

OPINION PIECE

No future for Euro-Arctic ocean fishes?

Jørgen S. Christiansen*

Department of Arctic and Marine Biology, UiT The Arctic University of Norway, 9037 Tromsø, Norway

ABSTRACT: In this essay, I outline how vanishing sea ice may unveil costs and benefits for fishes native to the Euro-Arctic seas. Most arctic fishes are not directly associated with the sea ice, but constitute an integral part of the seafloor biota. Arctic seafloor fishes may temporarily benefit from improved feeding conditions but may also lose to novel predators such as invading southern fishes and emerging industrial enterprises on the Arctic shelves. Polar cod *Boreogadus saida*, on the other hand, an abundant and prominent member of the ice-associated biota, uses sea ice as spawning substrate, shelter and feeding ground. Thus loss of sea ice likely has severe and explicit costs for this focal species with profound ecological consequences. Time series and biological baselines for arctic fishes are fragmentary at best. As I see it, we need to diagnose our ignorance and put the precautionary principle into full effect while awaiting for knowledge gaps to be filled. Here I offer a sneak peek into the future of ocean fishes in the Nordic Seas, primarily in the Arctic sector, with my opinion based on recent studies in Arctic marine ecology and climatology.

KEY WORDS: Arctic fisheries · *Boreogadus saida* · Climate change · Euro-Arctic ocean fishes · Sea-ice loss

— Resale or republication not permitted without written consent of the publisher —

THE ENVIRONMENTAL SETTING

Sea ice and glacial icebergs structure and support Arctic marine life (Gutt 2001, Arrigo 2014). As the climate changes, both ice forms undergo rapid changes: at the same time as icebergs calve heavily from the Greenland ice sheet, the sea-ice cover diminishes (Straneo & Cenedese 2015, Schaefer et al. 2016, Polyakov et al. 2017). This is particularly evident for September (Arctic summer minimum) when the sea-ice cover in 2015 ($4.6 \times 10^6 \text{ km}^2$) was nearly 30% less than the September mean for the period 1981–2010. March (Arctic winter maximum), on the other hand, seems more stable with an average loss of 7% during the same period and a sea-ice extent of $14.5 \times 10^6 \text{ km}^2$ in 2015 (NSIDC 2016). In addition to the overall loss of sea ice, multi-year ice is gradually being replaced by annually formed first-year ice (Hunt et al. 2016). There are however large regional differences in sea-ice loss across the Arctic seas. Spitsbergen in the Northeast Atlantic is displaying particularly dramatic

changes, with Kongsfjorden ($\sim 79^\circ \text{N}$) being virtually free of sea ice all year round (Wiencke & Hop 2016). Lengthened periods of open water are evident across the Arctic (Barnhart et al. 2016) and, as the overall decline in sea ice proceeds, parts of the Arctic shelves will become permanently free of sea ice in the coming decades. The deep Arctic Ocean, on the other hand, may still maintain ice cover in winter but with open water in summer (Wang & Overland 2012, Notz & Stroeve 2016).

This environmental setting fundamentally affects the entire Arctic biota from phototrophic microorganisms via benthic consumers to top predators (Post et al. 2013). Fishes are excellent tellers of climate change because environmental and ecological chronologies are readily archived in metabolically inert tissues such as otoliths (Izzo et al. 2016) and eye lenses (Nielsen et al. 2016). What then is the ecological role of fishes native to icy waters, how are they affected by dwindling sea ice, and how do they tackle invading fishes and industrial fisheries from

lower latitudes? These questions are addressed but not answered in the recent Arctic Biodiversity Assessment Report of the Arctic Council (Christiansen & Reist 2013). Case studies build ecological concepts, but the lack of time series and deficient key data on biodiversity, life histories and physiological constraints clearly prevent credible assessments and forecast modeling (Flyvbjerg 2006, Christiansen et al. 2014, Boero et al. 2015, Planque 2016). 'The fewer the facts, the stronger the opinion': this cliché governs the current strife over Arctic resources. Environmental and ecological conditions differ greatly between the Pacific and Atlantic sectors of the Arctic Ocean (Hunt et al. 2013, 2016, Tremblay et al. 2015) and the regional peculiarities preclude holistic scenarios of climate change. Here, I offer a sneak peek into the future and alleged fate of ocean fishes primarily in the Arctic sector of the Nordic Seas (Paasche et al. 2015). I base my opinion on qualified guestimates from recent case studies and reviews in Arctic marine ecology and climatology.

PRESENT STATE OF ARCTIC OCEAN FISHES

The study of Arctic ocean fishes is still exploratory but about 220 species are currently described from the Arctic seas *sensu strictu*, i.e. excluding larger parts of the sub-Arctic Bering, Barents and Norwegian Seas (cf. delineations in Mecklenburg et al. 2011). This number is likely to change as new areas become accessible for scientific surveys (Witze 2016), taxonomic issues are addressed (Mecklenburg & Steinke 2015), and as more species from lower latitudes move into the Arctic Ocean proper (Fossheim et al. 2015). Although the terms 'Arctic' (capital A) and 'arctic' (lower case a) are often considered synonyms, care is required for the ocean fishes: the noun 'Arctic' is a mere toponym whereas the adjective 'arctic' specifies a zoogeographic category of fishes constrained by functional biodiversity and oceanography. In other words, 'Arctic fishes' comprise all species occurring within the geographic realm of the Arctic seas whereas 'arctic fishes' are further restricted to those species that are distributed and reproduce mainly in ice-laden waters (i.e. with water temperature $\leq 0^{\circ}\text{C}$), and only infrequently occur in adjacent boreal waters (Mecklenburg & Steinke 2015). Table 1 shows the zoogeographic affiliation

Table 1. Number of fishes and fish-like vertebrates in the Arctic seas ($n = 221$) and their zoogeographic affiliation (cf. Mecklenburg et al. 2013)

Class	Zoogeographic affiliation			
	Arctic	Arctic-boreal	Boreal	Widely distributed
Hagfishes (Myxini)			1	
Sharks and rays (Chondrichthyes)	1	1	11	2
Ray-finned fishes (Actinopterygii)	56	31	106	12
Proportion across classes (%)	25.8	14.5	53.4	6.3

among Arctic fishes, and follows the delineations and definitions outlined in Mecklenburg et al. (2011) and Mecklenburg & Steinke (2015). From a zoogeographic standpoint more than half of the species are boreal (53.4%), barely 26% are considered true arctic and only 3 of these—polar cod *Boreogadus saida*, navaga *Eleginus nawaga* and Arctic flounder *Liopsetta glacialis*—are of commercial interest and also support subsistence fisheries of indigenous peoples (Ellis 1962, Christiansen et al. 2014).

Conservation and ecological outcomes of dwindling sea ice must be viewed in context of species' life histories, physiological constraints and trophic roles (e.g. Cooke et al. 2014). Arctic fishes occur from the littoral zone and deep waters of fjords, via troughs and shelves to the abyssal plains of the Arctic Ocean. But most are not directly associated with the sea ice (Fig. 1) and the most prominent and species-rich fish families found in the Arctic, i.e. eelpouts (Zoarcidae, $n = 39$), sculpins (Cottidae, $n = 30$), snail-fishes (Liparidae, $n = 20$) and pricklebacks (Stichaeidae, $n = 12$), are all considered non-migratory residents of the seafloor ('demersal') as adults (Mecklenburg et al. 2013, Mecklenburg & Steinke 2015). A few fishes such as gelatinous seasnail *Liparis fabricii*, Arctic staghorn sculpin *Gymnocanthus tricuspis* and daubed shanny *Leptoclinus maculatus* have planktonic larvae but most species lay few demersal eggs and often display parental care, while larval development is direct with no intermediate planktonic stages (Christiansen et al. 1998). Arctic fishes primarily feed on zoobenthos (e.g. Atkinson & Percy 1992). Few are detritus feeders, scavengers or predate other fishes and, beneath the photic zone, they rely on olfactory cues and chemo-tactile senses instead of eyesight, as in the case of the Greenland shark *Somniosus microcephalus* (Ferrando et al. 2016). Many arctic fishes are slow-growing, long-lived and likely respond to and reflect long-term environmental trends rather than seasonal fluctuations. In other words, arctic fishes share many functional traits with benthic in-

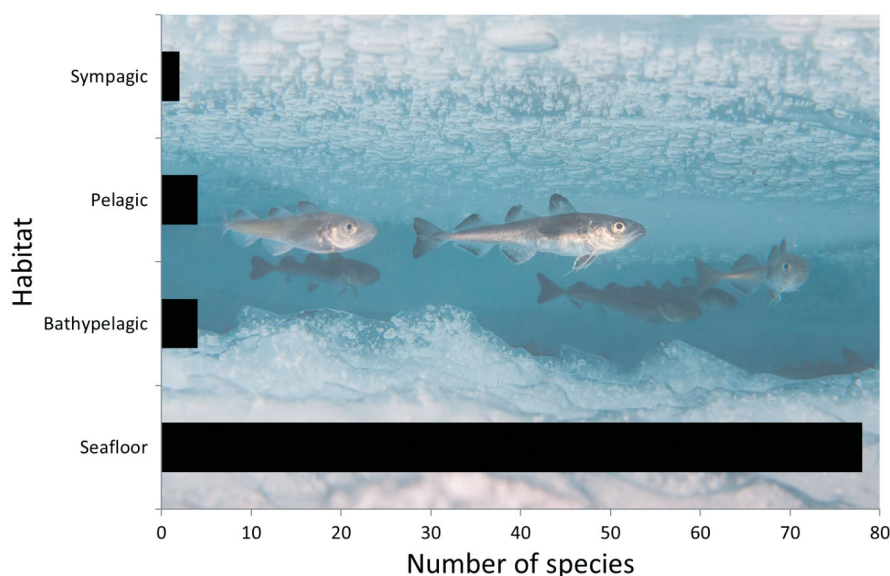


Fig. 1. Habitat of arctic and arctic-boreal fish species (black bars, $n = 89$), cf. Mecklenburg et al. (2013, Table 1). The seafloor species account for ~88% of the fish fauna. Background: Polar cod *Boreogadus saida* within Arctic sea ice. Photo credit: Peter Leopold, UiT The Arctic University of Norway

vertebrates and therefore form an integral part of the Arctic megabenthos (Fig. 1; Renaud et al. 2015a). Future studies of Arctic benthic communities can be expected to underscore this fact (Johannesen et al. 2017).

By contrast, the cryopelagic (sensu Andriashev 1970) gadoids—the elusive ice cod *Arctogadus glacialis* and the omnipresent polar cod—are the only fishes living within sea-ice crevices for periods of their lives (i.e. 'sympagic'; see Fig. 1). Ice cod is largely confined to the Arctic shelves (Aschan et al. 2009) whereas polar cod also inhabits the Arctic Ocean proper (Melnikov & Chernova 2013, David et al. 2016). Although polar cod does occur in open waters, the intimate association between polar cod and sea ice, particularly in early life, has been repeatedly documented across the Arctic seas (e.g. Ponomarenko 1968, Andriashev 1970, Lønne & Gulliksen 1991, Karamushko et al. 1997, Bouchard & Fortier 2008, Geoffroy et al. 2011, Hop & Gjørseter 2013, Eriksen et al. 2015, Kohlbach et al. 2017).

Polar cod spawns mainly in January and February and eggs may occur as late as in June in the Pechora Sea (Rass 1968). The floating eggs accumulate in the surface layers and develop mainly beneath the sea-ice cover, which acts as an upturned spawning substrate, shelter and feeding ground in early life (Rass 1968, Andriashev 1970, Lønne & Gulliksen 1991). In the laboratory, polar cod eggs (1.5 to 1.9 mm diameter) develop normally at -1.0 to 3.5°C in ice-free

surface layers and hatch after between 11 wk (at -1.0°C) and 4 wk (at 3.5°C) (Sakurai et al. 1998, Kent et al. 2016). Moreover, eggs and larvae are euryhaline, surviving in brackish water as low as 5 ppt (Doroshev & Aronovich 1974).

Besides being a notable member of the sympagic biota (Lønne & Gulliksen 1991), polar cod is the utterly dominant and abundant fish species in both inshore and offshore Arctic waters (e.g. Hop & Gjørseter 2013, Majewski et al. 2017) and throughout the entire water column from surface to ~1000 m depth (Geoffroy et al. 2016).

Polar cod, a focal species that makes ecosystems swing, displays the main attributes of a 'wasp-waist species' (sensu Bakun 2006) because it acts at the mid-trophic level and so regulates the abundance of both lower and higher trophic organisms, by preying on zooplankton and being preyed upon by other fishes, marine birds and mammals (Welch et al. 1993, Christiansen et al. 2012, Griffiths et al. 2013, Hop & Gjørseter 2013, Atkinson et al. 2014). Importantly, polar cod is the only true arctic fish species that swarms, undertakes migrations en masse between spawning and feeding grounds (Ponomarenko 1968, Welch et al. 1993, Karamushko et al. 1997), and so may teleconnect and drive the horizontal flow of energy and nutrients from the inner parts of fjords, across the shelves, into the ice-covered Arctic Ocean and vice versa (see also Kessel et al. 2017).

PUTATIVE PROSPECTS FOR ARCTIC OCEAN FISHES

Sea-ice loss raises a *quaestio vexata* about the flow of energy and matter between newly opened surface waters and the seafloor biota. Arctic benthic communities are sustained by the export of biogenic matter ('marine snow') from the photic zone to the seafloor and, near-shore, macroalgal detritus (Kędra et al. 2015, Renaud et al. 2015b). As climate change progresses, rivers increasingly advect terrestrial organic matter to the Arctic shelves and slopes (McClelland et al. 2012, Bell et al. 2016, Hunt et al. 2016), and ice-

rafted debris from discharged icebergs and melting sea ice may constitute a source of nutrients to benthic food webs (Hemming 2004). Also swarming planktonic tunicates such as salps (Thaliacea) may efficiently enhance the export of nutrients to the seafloor (Henschke et al. 2016).

In summary, the magnitude of export following the loss of sea ice depends inter alia on subtle interactions between sunlight, stratification, nutrient supply and advection, timing of ice algae and phytoplankton blooms, microbial processes, and mismatch gaps among producers and consumers (Arrigo 2014, Leu et al. 2015, Tremblay et al. 2015, Hunt et al. 2016, Polyakov et al. 2017).

Scenarios of sea-ice loss are probabilistic and seem inconclusive across and within Arctic and Antarctic ecosystems (Renaud et al. 2015a, Hunt et al. 2016). Some argue there will be a diminished supply of biogenic matter to the seafloor due to pronounced stratification and increased recycling in the photic zone (Wassmann & Reigstad 2011). Others maintain that pelagic-benthic coupling will tighten, advection and benthic productivity will increase, and there will be intensified invasions of benthic taxa from lower latitudes (Peck et al. 2010, Barnes 2015, Renaud et al. 2015a, Bell et al. 2016). In light of climate change, the study of advection and pelagic–benthic coupling is

key in order to understand temporal shifts in abundance and functional diversity of benthic communities (Lovvorn et al. 2016, Griffiths et al. 2017). What then are the putative prospects for the arctic seafloor fishes and the cryopelagic polar cod (Table 2)?

Phytoplankton blooms and lumps of sinking ice algae coincide with the melt of sea ice and ultimately underpin and nourish seafloor communities on the Arctic shelves (Dünweber et al. 2010, Szymanski & Gradinger 2016) and even in the deep Arctic basins (Assmy et al. 2013, Boetius et al. 2013). In this scenario, a flourishing benthic environment would favour the arctic fishes beneath the photic zone. Nearshore, prolonged periods of sunlight stimulate the growth of kelp, other seaweed and even seagrass (Clark et al. 2013, Bartsch et al. 2016, Duarte & Krause-Jensen 2016). Arctic littoral fish communities are little studied (Brand & Fischer 2016), but at lower latitudes it is well established that subsea vegetation provides an essential habitat as shelter and nursery for young fishes (Steneck et al. 2002). Moreover, enhanced kelp photosynthesis and carbon sequestration counteract local acidification, which may sustain habitats for calcifying prey organisms (Krause-Jensen et al. 2016). It is therefore conceivable that arctic fishes in the vegetation zone could benefit from an early breakup of shore-fast ice and declining sea ice (Table 2).

Table 2. Dwindling sea ice and alleged costs (dark shade), benefits (no shade) and uncertain (light shade) outcomes for arctic fishes of the seafloor and the sea-ice associated (sympagic) polar cod *Boreogadus saida*. Costs and benefits are evaluated against key ecological traits and man-made disturbances, as discussed in the text

HABITAT & FISH TAXA	BENTHIC REALM Seafloor fishes		PELAGIC REALM Polar cod (<i>Boreogadus saida</i>)
	Littoral zone	Deeper waters	Sympagic
Ecological traits			
Prey availability	Likely improved – higher prey diversity in subsea vegetation	Likely improved – increased biogenic export from euphotic waters to the benthic biota	Likely reduced – potential competition with Atlantic herring and Atlantic capelin
Predatory pressure	Alleviated – subsea vegetation as safe haven from predators	Heavier – Atlantic cod and Atlantic haddock	Heavier – Atlantic cod (ongoing) and Atlantic mackerel (potential)
Reproduction and early life	Improved – subsea vegetation as shelter and nursery	Worsened – ovivorous Atlantic haddock predated demersal eggs	Critical – ongoing loss of spawning habitat and shelter (i.e. sea ice) due to climate change
Man-made disturbances			
Industrial fisheries	None	Critical – bycatch fisheries and degraded habitats inflicted by bottom trawls	Bycatch and targeted fisheries (pro tem Russia)
Petroleum exploitation and shipping	Critical – oil spills widespread on and near shore habitats	Blowouts from subsea oil wells may affect local biota	Critical – at the egg and larval stages. Oil spills widespread in surface layers and within sea-ice crevices

Yet loss of sea ice, multi-year ice in particular, most likely poses a severe threat to the migratory polar cod. Polar cod shows an interesting dichotomy in thermal biology. Although largely confined to sub-zero ice-laden waters in its realised habitat, laboratory studies show that polar cod seeks ambient temperatures between 3 and 6°C (Schurmann & Christiansen 1994) and attains maximum growth at 7 to 8°C (Kunz et al. 2016, Laurel et al. 2016). In effect, polar cod acts as a cold arctic stenotherm in terms of ecology and habitat choice but it also reveals signs of eurythermy in physiological capacity within a temperature span of at least 10°C (from -2 to 8°C) (Whiteley et al. 2006). The idea of partial eurythermy in polar cod is well supported in recent laboratory studies by Drost et al. (2014), who demonstrated recovery after acute heating to 9.5°C and first symptoms of cardiac arrhythmia only at between 10 and 13.6°C. It is therefore unlikely that polar cod will succumb to elevated temperatures per se. The immediate and direct threat, however, lies in the fact that polar cod uses sea ice to propagate offspring.

Polar cod eggs are positively buoyant (Aronovich et al. 1975) and both eggs and newly hatched larvae (~6 mm) accumulate in contact with the sea ice (Rass 1968, Graham & Hop 1995). The eggs are delicate and transparent and sun-protective pigments develop only in larvae >10 mm (Aronovich et al. 1975, Matarese et al. 1989, Andersen et al. 1994). These features, combined with an early break-up of sea ice, make the earliest life stages of polar cod particularly vulnerable to UV-B radiation, wave motions, visual predators and potential petroleum spills (Rass 1968, Browman et al. 2000, Gradinger & Bluhm 2004, Nahrgang et al. 2016). Indeed, a time series (1984–2014) from the Pechora Sea spawning grounds already suggests a direct link between reduced sea-ice cover and failed recruitment of polar cod (Eriksen et al. 2015). Polar cod is shown to be half as fecund in the Atlantic waters off Spitsbergen compared with conspecifics in ice-laden waters (life time fecundity ~39 000 vs. 75 000 eggs per female). The underlying causes are unclear but may lie in the distinct ecological peculiarities of the 2 water masses rather than the ambient temperature (Nahrgang et al. 2014).

Ocean warming and loss of sea ice also lead to conspicuous range shifts of fishes from lower latitudes into Arctic waters (Fossheim et al. 2015, Kortsch 2016). Harvested species such as Atlantic cod *Gadus morhua*, Atlantic haddock *Melanogrammus aeglefinus*, deepwater redfish *Sebastes mentella* and Atlantic herring *Clupea harengus* are often reported to be 'newcomers' to the Arctic. Nonetheless, they were

not uncommon at high latitudes in periods with warmer climate in the past (Hamilton et al. 2000), and Atlantic cod even supported industrial fisheries in Spitsbergen (latitude 80°N) in the 1870s (Iversen 1923). So it is imperative that museum collections and older analogue sources are consulted to avoid misconceptions about the effects of climate change and temporal occurrences of fishes for given Arctic seas (Ricklefs 2012, Christiansen et al. 2016).

Atlantic mackerel *Scomber scombrus*, on the other hand, has recently displayed a remarkable surge in abundance and a northward shift in distribution range. It has been recorded around Jan Mayen Island since 1978. Larvae have been recorded off Spitsbergen since 2004, and adults in Isfjorden, Spitsbergen since 2013, while the harvest in southeast Greenland rose from about 160 t in 2011 to 78 500 t in 2014 (Wienerroither et al. 2011, Berge et al. 2015, Jansen et al. 2016). Atlantic herring and Atlantic mackerel are opportunistic predators on zooplankton and fish larvae. Being largely epipelagic and visual predators, they would likely benefit from loss of sea ice and improved optical conditions with prolonged periods of sunlight across large areas (Varpe et al. 2015). Adult Atlantic mackerel also hunt larger fishes and may thus pose a novel risk to polar cod. Atlantic cod is a well-known predator on polar cod, other fishes and zoobenthos (Link et al. 2009). Atlantic haddock also feeds heavily on demersal fish eggs (Richardson et al. 2011). In effect, the predatory behaviour by the 2 gadoids likely threatens both polar cod in open waters and the arctic fishes of the seafloor (Table 2). The diadromous Arctic charr *Salvelinus alpinus* is a well-known predator on polar cod (Ellis 1962), and range shifts of other salmonids (Salmonidae) into Arctic waters may restructure trophic relationships even further (Dunmall et al. 2013, Nielsen et al. 2013).

EMERGING INDUSTRIAL FISHERIES IN THE ARCTIC

About 60 fish species ('stocks') are currently targeted by industrial fisheries in West Greenland, around Iceland and in the Norwegian, Barents and Bering Seas (Christiansen & Reist 2013). Most fisheries target boreal species in the sub-Arctic seas south of the Arctic Circle, except for in the northeast Atlantic (Christiansen et al. 2014), where extensive fisheries for Atlantic cod and Atlantic haddock and other species occur even on the Arctic shelves around Svalbard archipelago at latitude 80° N (Mis-

und et al. 2016). The most numerous stocks belong to the righteye flounders (Pleuronectidae, $n = 18$ species), the cods (Gadidae, $n = 14$) and the rockfishes (Scorpaenidae, $n = 9$) (Fig. 2). Harvesting of demersal stocks is particularly disturbing because bottom trawls lead to bycatch of arctic fishes. Bycatch fishes have no direct commercial value but they make ecosystems work and support wildlife central to the livelihoods of indigenous peoples (Christiansen et al. 2014 and references therein). So which fishes and concomitant industrial fisheries may expand further and penetrate into as yet unregulated parts of the Arctic Ocean (Lam et al. 2016, Norris & McKinley 2017)? There is no clear-cut answer to this key question. Fishes of the Arctic Ocean proper are hardly studied and expanded scientific surveys may disclose unexpected distributions (Christiansen et al. 2016).

Ice cover prevents physostome fishes from gulping air at the sea surface, which is necessary to maintain normal gas bladder function (e.g. Solberg & Kaartvedt 2014). So loss of sea ice expands the distribution potential for physostome salmonids, Atlantic capelin and Atlantic herring, at least seasonally. The salmonids and Atlantic capelin lack the antifreeze required to endure sub-zero ice-laden waters. Atlantic herring, on the other hand, seems well suited to enter the epipelagic Arctic Ocean because it efficiently synthesises antifreeze all year round (Christiansen & Lynghammar 2012). The amphiboreal fishes (sensu Berg 1934) such as Pacific herring *Clupea pallasii* and walleye pollock *Gadus chalcogram-*

mus are especially intriguing. Their exceptional, disjunctive distribution in either the Atlantic or the Pacific sector of the Arctic Ocean would suggest that they represent the marginal remnants of a phylogeographic continuum, which broke up and disappeared from the intervening seas as the Arctic cooled (Christiansen & Reist 2013). For example, the Pacific population of walleye pollock supports one of the largest whitefish fisheries in the world whereas a minuscule population in the northeast Atlantic is known to science from <100 specimens since its discovery in 1932 (Christiansen et al. 2005, Byrkjedal et al. 2008). Pacific herring is common in the East Siberian, Chukchi and Beaufort Seas with genetic lineages that also extend into the White Sea, the Barents Sea and in secluded fjords in northern Norway (Mikkelsen et al. 2016 and references therein). In other words, it is conceivable that the 2 species may repopulate the Arctic seas once suitable environmental conditions are present. It is noteworthy that the walleye pollock has recently been recorded north of the Bering Strait, i.e. in the Chukchi and Beaufort Seas (Mecklenburg & Steinke 2015).

The bathypelagic Greenland halibut *Reinhardtius hippoglossoides* and deepwater redfish are believed primary candidates to disperse further into the deeper parts of the Arctic Ocean (Hollowed et al. 2013, Chernova 2017, Haug et al. 2017). They apparently lack antifreeze but may survive in a supercooled state in deeper oceanic waters (Enevoldsen et al. 2003, Christiansen & Lynghammar 2012). Deepwater redfish is mesopelagic, occurring from 200 to 900 m above bottom depth of 3000 m, and this species seems particularly fit for the Arctic Ocean given the presence of suitable prey such as other mesopelagic fishes and zooplankton which are abundant at high latitudes in the northeast Atlantic (Siegelman-Charbit & Planque 2016). Atlantic cod synthesises antifreeze in sub-zero waters (Christiansen & Lynghammar 2012), and it is conceivable that it may leave the Arctic shelf for an epipelagic life into the Arctic Ocean proper; however more hard data are needed to support this conjecture (Christiansen et al. 2016, Ingvaldsen et al. 2017).

In the open water masses, Greenland halibut and Atlantic cod spawn pelagic eggs while deepwater redfish gives birth to live offspring.

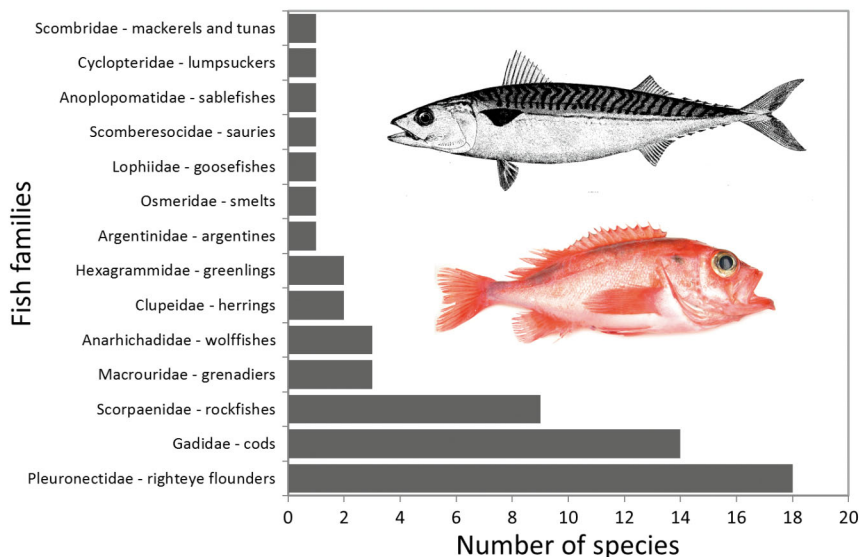


Fig. 2. Number of harvested fish species ('stocks') within fish families of the Arctic Ocean and adjacent seas (cf. Christiansen et al. 2014). Insets: Atlantic mackerel *Scomber scombrus* and deepwater redfish *Sebastes mentella*—emerging species in the Arctic (see text). Photo credit: Institute of Marine Research, Norway

Atlantic herring and Atlantic capelin, on the other hand, are substrate spawners and require spawning grounds in shallower coastal waters to close their reproductive cycle. But both species are also known to undertake extensive epipelagic migrations across deeper oceanic waters and one could foresee that they would enter the Arctic Ocean on a seasonal basis.

OUTLOOK

Loss of sea ice is not irreversible. The extent and quality of Arctic sea ice have changed considerably over historic time (Falk-Petersen et al. 2015, Hunt et al. 2016) and the Arctic marine biota was exposed to numerous glacial and interglacial cycles, abrupt shifts in climate and loss of sea ice during the Quaternary Period—well before humans made their mark on global change (Cronin & Cronin 2015, Hoff et al. 2016, Schaefer et al. 2016, Hoffman et al. 2017). Although blurred by recent human activity, climate cycles are still natural and recurring phenomena that Arctic biota likely withstood in the past.

The 2016 slogan of the annual conference Arctic Frontiers (www.arcticfrontiers.com/), 'Industry and environment', underscores that big business sets the agenda in exploiting Arctic resources often at the expense of indigenous peoples (e.g. Christiansen et al. 2014, Crook et al. 2016, Ford et al. 2016, Nystø 2017). As I see it, the most blatant and unprecedented consequences of dwindling sea ice relate to emerging industrial enterprises in hitherto ice-covered seas (Norris & McKinley 2017). Large-scale groundfish fisheries pose a real, momentous and novel threat to the arctic fishes and other megabenthos in terms of loss to bycatch and habitat destruction (Christiansen et al. 2014, Degen et al. 2016). Moreover, increased seismic and naval activity, shipping and accompanying noise pollution have wide-ranging but yet little understood consequences for Arctic wildlife (Eguíluz et al. 2016, Simpson et al. 2016). On the bright side, man-made disturbances are manageable even though they may not be completely eliminated (Moreno-Mateos et al. 2017).

Recent model projections of industrial fisheries show that ocean warming enhances species turnover across marine ecosystems but also decreases the maximum catch potential in tropical waters such as the Indo-Pacific. By contrast, one may expect a many-fold rise in catches in Arctic waters (Cheung et al. 2016). So how is the future for the Euro-Arctic ocean fishes? Promising—for boreal species that are

invading and taking advantage of Arctic ecosystems. Complex—for native arctic fishes that may temporarily benefit from improved feeding conditions but also face novel competitors and predators, as well as being threatened (as bycatch) by industrial fisheries. Moreover, with the notable exception of polar cod, heat thresholds for arctic fishes are barely studied (Drost et al. 2016, Leo et al. 2017). In my opinion, the bleakest and clearest prospects concern the polar cod, with loss of sea ice being probably the single most important stressor for this cryopelagic species (Table 2).

Timescale (years, decades, centuries) and geographical scale (fjords, shelves, deep open seas) shape our perception and interpretation of climate change (Jenkins & Uya 2016). The Arctic seas are diverse and dwindling sea ice may temporarily enrich benthic habitats in one region but impoverish them in another. The strength of stratification (Wassmann & Reigstad 2011, Tremblay et al. 2015, Polyakov et al. 2017) and advection (Hunt et al. 2016) seem key factors affecting the extent of energy and biogenic matter exported to benthic communities to which most of the arctic fishes belong (Fig. 1).

As an immediate step, it is wise to recognize our ignorance by fully adopting the precautionary principle, for example through a provisional ban on bottom trawling on the Arctic shelves (Christiansen et al. 2014, Jensen 2016). An upcoming fleet of ice-going research vessels will soon form the backbone of scientific endeavours to close knowledge gaps and, provided politicians take note, will help mitigate our environmental footprint in the Arctic seas (Witze 2016).

Acknowledgements. I am indebted to my colleagues and friends of the TUNU-Programme, UiT The Arctic University of Norway, for years of fruitful collaboration and inspiration. I particularly thank Ingvar Byrkjedal, Oleg V. Karamushko, Arve Lynghammer and Catherine W. Mecklenburg for their insights. I thank Malcolm Jobling for literature support, and the captain and his crew of RV 'Helmer Hanssen' (former RV 'Jan Mayen') and the Government of Greenland for access to the Northeast Greenland National Park. Three anonymous referees provided useful comments that improved the manuscript. This opinion piece has received neither public nor private funding thus preventing Open Access publication.

LITERATURE CITED

- Andersen OGN, Nielsen JR, Smidt ELB (1994) Description and comparison of eggs and yolk sac larvae of Greenland cod (*Gadus ogac*), Atlantic cod (*Gadus morhua*) and Arctic cod (*Boreogadus saida*) from West Greenland waters. *J Northw Atl Fish Sci* 16:19–32

- Andriashev AP (1970) Cryopelagic fishes of the Arctic and Antarctic and their significance in polar ecosystems. In: Holdgate MW (ed) Antarctic ecology. Academic Press, London, p 297–304
- ✦ Aronovich TM, Doroshev SI, Spectorova LV, Makhotin VM (1975) Egg incubation and larval rearing of navaga (*Eleginus navaga* Pall.), polar cod (*Boreogadus saida* lepechin) and arctic flounder (*Liopsetta glacialis* Pall.) in the laboratory. *Aquaculture* 6:233–242
- ✦ Arrigo KR (2014) Sea ice ecosystems. *Annu Rev Mar Sci* 6: 439–467
- ✦ Aschan M, Karamushko OV, Byrkjedal I, Wienerroither R, Borkin IV, Christiansen JS (2009) Records of the gadoid fish *Arctogadus glacialis* (Peters, 1874) in the European Arctic. *Polar Biol* 32:963–970
- ✦ Assmy P, Ehn JK, Fernandez-Mendez M, Hop H and others (2013) Floating ice-algal aggregates below melting Arctic sea ice. *PLOS ONE* 8:e76559
- ✦ Atkinson EG, Percy JA (1992) Diet comparison among demersal marine fish from the Canadian Arctic. *Polar Biol* 11: 567–573
- ✦ Atkinson A, Hill SL, Barange M, Pakhomov EA and others (2014) Sardine cycles, krill declines, and locust plagues: revisiting ‘wasp-waist’ food webs. *Trends Ecol Evol* 29: 309–316
- ✦ Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the ‘predator pit’ topographies. *Prog Oceanogr* 68:271–288
- ✦ Barnes DKA (2015) Antarctic sea ice losses drive gains in benthic carbon drawdown. *Curr Biol* 25:R789–R790
- ✦ Barnhart KR, Miller CR, Overeem I, Kay JE (2016) Mapping the future expansion of Arctic open water. *Nat Clim Chang* 6:280–285
- ✦ Bartsch I, Paar M, Fredriksen S, Schwanitz M, Daniel C, Hop H, Wiencke C (2016) Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biol* 39:2021–2036
- ✦ Bell LE, Bluhm BA, Iken K (2016) Influence of terrestrial organic matter in marine food webs of the Beaufort Sea shelf and slope. *Mar Ecol Prog Ser* 550:1–24
- Berg LS (1934) On the amphiboreal (discontinuous) distribution of marine fauna in the northern hemisphere. *Izvest Gos Geogr Obshch* 66:69–78 [in Russian]
- ✦ Berge J, Heggland K, Lønne OJ, Cottier F and others (2015) First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic* 68:54–61
- ✦ Boero F, Kraberg AC, Krause G, Wiltshire KH (2015) Time is an affliction: why ecology cannot be as predictive as physics and why it needs time series. *J Sea Res* 101:12–18
- ✦ Boetius A, Albrecht S, Bakker K, Bienhold C and others (2013) Export of algal biomass from the melting Arctic sea ice. *Science* 339:1430–1432
- ✦ Bouchard C, Fortier L (2008) Effects of polynyas on the hatching season, early growth and survival of polar cod *Boreogadus saida* in the Laptev Sea. *Mar Ecol Prog Ser* 355:247–256
- ✦ Brand M, Fischer P (2016) Species composition and abundance of the shallow water fish community of Kongsfjorden, Svalbard. *Polar Biol* 39:2155–2167
- ✦ Browman HI, Rodriguez CA, Béland F, Cullen JJ and others (2000) Impact of ultraviolet radiation on marine crustacean zooplankton and ichthyoplankton: a synthesis of results from the estuary and Gulf of St. Lawrence, Canada. *Mar Ecol Prog Ser* 199:293–311
- ✦ Byrkjedal I, Rees DJ, Christiansen JS, Fevolden SE (2008) The taxonomic status of *Theragra finnmarchica* Koefoed, 1956 (Teleostei: Gadidae): perspectives from morphological and molecular data. *J Fish Biol* 73:1183–1200
- ✦ Chernova NV (2017) Catching of Greenland halibut *Reinhardtius hippoglossoides* (Pleuronectidae) on the shelf edge of the Laptev and East Siberian Seas. *J Ichthyol* 57: 219–227
- ✦ Cheung WWL, Reygondeau G, Frölicher TL (2016) Large benefits to marine fisheries of meeting the 1.5°C global warming target. *Science* 354:1591–1594
- Christiansen JS, Lynghammar A (2012) Industrial potential of antifreeze proteins (AF[G]Ps) from marine fishes in Arctic Norway – initial screening of species. MABIT Scientific Report BS0040, UiT The Arctic University of Norway, Tromsø
- ✦ Christiansen JS, Reist JD (2013) Fishes. Arctic Biodiversity Assessment, Conservation of Arctic Flora and Fauna. www.arcticbiodiversity.is/the_report/chapters/fishes (accessed on 24 March 2017)
- Christiansen JS, Fevolden SE, Karamushko OV, Karamushko LI (1998) Maternal output in polar fish reproduction. In: di Prisco G, Pisano E, Clarke A (eds) *Fishes of Antarctica; a biological review*. Springer Italia, Milan, p 41–52
- ✦ Christiansen JS, Fevolden SE, Byrkjedal I (2005) The occurrence of *Theragra finnmarchica* Koefoed, 1956 (Teleostei, Gadidae), 1932–2004. *J Fish Biol* 66:1193–1197
- ✦ Christiansen JS, Hop H, Nilssen EM, Joensen J (2012) Trophic ecology of sympatric Arctic gadoids, *Arctogadus glacialis* (Peters, 1872) and *Boreogadus saida* (Lepechin, 1774), in NE Greenland. *Polar Biol* 35:1247–1257
- ✦ Christiansen JS, Mecklenburg CW, Karamushko OV (2014) Arctic marine fishes and their fisheries in light of global change. *Glob Change Biol* 20:352–359
- ✦ Christiansen JS, Bonsdorff E, Byrkjedal I, Fevolden SE and others (2016) Novel biodiversity baselines outpace models of fish distribution in Arctic waters. *Sci Nat* 103:8
- ✦ Clark GF, Stark JS, Johnston EL, Runcie JW, Goldsworthy PM, Raymond B, Riddle MJ (2013) Light-driven tipping points in polar ecosystems. *Glob Change Biol* 19: 3749–3761
- ✦ Cooke SJ, Killen SS, Metcalfe JD, McKenzie DJ, Mouillot D, Jørgensen C, Peck MA (2014) Conservation physiology across scales: insights from the marine realm. *Conserv Physiol* 2:cou024
- ✦ Cronin TM, Cronin MA (2015) Biological response to climate change in the Arctic Ocean: the view from the past. *Arktos* 1:4
- ✦ Crook DA, Douglas MM, King AJ, Schnierer S (2016) Towards deeper collaboration: stories of Indigenous interests, aspirations, partnerships and leadership in aquatic research and management. *Rev Fish Biol Fish* 26: 611–615
- ✦ David C, Lange B, Krumpfen T, Schaafsma F, van Franeker JA, Flores H (2016) Under-ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their association with sea-ice habitat properties. *Polar Biol* 39: 981–994
- ✦ Degen R, Jørgensen LL, Ljubin P, Ellingsen IH, Pehlke H, Brey T (2016) Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. *Mar Ecol Prog Ser* 546:1–16

- ✦ Doroshev SI, Aronovich TM (1974) The effects of salinity on embryonic and larval development of *Eleginus navaga* (Pallas), *Boreogadus saida* (Lepechin) and *Liopsetta glacialis* (Pallas). *Aquaculture* 4:353–362
- ✦ Drost HE, Carmack EC, Farrell AP (2014) Upper thermal limits of cardiac function for Arctic cod *Boreogadus saida*, a key food web fish species in the Arctic Ocean. *J Fish Biol* 84:1781–1792
- ✦ Drost HE, Lo M, Carmack EC, Farrell AP (2016) Acclimation potential of Arctic cod (*Boreogadus saida*) from the rapidly warming Arctic Ocean. *J Exp Biol* 219: 3114–3125
- ✦ Duarte CM, Krause-Jensen D (2017) Export from seagrass meadows contributes to marine carbon sequestration. *Front Mar Sci* 4:13
- Dunmall KM, Reist JD, Carmack EC, Babaluk JA, Heide-Jørgensen MP, Docker MF (2013) Pacific Salmon in the Arctic: harbingers of change. In: Mueter FJ et al. (eds) Responses of Arctic marine ecosystems to climate change. Alaska Sea Grant, University of Alaska Fairbanks, AK, p 141–160
- ✦ Dünweber M, Swalethorp R, Kjellerup S, Nielsen TG and others (2010) Succession and fate of the spring diatom bloom in Disko Bay, western Greenland. *Mar Ecol Prog Ser* 419:11–29
- ✦ Eguíluz VM, Fernández-Gracia J, Irigoien X, Duarte CM (2016) A quantitative assessment of Arctic shipping in 2010–2014. *Sci Rep*
- ✦ Ellis DV (1962) Observations on the distribution and ecology of some Arctic fish. *Arctic* 15:179–189
- Enevoldsen LT, Heiner I, DeVries AL, Steffensen JF (2003) Does fish from the Disko Bay area of Greenland possess antifreeze proteins during the summer? *Polar Biol* 26: 365–370
- ✦ Eriksen E, Ingvaldsen RB, Nedreaas K, Prozorkevich D (2015) The effect of recent warming on polar cod and beaked redfish juveniles in the Barents Sea. *Reg Stud Mar Sci* 2:105–112
- ✦ Falk-Petersen S, Pavlov V, Berge J, Cottier F, Kovacs KM, Lydersen C (2015) At the rainbow's end: high productivity fueled by winter upwelling along an Arctic shelf. *Polar Biol* 38:5–11
- ✦ Ferrando S, Gallu L, Ghigliotti L, Vacchi M, Nielsen J, Christiansen JS, Pisano E (2016) Gross morphology and histology of the olfactory organ of the Greenland shark *Somniosus microcephalus*. *Polar Biol* 39:1399–1409
- ✦ Flyvbjerg B (2006) Five misunderstandings about case-study research. *Qual Inq* 12:219–245
- ✦ Ford JD, Cameron L, Rubis J, Maillet M, Nakashima D, Willox AC, Pearce T (2016) Including indigenous knowledge and experience in IPCC assessment reports. *Nat Clim Chang* 6:349–353
- ✦ Fosheim M, Primercerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat Clim Chang* 5:673–677
- ✦ Geoffroy M, Robert D, Darnis G, Fortier L (2011) The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. *Polar Biol* 34:1959–1971
- ✦ Geoffroy M, Majewski A, LeBlanc M, Gauthier S, Walkusz W, Reist JD, Fortier L (2016) Vertical segregation of age-0 and age-1+ polar cod (*Boreogadus saida*) over the annual cycle in the Canadian Beaufort Sea. *Polar Biol* 39: 1023–1037
- ✦ Gradinger RR, Bluhm BA (2004) In-situ observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the High Arctic Canada Basin. *Polar Biol* 27:595–603
- ✦ Graham M, Hop H (1995) Aspects of reproduction and larval biology of Arctic cod *Boreogadus saida*. *Arctic* 48: 130–135
- ✦ Griffiths JR, Kadin M, Nascimento FJA, Tamelander T and others (2017) The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Glob Change Biol* 23:2179–2196
- ✦ Griffiths SP, Olson RJ, Watters GM (2013) Complex wasp-waist regulation of pelagic ecosystems in the Pacific Ocean. *Rev Fish Biol Fish* 23:459–475
- ✦ Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. *Polar Biol* 24:553–564
- ✦ Hamilton L, Lyster P, Otterstad O (2000) Social change, ecology and climate in 20th-century Greenland. *Clim Change* 47:193–211
- ✦ Haug T, Bogstad B, Chierici M, Gjørseter H and others (2017) Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fish Res* 188:38–57
- ✦ Hemming SR (2004) Heinrich events: massive late Pleistocene detritus layers of the North Atlantic and their global climate imprint. *Rev Geophys* 42:RG1005
- ✦ Henschke N, Everett JD, Richardson AJ, Suthers IM (2016) Rethinking the role of salps in the ocean. *Trends Ecol Evol* 31:720–733
- ✦ Hoff U, Rasmussen TL, Stein R, Ezat MM, Fahl K (2016) Sea ice and millennial-scale climate variability in the Nordic seas 90 kyr ago to present. *Nat Commun* 7:12247
- ✦ Hoffman JS, Clark PU, Parnell AC, He F (2017) Regional and global sea-surface temperatures during the last interglaciation. *Science* 355:276–279
- ✦ Hollowed AB, Planque B, Loeng H (2013) Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. *Fish Oceanogr* 22:355–370
- ✦ Hop H, Gjørseter H (2013) Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Mar Biol Res* 9: 878–894
- ✦ Hunt GL Jr, Blanchard AL, Boveng P, Dalpadado P and others (2013) The Barents and Chukchi Seas: comparison of two Arctic shelf ecosystems. *J Mar Syst* 109–110:43–68
- ✦ Hunt GL Jr, Drinkwater KF, Arrigo K, Berge J and others (2016) Advection in polar and sub-polar environments: impacts on high latitude marine ecosystems. *Prog Oceanogr* 149:40–81
- ✦ Ingvaldsen RB, Gjørseter H, Ona E, Michaelsen K (in press) (2017) Atlantic cod (*Gadus morhua*) feeding over deep water in the high Arctic. *Polar Biol* doi:10.1007/s00300-017-2115-2
- Iversen T (1923) Torskfiske ved Spitsbergen i gamle dage. Torskperioder. *Norsk Fiskeritidende* 42:115–129 [in Norwegian]
- ✦ Izzo C, Doubleday ZA, Grammer GL, Gilmore KL and others (2016) Fish as proxies of ecological and environmental change. *Rev Fish Biol Fish* 26:265–286
- ✦ Jansen T, Post S, Kristiansen T, Óskarsson GJ and others (2016) Ocean warming expands habitat of a rich natural resource and benefits a national economy. *Ecol Appl* 26: 2021–2032
- ✦ Jenkins SR, Uya M (2016) Temporal scale of field experiments in benthic ecology. *Mar Ecol Prog Ser* 547:273–286

- Jensen T (2016) Begrenser trålfisket. Fiskeribladet Fiskaren Week 38:17 [in Norwegian]
- ✦ Johannesen E, Jørgensen LL, Fossheim M, Primicerio R and others (2017) Large-scale patterns in community structure of benthos and fish in the Barents Sea. *Polar Biol* 40: 237–246
- Karamushko OV, Karamushko LI, Sandler H, Stasenkova VA (1997) The fish fauna of the Pechora Sea (South-Eastern Barents Sea). In: Sandler H, Grönlund L, Denisenko N (eds) Pechora Sea Ecological Studies in 1992–1995. Report B13, Finnish-Russian Offshore Technology Working Group, Helsinki, p 157–177
- Kędra M, Moritz C, Choy ES, David C and others (2015) Status and trends in the structure of Arctic benthic food webs. *Polar Res* 34:23775
- ✦ Kent D, Drost HE, Fisher J, Oyama T, Farrell AP (2016) Laboratory rearing of wild Arctic cod *Boreogadus saida* from egg to adulthood. *J Fish Biol* 88:1241–1248
- ✦ Kessel ST, Hussey NE, Crawford RE, Yurkowski DJ, Weber DM, Dick TA, Fisk AT (2017) First documented large-scale horizontal movements of individual Arctic cod (*Boreogadus saida*). *Can J Fish Aquat Sci* 74: 292–296
- ✦ Kohlbach D, Schaafsma FL, Graeve M, Lebreton B and others (2017) Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: Evidence from stomach content, fatty acid and stable isotope analyses. *Prog Oceanogr* 152:62–74
- Kortsch S (2016) Marine food-web structure and community patterns in high-latitude marine ecosystems—ecological responses to warming. PhD dissertation, UiT The Arctic University of Norway, Tromsø
- ✦ Krause-Jensen D, Marbà N, Sanz-Martin M, Hendriks IE and others (2016) Long photoperiods sustain high pH in Arctic kelp forests. *Sci Adv* 2:e1501938
- ✦ Kunz KL, Frickenhaus S, Hardenberg S, Johansen T and others (2016) New encounters in Arctic waters: a comparison of metabolism and performance of polar cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*) under ocean acidification and warming. *Polar Biol* 39: 1137–1153
- ✦ Lam VWY, Cheung WWL, Reygondeau G, Sumaila UR (2016) Projected change in global fisheries revenues under climate change. *Sci Rep* 6:32607
- ✦ Laurel BJ, Spencer M, Iseri P, Copeman LA (2016) Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. *Polar Biol* 39:1127–1135
- ✦ Leo E, Kunz KL, Schmidt M, Storch D, Pörtner HO, Mark FC (2017) Mitochondrial acclimation potential to ocean acidification and warming of Polar cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*). *Front Zool* 14:21
- ✦ Leu E, Mundy CJ, Assmy P, Campbell K and others (2015) Arctic spring awakening—steering principles behind the phenology of vernal ice algal blooms. *Prog Oceanogr* 139:151–170
- ✦ Link JS, Bogstad B, Sparholt H, Lilly GR (2009) Trophic role of Atlantic cod in the ecosystem. *Fish Fish* 10:58–87
- Lønne OJ, Gulliksen B (1991) Source, density and composition of sympagic fauna in the Barents Sea. *Polar Res* 10: 289–294
- ✦ Lovvorn JR, North CA, Kolts JM, Grebmeier JM, Cooper LW, Cui X (2016) Projecting the effects of climate-driven changes in organic matter supply on benthic food webs in the northern Bering Sea. *Mar Ecol Prog Ser* 548:11–30
- ✦ Majewski AR, Atchison S, MacPhee S, Eert J, Niemi A, Michel C, Reist JD (2017) Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. *Deep Sea Res I* 121:169–182
- Matarese AC, Kendall AW Jr, Blood DM, Vinter BM (1989) Laboratory guide to early life history stages of Northeast Pacific fishes. NOAA Technical Report NMFS 80:190–191
- ✦ McClelland JW, Holmes RM, Dunton KH, Macdonald RW (2012) The Arctic Ocean estuary. *Estuaries Coasts* 35: 353–368
- ✦ Mecklenburg CW, Steinke D (2015) Ichthyofaunal baselines in the Pacific Arctic region and RUSALCA study area. *Oceanography* 28:158–189
- ✦ Mecklenburg CW, Møller PR, Steinke D (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Mar Biodivers* 41:109–140
- ✦ Mecklenburg CW, Byrkjedal I, Christiansen JS, Karamushko OV, Lynghammar A, Møller PR (2013) List of marine fishes of the arctic region annotated with common names and zoogeographic characterizations. Conservation of Arctic Flora and Fauna. <http://caff.is/monitoring-series/> (accessed on 24 March 2017)
- ✦ Melnikov IA, Chernova NV (2013) Characteristics of under-ice swarming of polar cod *Boreogadus saida* (Gadidae) in the central Arctic Ocean. *J Ichthyol* 53:7–15.
- ✦ Mikkelsen N, Pedersen T, dos Santos Schmidt TC, Falk-Petersen IB, Slotte A (2016) Are life histories of Norwegian fjord herring populations of Pacific ancestry similar to those of Atlantic or Pacific herring? *J Mar Syst* doi: 10.1016/j.jmarsys.2016.12.004
- ✦ Misund OA, Heggland K, Skogseth R, Falck E and others (2016) Norwegian fisheries in the Svalbard zone since 1980. Regulations, profitability and warming waters affect landings. *Polar Sci* 10:312–322
- ✦ Moreno-Mateos D, Barbier EB, Jones PC, Jones HP and others (2017) Anthropogenic ecosystem disturbance and the recovery debt. *Nat Commun* 8:14163
- ✦ Nahrgang J, Varpe Ø, Korshunova E, Murzina S, Hallanger IG, Vieweg I, Berge J (2014) Gender specific reproductive strategies of an Arctic key species (*Boreogadus saida*) and implications of climate change. *PLOS ONE* 9: e98452
- ✦ Nahrgang J, Dubourg P, Frantzen M, Storch D, Dahlke F, Meador JP (2016) Early life stages of an arctic keystone species (*Boreogadus saida*) show high sensitivity to a water-soluble fraction of crude oil. *Environ Pollut* 218: 605–614
- ✦ Nielsen JL, Ruggerone GT, Zimmerman CE (2013) Adaptive strategies and life history characteristics in a warming climate: salmon in the Arctic? *Environ Biol Fishes* 96: 1187–1226
- ✦ Nielsen J, Hedeholm RB, Heinemeier J, Bushnell PG and others (2016) Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). *Science* 353:702–704
- ✦ Norris AJ, McKinley P (2017) The central Arctic Ocean—preventing another tragedy of the commons. *Polar Record* 53:43–51
- ✦ Notz D, Stroeve J (2016) Observed Arctic sea-ice loss directly follows anthropogenic CO₂ emission. *Science* 354:747–750
- NSIDC (2016) The National Snow & Ice Data Center. <https://nsidc.org/> (accessed on 24 March 2017)
- Nystø SR (2017) Næringsliv og urfolksrettigheter. *Fiskeribladet Fiskaren Week* 4:23 [in Norwegian]

- Paasche Ø, Österblom H, Neuenfeldt S, Bonsdorff E and others (2015) Connecting the seas of Norden. *Nat Clim Chang* 5:89–92
- Peck LS, Barnes DKA, Cook AJ, Fleming AH, Clarke A (2010) Negative feedback in the cold: ice retreat produces new carbon sinks in Antarctica. *Glob Change Biol* 16:2614–2623
- Planque B (2016) Projecting the future state of marine ecosystems, “la grande illusion”? *ICES J Mar Sci* 73:204–208
- Polyakov IV, Pnyushkov AV, Alkire MB, Ashik IM and others (2017) Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science* 356:285–291
- Ponomarenko VP (1968) Some data on the distribution and migrations of polar cod in the seas of the Soviet Arctic. *Rapp P-V Reün Cons Int Explor Mer* 158:131–135
- Post E, Bhatt US, Bitz CM, Brodie JF and others (2013) Ecological consequences of sea-ice decline. *Science* 341: 519–524
- Rass TS (1968) Spawning and development of polar cod. *Rapp P-V Reün Cons Int Explor Mer* 158:135–137
- Renaud PE, Sejr MK, Bluhm A, Sirenko B, Ellingsen IH (2015a) The future of Arctic benthos: expansion, invasion, and biodiversity. *Prog Oceanogr* 139:244–257
- Renaud PE, Løkken TS, Jørgensen LL, Berge J, Johnson BJ (2015b) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Front Mar Sci* 2:31
- Richardson DE, Harea JA, Fogarty MJ, Link JS (2011) Role of egg predation by haddock in the decline of an Atlantic herring population. *Proc Natl Acad Sci USA* 108: 13606–13611
- Ricklefs RE (2012) Naturalists, natural history, and the nature of biological diversity. *Am Nat* 179:423–435
- Sakurai Y, Ishii K, Nakatani R, Yamaguchi H, Anma G, Jin M (1998) Reproductive characteristics and effects of temperature and salinity on the development and survival of eggs and larvae of Arctic cod (*Boreogadus saida*). *Mem Fac Fish Hokkaido Univ* 44:77–89
- Schaefer JM, Finkel RC, Balco G, Alley RB and others (2016) Greenland was nearly ice-free for extended periods during the Pleistocene. *Nature* 540:252–255
- Schurmann H, Christiansen JS (1994) Behavioural thermoregulation and swimming activity of 2 Arctic teleosts (subfamily Gadinae)—the polar cod (*Boreogadus saida*) and the navaga (*Eleginus navaga*). *J Therm Biol* 19: 207–212
- Siegelman-Charbit L, Planque B (2016) Abundant mesopelagic fauna at oceanic high latitudes. *Mar Ecol Prog Ser* 546:277–282
- Simpson SD, Radford AN, Nedelec SL, Ferrari MCO, Chivers DP, McCormick MI, Meekan MG (2016) Anthropogenic noise increases fish mortality by predation. *Nat Commun* 7:10544
- Solberg I, Kaartvedt S (2014) Surfacing behavior and gas release of the physostome sprat (*Sprattus sprattus*) in ice-free and ice-covered waters. *Mar Biol* 161:285–296
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459
- Straneo F, Cenedese C (2015) The dynamics of Greenland’s glacial fjords and their role in climate. *Annu Rev Mar Sci* 7:89–112
- Szymanski A, Gradinger R (2016) The diversity, abundance and fate of ice algae and phytoplankton in the Bering Sea. *Polar Biol* 39:309–325
- Tremblay JÉ, Anderson LG, Matrai P, Coupel P, Bélanger S, Michel C, Reigstad M (2015) Global and regional drivers of nutrient supply, primary production and CO₂ draw-down in the changing Arctic Ocean. *Prog Oceanogr* 139: 171–196
- Varpe Ø, Daase M, Kristiansen T (2015) A fish-eye view on the new Arctic lightscape. *ICES J Mar Sci* 72:2532–2538
- Wang M, Overland JE (2012) A sea ice free summer Arctic within 30 years: An update from CMIP5 models? *Geophys Res Lett* 39:L18501
- Wassmann P, Reigstad M (2011) Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography* 24:220–231
- Welch HE, Crawford RE, Hop H (1993) Occurrence of Arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian high Arctic. *Arctic* 46: 331–339
- Whiteley NM, Christiansen JS, Egginton S (2006) Polar cod, *Boreogadus saida* (Gadidae), show an intermediate stress response between Antarctic and temperate fishes. *Comp Biochem Physiol A* 145:493–501
- Wiencke C, Hop H (2016) Ecosystem Kongsfjorden: new views after more than a decade of research. *Polar Biol* 39: 1679–1687
- Wienerroither RM, Nedreaas KH, Uiblein F, Christiansen JS, Byrkjedal I, Karamushko O (2011) The marine fishes of Jan Mayen Island, NE Atlantic—past and present. *Mar Biodivers* 41:395–411
- Witze A (2016) Fleet of polar ships raises science stakes. *Nature* 533:302–303

Editorial responsibility: Ivan Nagelkerken,
Adelaide, South Australia, Australia

Submitted: September 5, 2016; Accepted: May 13, 2017
Proofs received from author(s): June 30, 2017