo *et al.*, 2007).

While cold water lowers metabolism, which may benefit overwintering during the non-feeding period (e.g. Kooka *et al.*, 2007), we speculate that the constraint by ice on access to air may be a

factor in defining the overwintering areas *per se*. The southeastern Bering Sea exhibits extreme variability in sea ice extent (Stabeno *et al.*, 2012), which also fluctuates across the overwintering habitat of herring (Tojo *et al.*, 2007). Distribution and diet of Pacific herring vary largely between cold and warm years, including in relation to ice (Andrews III *et al.*, 2015). However, it remains uncertain if ice *per se* constrains distributions of the Pacific herring. On the contrary, it has been suggested that ice-covered Alaskan bays may facilitate survival of overwintering juvenile Pacific herring by providing cover from predatory birds and mammals (Lewandoski and Bishop, 2017). Also, herring in the Baltic persists in habitats that regularly become ice covered (e.g. Lamichhaney *et al.*, 2012), though to what extent the ice affects the population is unknown.

The apparently only systematic field studies of how ice may hamper access to air in any physostome are for another clupeid, sprat (*Sprattus sprattus*). These document changes in vertical distribution, smaller swimbladder, altered swimming behaviour including more frequent, but unsuccessful, search for air under the ice, and termination of gas release when their fjord habitat froze over (Solberg *et al.*, 2012; Solberg and Kaartvedt, 2014). In ice-free conditions the sprat seeks out the surface approximately four times per day, indicating the importance of access to new air (Solberg and Kaartvedt, 2014). The sprat straightaway changed to a shallower distribution upon the fjord freezing over, and moved even shallower upon heavy snowfall (Solberg *et al.*, 2012). The distinction between the responses to ice *per se* and the lower light due to the snow is supported by observations of krill in the same habitat. Krill moved shallower only when snow covered the ice (Vestheim *et al.*, 2014). Presumably, the ice represents a constraint to the fish that it is to some extent able to handle, albeit at an unknown cost.

The small capelin (*Mallotus villosus*) inhabits the circumpolar northern boreal oceans at the margins of cold Arctic waters (Rose, 2005). Capelin dominates the pelagic fish in the Barents Sea (Gjøsæter, 1998). There, and elsewhere, capelin plays a key role in the food web, both as a planktivore and as prey for other fish, marine mammals, and birds (Gjøsæter, 1998; Rose 2005). Capelin performs long migrations and while being able to forage in cold water (-1.5°C), it requires warmer waters to reproduce (Rose, 2005). Because its distribution extends further to the north and east in the Barents Sea during warm years than in cold years, both its oceanic distribution and its spawning grounds are anticipated to change with warming (Huse and Ellingsen, 2008).

While the Barents Sea capelin may be associated with the productive marginal ice zone during summer (Hop and Gjøsæter, 2013), its relation to ice in winter is unknown. In Icelandic waters, capelin may be common near the ice edge also in winter,

Table 1. Summary of hypotheses for fish in a future warmer Arctic Ocean and suggested consequences for plankton.

Hypothesis	Suggested consequence for plankton
<i>Ice constrains the geographic distribution of physostomous fish by preventing filling of the swimbladder</i>	Lower plankton mortality with ice
<i>The release of ice constraints to the future, warmer, ocean may facilitate northward expansion of physostomous fish</i>	Increased predation pressure on plankton during summer
<i>If constraints related to the photoperiod override that of temperature, biogeographic boundaries of mesopelagic fish may be relatively unaffected by climate change</i>	Low size-selective mortality of large Arctic copepods during winter in habitats without mesopelagic fish and little change with warming
<i>If cold waters currently constrain mesopelagic fish toward the poles; then mesopelagic fish may invade a warmer Arctic Ocean. Switching antipredator behaviour to schooling in light summer nights may facilitate northward extensions</i>	Increased mortality of plankton. High accumulated mortality of large, seasonally migrating Arctic copepods during overwintering at mesopelagic depths

Table 2. Literature on physostomous fish affected by ice or air constraints.

Species	Location and conditions	Change with constrained surface access	Reference
Sprat (<i>S. sprattus</i>)	Oslofjorden, Norway. Upward-looking echo-sounder in temporarily ice covered fjord	Altered vertical distribution, smaller swimbladder volume, altered behaviour, and increased, yet unsuccessful searches for air underneath the ice	Solberg <i>et al.</i> (2012) Solberg and Kaartvedt (2014)
Atlantic salmon (<i>Salmo salar</i>)	Aquaculture, submerged cages	Deflated swimbladder with time during 25 d experiment. Tilted swimming and deformation in vertebra. Increased swimming near top of cage. Searching for air	Korsøen <i>et al.</i> (2009)
Atlantic salmon (<i>S. salar</i>)		Unable to replace gas lost from the swimbladder	Jakobs (1934, cited in Harden Jones and Marshall, 1953)
Atlantic salmon (<i>S. salar</i>)	Aquaculture submerged cage	Negatively buoyant, increased swimming speed, reduced welfare, and increased mortality	Fosseidengen <i>et al.</i> (1982), Ablett <i>et al.</i> (1989), and Dempster <i>et al.</i> (2009)
Herring (<i>C. harengus</i>)	Experiments	Fish with artificially emptied swimbladders died when denied access to the surface	Blaxter and Batty (1984)
Central mudminnow <i>Umbra limi</i>	Experiments and field study in lake	Facultative air-breathing fish in low oxygen waters searching for air bubbles under the ice	Klinger <i>et al.</i> (1982)
Grayling <i>Thymallus thymallus</i>	Field study lake	Acoustically tagged individuals immediately changing vertical distribution with ice cover, swimming in the upper 50 cm	Bass <i>et al.</i> (2014)

but for logistic reasons monitoring does not include ice-covered waters (Birkir Bardarson, Marine Research Institute Iceland, pers. com.). It remains unknown if capelin accumulates at an ice border, such that ice is a constraint *per se* or the border zone represents a favourable habitat, or if observed distributions just represent fringes of a population that extends into ice-covered waters.

In summary, both experimental and field studies suggest that hampered access to air may impact physostomes negatively (Table 2). On the other hand, populations of clupeids, osmerids, and salmonids do persist in environments, particularly lakes, which freeze over in winter (Steinhart and Wurtsbaugh, 1999; Jurvelius *et al.*, 2000; Klemetsen *et al.*, 2003; Dunlop and Riley, 2013; Bass *et al.*, 2014). At present, large-scale ecological consequences of increased access to the surface in a future ocean with reduced ice cover remains unknown. Upward-looking echo sounders represent a powerful tool for studying fish behaviour in ice-free and iced-covered habitats (Solberg & Kaartvedt, 2014). This approach might represent one way to further test how ice affects other physostomes, including in lakes that are more readily accessible than are comparable marine habitats.

Photoperiod and light

The extreme photoperiod and light climate of the Arctic alter the trade-offs in diel vertical migration in which mesopelagic fish, and other pelagic organisms, exploit the rich pastures of upper waters in shelter of darkness at night and seek refuge in deep, dim waters in daytime. Midnight sun likely limits the options for safe nocturnal foraging by mesopelagic fish in upper layers in summer (Sameoto, 1989; Norheim *et al.*, 2016), and continuous darkness during winter expectedly hampers visual feeding in deep water any time of day. In northern boreal, waters with more equal diel light cycles dark adapted mesopelagic fish hunt even at several

hundred metres depth during daytime (Bagoien *et al.*, 2001; Dypvik *et al.*, 2012).

Deep scattering layers of mesopelagic fish occur in all oceans, with an estimated global abundance of 10 billion tonnes (Irigoin *et al.*, 2014). However, mesopelagic fish abundance declines toward Arctic waters (Sameoto, 1989; Dale *et al.*, 1999; Sutton *et al.*, 2017). Mesopelagic fish distribute vertically relative to limited bands of light intensities, so-called light comfort zones, both locally (Røstad *et al.*, 2016a, b) and globally (Aksnes *et al.*, 2017). About half of the mesopelagic fish migrate between upper layers and the mesopelagic zone on a daily scale (Klevjer *et al.*, 2016).

The light summer nights in the Arctic apparently prevent the light comfort zone of mesopelagic fishes to overlap with abundant prey resources during much of the productive season. The hampering of nocturnal ascent of mesopelagic scattering layers at high latitude in summer concurs with weakening of the backscatter layers northwards (Norheim *et al.*, 2016). Another challenge is the constant darkness during winter, which might deprive feeding conditions for mesopelagic fish in deep water, like on overwintering *Calanus*. This prediction has not been tested in the Arctic, but finds support in data from the boreal Lurefjorden, which is characterized by high light extinction and particularly dark mesopelagic waters. Lurefjorden is basically devoid of mesopelagic fish, presumably because dark waters prohibits visual search at mesopelagic depths (Eiane *et al.*, 1999). Yet, in the Arctic, there is unexpected biological activity during the polar night, and gut content of visual predators is evident in shallow moon lit waters (Berge *et al.*, 2015). To what extent this relates to any deeper-living mesopelagic fishes is unknown, as is their use of any non-visual search for prey (e.g. Boscarino *et al.*, 2010).

In sum, one may hypothesize that *if the importance of photoperiod at high latitudes overrides that of temperature, biogeographic boundaries of mesopelagic fish may be relatively unaffected by*

climate change (Kaartvedt, 2008). However, if distributions are less tightly linked with the optical environment (Siegelman-Charbit and Planque, 2016) and cold waters currently constrain mesopelagic fish toward the poles (Proud *et al.*, 2017); then mesopelagic fish may invade a future Arctic Ocean. There is some mesopelagic fish (*Maurolicus muelleri*) switching to schooling in upper layers during light Norwegian summer nights (Kaartvedt *et al.*, 1998; Prihartato *et al.*, 2015). Such behaviour might facilitate further northward extension if other conditions like temperature became more favourable.

The glacier lanternfish (*Benthoosema glaciale*) is the most common mesopelagic fish in the northern Atlantic (Gjøsæter, 1973). The glacier lanternfish drifts passively with currents (Kaartvedt *et al.*, 2009). Their occurrence in the Arctic apparently results from immigration via advection (Sameoto, 1989) and is thus not proof of sustainable populations. Yet, the presence of such apparent expatriates may allow for testing the hypothesis of inferior feeding conditions in the Arctic photoperiod both summer and winter by examining their actual stomach contents and body condition.

Top-down effects in a future Arctic Ocean

To the extent that ice constrains the geographic distribution of physostomous fish, either for overwintering or during summer foraging migrations, changes in their distribution will inflict altered predation pressures on prey. This relates both to summer and winter ice, as any change in location for overwintering may cause spatial changes in predation on plankton in other seasons. In contrast to vertically migrating mesopelagic fish, horizontally migrating fish like herring and capelin may benefit from the extreme Arctic photoperiod in several ways. As ice melts, the optical habitat may be enhanced allowing for more efficient prey detection (Varpe *et al.*, 2015; Langbehn and Varpe, 2017). Also, these fishes school and use rapid swimming as antipredator strategies (Vabø and Nøttestad, 1997; Crook and Davoren, 2014), allowing them to inhabit upper waters and forage visually throughout the day. Such benefits connected with the high latitude photoperiod providing 24 hours daily for visual search in summer are for example manifested in high growth rates of juvenile cod under midnight sun (Suthers and Sundby, 1996).

Visually searching fish select larger prey organisms as these are more easily detected (Brooks and Dodson, 1965). Hence, large Arctic copepods like *Calanus* would be vulnerable with distributions of planktivorous fish being shifted poleward. Varpe *et al.* (2015) predicted changed selection pressure on copepods and that large prey would be most impacted by any increased fish predation. This would have enormous ramifications, since the large and lipid-rich *Calanus* copepods of the Arctic are central in the energy transfer of the marine ecosystem (Steen *et al.*, 2007; Leu *et al.*, 2011; Jónasdóttir *et al.*, 2016).

While summer predation may increase on *Calanus* by horizontally migrating fishes like herring and capelin, any expansion of mesopelagic fish into the Arctic likely will increase predation during winter. Among the main characteristics of marine ecosystems at high latitudes is the seasonal vertical migration of *Calanus* for overwintering at mesopelagic depths and beyond. Depending on species, *Calanus* overwinters at several hundred metres to > 1000 m while sustained by stored lipids (Falk-Petersen *et al.*, 2009; Jónasdóttir *et al.*, 2016). Although phenotypic plasticity is large, *Calanus finmarchicus* normally goes through 1 diapause period (Jónasdóttir *et al.*, 2016), while the larger *Calanus glacialis*

and largest *Calanus hyperboreus* requires 1–2 and at least 2, respectively. Each overwintering spans 4–9 months (Hirche, 1997; Jónasdóttir *et al.*, 2016). With such long time spent immobile at mesopelagic depths, low mortality rate during diapause is a prerequisite for sustainable rich *Calanus* populations.

Studies in boreal Norwegian fjords indicate that mesopelagic fish are more efficient predators on overwintering *Calanus* than are invertebrate predators (Bagoien *et al.*, 2001). Winter mortality rates are very high for *Calanus* exposed to mesopelagic fish and much lower without (Bagoien *et al.*, 2001). Furthermore, in dark fjords without mesopelagic fish, plankton are larger (Eiane *et al.*, 1999; Aksnes *et al.*, 2004). Strikingly, the presumably Arctic *C. glacialis* dominates over its smaller temperate cousin *C. finmarchicus* (Bucklin *et al.*, 2000; Bagoien *et al.*, 2001; Niehoff & Hirche, 2005) in Lurefjorden, where mesopelagic fish are lacking, despite overwintering temperatures (~7 °C) exceeding the representative upper comfort temperature of *C. glacialis* (~5–6 °C, Kosobokova, 1999; Hirche and Kosobokova, 2007). A consequent assumption may be that the success of large Arctic copepods relates to strongly reduced size-selective mortality during winter in habitats without mesopelagic fish. A subsequent prediction is that—as in Lurefjorden—large Arctic copepods can prevail also at lower latitudes (higher temperatures) when mesopelagic fish are absent. This can be tested by addressing the *Calanus* species composition in habitats with and without mesopelagic fish. The mesopelagic waters of an increasing number of Norwegian fjords appear to become dominated by invertebrates at the expense of mesopelagic fish, possibly related to coastal water darkening (Aksnes *et al.*, 2009).

If the success of large Arctic copepods indeed is related to limited top-down control at mesopelagic depths during winter due to low abundance of mesopelagic fish, in turn being related to photoperiod rather than temperature (Kaartvedt, 2008), there might be more resilience to warming than suggested in scenarios predicting substitution of larger Arctic forms of *Calanus* with smaller, boreal cousins (Falk-Petersen *et al.*, 2007; Hirche and Kosobokova, 2007; Kjellerup *et al.*, 2012). On the other hand, if the hypothesis that photoperiod prevents mesopelagic fish from invading the Arctic turns out to be incorrect and mesopelagic fish indeed expand into a warmer Arctic (Proud *et al.*, 2017), implications for the *Calanus* and the ecosystem at large may be huge.

In sum, the fate of planktivorous fish in a future Arctic Ocean likely depends on more factors than temperature *per se*. Predicting effects of climate change on plankton like *Calanus* also requires an understanding of the predation risk, both during overwintering in deep water and when foraging in upper waters during the productive season. The prevailing focus is on direct impacts of temperature and toward potential bottom-up processes like feeding or growth of the *Calanus per se* (e.g. Søreide *et al.*, 2010; Alcaraz *et al.*, 2014), while top-down processes receive limited attention. We here have outlined some potential scenarios for planktivorous fish and subsequent impacts on their prey (Table 1). We hope to see an increase in studies targeting the role of top-down processes in future assessments.

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