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RESEARCH/REVIEW ARTICLE

Status and trends in the structure of Arctic benthic food webs

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Keywords

Arctic; food web; climate change; sea-ice retreat; trophic transfer; pelagic–benthic coupling.

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Abstract

Ongoing climate warming is causing a dramatic loss of sea ice in the Arctic Ocean, and it is projected that the Arctic Ocean will become seasonally ice-free by 2040. Many studies of local Arctic food webs now exist, and with this review paper we aim to synthesize these into a large-scale assessment of the current status of knowledge on the structure of various Arctic marine food webs and their response to climate change, and to sea-ice retreat in particular. Key drivers of ecosystem change and potential consequences for ecosystem functioning and Arctic marine food webs are identified along the sea-ice gradient, with special emphasis on the following regions: seasonally ice-free Barents and Chukchi seas, loose ice pack zone of the Polar Front and Marginal Ice Zone, and permanently sea-ice covered High Arctic. Finally, we identify knowledge gaps in different Arctic marine food webs and provide recommendations for future studies.

The Arctic Ocean is experiencing significant warming of approximately three times the global average (Steele et al. 2008; Serreze et al. 2009; Polyakov et al. 2010) and, despite a very pronounced seasonality, recent winter warming far exceeds that occurring in summer (Screen & Simmonds 2010). One of the characteristic features of the Arctic Ocean is sea ice, present permanently at high latitudes and seasonally at lower latitudes in winter (Fig. 1). The most conspicuous sign of warming is the dramatic loss of sea ice (Higgins & Cassano 2009; Parkinson & Comiso 2013): its summer extent has decreased by nearly 50% over the past decade (Fig. 1), and the Arctic Ocean

has undergone a regime shift from multi-year ice to largely seasonal and much thinner ice cover (Comiso 2012). The Arctic Ocean may become seasonally ice-free by as early as 2040 (Polyakov et al. 2010). Reductions in sea-ice cover are being further amplified by increased heat fluxes into the Arctic Ocean through the Bering (Woodgate et al. 2006; Woodgate et al. 2010; Woodgate et al. 2012) and Fram straits (Piechura & Walczowski 2009). This enhanced ocean temperature further delays the growth of sea ice in the fall (Steele et al. 2008). In terms of ecosystem functioning, these patterns indicate a shift towards an earlier spring transition between sea-ice-covered and

sea-ice-free conditions (Grebmeier, Overland et al. 2006; Steele et al. 2008). Therefore, in the Arctic, climate change is not only affecting the physical structures such as sea ice, but is also responsible for multiple ecological changes on ecosystem functioning, including food-web structure, stability and efficiency, especially by affecting components at the base of the food web.

The two main sources of primary production in Arctic ecosystems are sea-ice algae and phytoplankton (Søreide et al. 2006). The growth of both ice algae and phytoplankton takes place within a one to four month period during spring and summer (Søreide et al. 2006; Renaud, Carroll et al. 2008; Iken et al. 2010). The productive season starts at the end of the polar night with sunlight triggering the bloom of sea-ice algae. Even though they constitute only a small-to-moderate portion (<20%) of total annual primary production (Hegseth 1998; Gradinger 2009), ice algae contribute to Arctic benthic food webs during springtime on shallow continental shelves with seasonal ice cover because they occur early and sink fast following sea-ice retreat (Hobson et al. 1995; Tamelander et al. 2006). This ice algal contribution is proportionally more important in areas where sea-ice cover lasts later in the year (Gosselin et al. 1997) but is expected to decrease with current sea-ice retreat (Leu et al. 2011). A phytoplankton spring bloom follows the ice algae bloom as the sea-ice cover melts (Leu et al. 2011). In the summer, limited nutrients support a low phytoplankton biomass (Wassmann & Reigstad 2011), with episodic bloom conditions facilitated by occasional nutrient availability (Grebmeier, Cooper et al. 2006). These phytoplankton blooms, although responsible for the bulk of annual production, are usually restricted to open waters (but see Arrigo et al. 2012; Mundy et al. 2014). Boetius et al. (2013) also showed that sinking ice algae aggregates constitute an important food input to benthos in the Arctic basins. In addition to phytoplankton and ice algal production, microbial oceanic phototrophs can contribute up to 50% of total inorganic carbon assimilation and play a leading role in nutrient cycling (Falkowski et al. 1998). Bacterial primary production ratios have been estimated to reach more than 240% above 81°N (Rich et al. 1997) compared to 1–143% ($32 \pm 6\%$) in the Barents Sea (Sturluson et al. 2008). The bacterial contribution to respiration in the water column may be substantial: 3–60% in the Chukchi Sea and Canada Basin, and 25% on average in the Arctic (Kirchman et al. 2009). Moreover, bacterial activity on sinking particles, an important habitat that harbours distinct communities of Arctic bacteria (Hansell & Ducklow 2003; Hodges et al. 2005), directly affects the quantity and quality of the organic matter that reaches the seafloor. In coastal areas and interior shelves,

coastal erosion, river and glacial discharge can become important sources of terrestrial organic matter that can also be further utilized in benthic food webs (Dunton et al. 2006; Dunton et al. 2012; Kędra et al. 2012; Kuliński et al. 2014).

The quality and quantity of primary production, including ice algae and phytoplankton, reaching the seafloor have a strong impact on benthic communities (Pearson & Rosenberg 1978), which further cascades through the whole food web, especially in the highly seasonal Arctic marine ecosystems. Shallow Arctic shelves in particular are characterized by tight pelagic–benthic coupling due to low grazing in the water column during the bloom (Grebmeier et al. 1988; Grebmeier & McRoy 1989; Renaud, Carroll et al. 2008; Tamelander et al. 2008). This results in large export of organic matter, produced in the surface layers and descending to the seafloor and benthos (Grebmeier, Cooper et al. 2006), especially in spring, when production is far greater than zooplankton consumption (Tamelander et al. 2006). For example, almost 70% of the organic carbon produced in the water column during spring in the Pacific Arctic region reaches the seafloor (Walsh et al. 1989), supporting high biomass, abundance and diversity of benthic organisms (Grebmeier & McRoy 1989; Grebmeier, Cooper et al. 2006; Iken et al. 2010; Bluhm, Gradinger et al. 2011), which are important prey items for higher trophic level animals foraging on the seafloor, including diving sea ducks (Merginae), bearded seals (*Erignathus barbatus*), walrus (*Odobenus rosmarus*) and grey whales (*Eschrichtius robustus*) (Lovvorn et al. 2003; Grebmeier, Cooper et al. 2006; Grebmeier & Barry 2007; Grebmeier 2012). This contrasts with the summer period, when grazing of phytoplankton by zooplankton may reach up to 97% of daily water column primary production in more pelagic-oriented areas like the Barents Sea (Tamelander et al. 2006), thus limiting carbon export to the benthos. During summer, reworked organic matter consisting of zooplankton faecal pellets and carcasses, moults and bacteria, as well as phytodetritus, primarily fuels benthic food webs. Many shallow shelf Arctic systems, especially in the Pacific Arctic, have a high efficiency of energy transfer from the water column to the benthos (Ambrose & Renaud 1995). Macro- and megafauna appear to play a prominent role in carbon recycling (up to 30% efficiency for Arctic benthos; Clough et al. 2005; Renaud et al. 2007), but studies focusing on partitioning of carbon recycling for bacterial, meiofaunal, macrofauna and megafaunal components are rare (Piepenburg et al. 1995).

Trophic transfer efficiency describes the efficiency with which energy is transferred from one trophic level to the next, in particular the relative percentage of primary

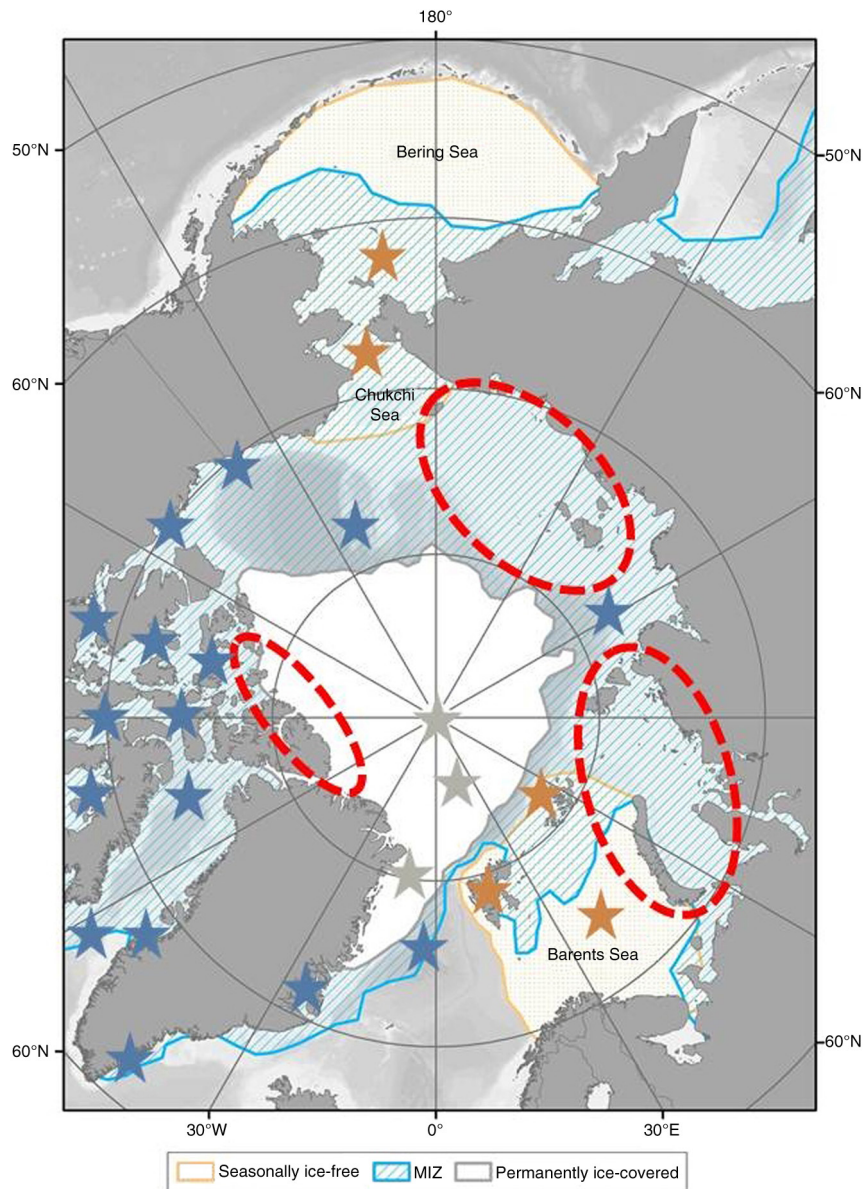


Fig. 1 Map of the Arctic Ocean showing the minimum sea-ice extent September 2012 and the median sea-ice extent February 1981–2010 (blue line). Locations of published food-web studies and the case study areas of this review are marked with yellow (seasonally ice-free areas), blue (Marginal Ice Zone [MIZ]) and grey (permanently ice-covered High Arctic) stars. Red circles indicate areas that require more investigation. Bathymetry after Amante & Eakins (2009); sea-ice data from Fetterer et al. (2002).

production that reaches top predators (Kozlovsky 1968). Species interactions, of which many are sea-ice related in Arctic ecosystems (Fortier et al. 2002; Gradinger & Bluhm 2004; Søreide et al. 2006; Gradinger 2009), control energy and organic matter flow which determine ecological efficiencies and can limit productivity and patterns of species dominance and food-web stability (McCann 2000). In the changing Arctic Ocean, species shifts and local extinctions and invasions may occur, leading to new

interactions between species that have not co-evolved (Hobbs et al. 2006). New or missing links in established food webs may lead to large energy inefficiencies, changes in energy pathways that currently support key top predators, and destabilization of food-web dynamics (Vander Zanden et al. 1999; Pauly et al. 2002). However, this process is also dependent on the level of trophic and functional redundancy in a system (Layman et al. 2007). Understanding how Arctic food webs will become

structured in the future will therefore entail disentangling the factors with most impact on interspecific interactions.

The aim of this paper is to present the current status of knowledge of the structure of various Arctic marine benthic food webs and their observed responses to ongoing climate change, in particular to sea-ice retreat. Potential changes to food-web trophic transfer efficiency are also discussed. To date, most focused studies of Arctic food webs are limited in space, time or taxonomic level (e.g., Iken et al. 2005; Aydin & Mueter 2007; Bergmann et al. 2009; Megrey & Aydin 2009; Iken et al. 2010; Feder et al. 2011; Dunton et al. 2012; Whitehouse et al. 2014), and large-scale syntheses across the Arctic are generally missing. Only a few pan-Arctic reviews have been published (Carmack & Wassmann 2006; Piepenburg et al. 2011; Wassmann et al. 2011), and none has focused on species interactions and trophic pathways of food webs nor on food-web structure and with trophic transfer efficiency. To complement existing studies, this review will focus on the key drivers of ecosystem changes in the Arctic, including sea-ice decline, temperature rise and changes in stratification and the consequences for important ecosystem functions that are susceptible to change, including nutrient regeneration, primary and secondary production, pelagic–benthic coupling, structure of food webs and consequences for top predators. In particular, we aim to: (1) identify key drivers of ecosystem change and potential consequences for ecosystem functioning; (2) present different scenarios and trends in Arctic marine food webs by analysing regional ecosystem case studies located along a sea-ice gradient: the seasonally ice-free Barents Sea and Chukchi Sea, the loose ice pack Polar Front (PF) and the Marginal Ice Zone (MIZ) and the permanent ice-covered High Arctic; and (3) identify knowledge gaps in Arctic marine food webs, and suggest possible methods to fill these gaps and provide recommendations for future studies.

Primary and secondary drivers of ecosystem change: potential consequences

Key drivers of ecosystem change

The primary driver of the observed ecosystem change in high latitudes is ongoing climate change, and warming in particular (Symon et al. 2005). Increasing air temperature is the main cause of sea-ice decline, along with the secondary drivers of Arctic ecosystem change, such as increase in sea-water temperature and altered stratification (Symon et al. 2005; Stocker et al. 2013). Sea ice is a major regulating component in controlling pelagic and benthic production through modulating water column

stratification and light fields (Bluhm & Gradinger 2008; Gradinger 2009) because it controls the exchange of heat between the atmosphere and ocean and, together with snow cover, limits the penetration of light into the water column. Also, in the Arctic Ocean, the thaw–freeze cycle of sea ice and large freshwater riverine inputs result in pronounced haline stratification within the surface layer (Carmack & Wassmann 2006). Shortly after the phytoplankton spring bloom, the polar mixed layer becomes and remains nitrogen-depleted because of strong vertical stratification, which prevents replenishment during the summer season (Tremblay et al. 2008). Analysis of model data shows that when less sea ice is produced and freshwater load is increasing in the Arctic Ocean, the water column stratification becomes stronger, which decreases winter mixing (Slagstad et al. 2011), subsequently affecting nutrient distribution in the water column (Li et al. 2009; Codispoti et al. 2013; Matrai et al. 2013). In general, patterns of nutrients availability in the euphotic zone are a function of the total transport at the Barents Sea Opening and Fram Strait, through Davis Strait in the Canadian Archipelago and Bering Strait in the Pacific Arctic region, along with nutrient input from rivers, upwelling, stratification patterns and local mixing of deep water (Codispoti et al. 2013). Both major sources of nutrients in the Arctic Ocean, oceanic inputs associated with waters of Pacific and Atlantic origin, and riverine nutrient fluxes, are likely to change with accelerating climate change (Peterson et al. 2002; McClelland et al. 2006; Peterson et al. 2006; Shiklomanov & Lammers 2009). Changes in riverine freshwater runoff will likely be associated with changes in the quality and quantity of the nutrient supply, and while the loads of silicate, phosphate and dissolved and particulate organic matter are expected to increase in the future, trend in riverine nitrogen loads remain largely unknown (Frey et al. 2007; Raymond et al. 2007; Frey & McClelland 2009). Differences between nutrient transport and availability over the shelf areas and central Arctic may increase in the future: the already nutrient-depleted central Arctic Basin will likely become more oligotrophic, while shelf areas will be further enriched by increased transport of Atlantic and Pacific water masses and runoff. Biogeochemical processes and changes in adjacent basins as well as circulation changes may affect the future productivity of the Arctic Ocean.

Primary production and its consumers

Alterations of the seasonal cycle of primary productivity at the base of the food web is one of the most important consequences of rising temperature, sea-ice retreat and

changes in nutrient patterns. In general, ice algae and pelagic phytoplankton production occur sequentially during the year, with the abundance of ice algae relative to pelagic phytoplankton increasing northward coincident with greater sea-ice cover (Leu et al. 2011; Wassmann et al. 2011; Rubao et al. 2013). Although light availability and nutrients are often the prime limiting factors for primary production (Gradinger 2009; Leu et al. 2011), the timing of pelagic phytoplankton blooms is likely controlled by sea-ice retreat, whereas the timing of ice algae blooms is influenced by snow and sea-ice melt and starts earlier than open-water blooms. In many Arctic marginal seas, the timing of sea-ice retreat may have a strong impact on the timing of phytoplankton production, but little or no impact on the timing of ice algae peaks. Changes in the timing of maximum phytoplankton production influence the variability in time-lags between ice algal and phytoplankton production peak production (from 45 to 90 days; Ji et al. 2013). The timing of the sea-ice algal bloom is an important driver of spring secondary production as an earlier ice algae bloom will export larger amounts of primary production to seafloor communities (Gradinger 1995), especially when water column grazing is low, strengthening pelagic–benthic coupling processes. Changes in timing of the pulses of ice algae and phytoplankton primary production and in the associated gap period between them will influence zooplankton grazer abundances and activities (Søreide et al. 2010; Varpe 2012). Although the timing of primary production varies greatly over time and space in different regions, systematic shifts in the timing of production and export processes have the potential to increase the frequency of mismatch between marine grazers and their food, which in turn can subsequently alter the organic matter flux to the seafloor and/or the transfer to the higher trophic levels (Rubao et al. 2013).

Because Arctic zooplankton reproduction is largely determined by the food quality of autotrophs (Müller-Navarra 2008), production of lipids in sea-ice diatoms early in the season is extremely important (Falk-Petersen et al. 2009; Søreide et al. 2010). These high-energy lipid compounds are rapidly transferred through the Arctic marine food chains. Changes in the initiation and duration of the growth season, and therefore in the timing, quality and quantity of sea-ice blooms, will directly affect, among others, calanoid copepods (Ji et al. 2012), which are critical to energy transfer between lower and higher trophic levels. Diatom lipids are accumulated in large amounts by *Calanus* species and ice amphipods, and further transferred to pelagic carnivorous zooplankton and pelagic fish stocks (Scott et al. 1999; Scott et al. 2001; Auel et al. 2002). Lipid levels increase from 10–20% in

phytoplankton to 50–70% in herbivorous zooplankton and ice fauna that then become available as nutritious prey items for upper trophic level consumers (Daase et al. 2014). Dominant Arctic zooplankton taxa, like *Calanus glacialis*, switch from a diet of ice algae in spring towards phytoplankton in late summer, while others, like the sympagic amphipod *Apherusa glacialis*, feed mainly on ice algae during early spring (Falk-Petersen et al. 1999; Scott et al. 1999; Falk-Petersen et al. 2006). Ice-associated amphipods *Onisimus* spp. switch from ice algae in spring to an omnivorous diet by the end of the productive season (Werner & Auel 2005). The young ice amphipod *Gammarus wilkitzkii* feeds on ice algae, while their adults have a carnivorous diet, feeding preferentially on calanoid copepods (Scott et al. 2001; Werner et al. 2002). Although most benthic species do not feed directly on algal cells, changes in the timing and quality of bloom sedimentation (the latter additionally influenced by microbial processing) may impact those species' composition and abundances (Ambrose & Renaud 1997). Changes in the availability or abundance of ice algae or dependent zooplankton communities may cause cascading impacts on higher trophic level populations.

Microbial processes

Earlier sea-ice melt and increased stratification of the water column will promote picophytoplankton occurrence. Because of their short generation times, microorganisms respond quickly to environmental changes and are the first to react to global changes, affecting key ecosystem functions at the base of food webs (Sarmiento et al. 2010). Significant changes in microbial communities and diversity have already been observed after a sharp decline of sea-ice cover in September 2007 (between 2002 and 2010; Comeau et al. 2011). Increased carbon supply from pelagic productivity and riverine discharge coupled with increased bottom water temperature could result in higher bacterial activity and rates of bacterial cycling of carbon (Kritzberg et al. 2010; Vaquer-Sunyer et al. 2010). The decreased quality and quantity of sinking particles (Wassmann & Reigstad 2011) and usable carbon (Renaud, Morata et al. 2008) being exported to the seafloor would decrease the efficiency of food webs. Picophytoplankton is believed to be relatively inaccessible as a prey for mesozooplankton (Li et al. 2009); however some studies suggest that protozoans may constitute a larger percentage of copepod diets (Campbell et al. 2009), even up to 80–90%, during summertime, when abundances, biomass and production are dominated by pico- and nanophytoplankton (Piwosz et al. 2009; De Laender et al. 2010; Piwosz et al. 2015) and when abundances of

microzooplankton are high (Kubiszyn et al. 2014). In herbivore-limited systems, copepod production is therefore closely linked with protozoan production and constitutes a direct link between the microbial loop and higher trophic levels (Campbell et al. 2009; Sherr et al. 2009; De Laender et al. 2010; Nelson et al. 2014). Still, it is likely that Arctic food webs will lengthen at their base with the increase in numbers of trophic transfers within the microbial food webs or the number of grazers in the water column, decreasing the amount of carbon available for the higher trophic levels in the original food chain.

Our knowledge of the possible impact of viruses and parasitic protists in terms of their capacity to terminate algal blooms in the Arctic is limited (Nelson et al. 2014). Viral infection has been shown to control blooms of the coccolithophore *Emiliana huxleyi* in the Northern Atlantic (Wilson et al. 2002), while parasitic protists in the order Syndiniales have been coupled with collapses of blooms of dinoflagellate species in the Mediterranean Sea (Chambouvet et al. 2008). Increased impact of algal viruses and parasites would decrease the amount of food available for pelagic and benthic grazers. How these processes affect current blooms in the Arctic Ocean remains largely unknown, but both viruses and parasitic Syndiniales have been reported from sea ice (Wells & Deming 2006; Bachy et al. 2011; Collins & Deming 2011; Comeau et al. 2013; Piwosz et al. 2013) and the water column (Howard-Jones et al. 2002; Lovejoy et al. 2006; Bachy et al. 2011; Comeau et al. 2011; Payet & Suttle 2013).

Pelagic–benthic coupling

The initiation of sea-ice retreat is important for the timing, quality and amount of primary production (Springer et al. 1996; Hunt & Stabeno 2002), and changes in the timing of both ice algae and phytoplankton primary production may cause changes in food webs by influencing the standing stock of zooplankton, which will in turn affect the direct, ungrazed deposition of phytoplankton (Cooper et al. 2002) and subsequently benthic species (Overland & Stabeno 2004; Grebmeier, Cooper et al. 2006; Grebmeier, Overland et al. 2006; Nelson et al. 2009; Grebmeier 2012). In areas with reduced summer sea ice, pelagic grazing pressure will be higher (Lalande et al. 2007), perhaps altering sedimentation of organic matter, resulting in more pelagic-oriented systems. With increased primary production (Arrigo & van Dijken 2011; Arrigo et al. 2014; Palmer et al. 2014), pelagic food webs could become more productive and intercept more organic matter before it reaches the seafloor (Renaud, Carroll et al. 2008); however, nutrient limitation may halt this process. Increased grazing would reduce the

export flux of carbon to the seafloor, weakening pelagic–benthic coupling processes. Studies in the Bering Sea found that with sea-ice cover the spring blooms were characterized by a higher proportion of diatoms, less recycling and greater export and, therefore, stronger pelagic–benthic coupling (Moran et al. 2012). In the case of open-water conditions, blooms were characterized by a higher proportion of dinoflagellates, greater carbon cycling in the water column and lower export to the seafloor, and consequently reduced pelagic–benthic coupling (Moran et al. 2012).

Upper trophic levels

Changes in primary and secondary production affect upper trophic levels and are predicted to have increasing impact with climate warming (Wassmann 2006; Daufresne et al. 2009; Moore et al. 2014). Arctic marine top predators will have to face extreme changes in their habitat and forage base, including density and distributional shifts of their prey, as well as potential losses of some of their favoured lipid-rich prey species (Kovacs & Lydersen 2008; Kovacs et al. 2011). Upper trophic levels usually respond in a non-linear fashion to changes in ecosystem structure and usually the response depends on their exact position in the food web (Moore et al. 2014). Although the resilience of Arctic top predators is largely dependent on an individual's adaptive capacity, in general their resilience capacity depends largely on the region, the intensity and range of ice cover change and species characteristics (e.g., ice-obligate species are more vulnerable than ice-associated or seasonally migrant ones [Moore & Huntington 2008]). Sea-ice associated and sea-ice obligate species such as walrus and bearded seals that use sea ice as a platform for breeding, resting and foraging will be most affected by changes in sea-ice cover (Laidre et al. 2008; Moore & Huntington 2008; Table 1). Reductions in prey quality have been observed to have ecosystem-wide effects, such as population crashes of Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska (Rosen & Trites 2000) and breeding failures of seabirds in the North Sea (Wanless et al. 2005). A decline in spawning and foraging areas will affect both predators and their prey. For instance, polar cod (*Boreogadus saida*) abundance might be significantly reduced, with tremendous consequences to the entire system as this species is believed to account for up to 75% of energy transfer between zooplankton and vertebrate predators (Darnis et al. 2012). In addition to changes in resource availability, top predators will likely face increased complexity within food webs that tend to dissipate energy flow (Węśławski et al. 2009). This will likely be followed by increased

Table 1 Circumpolar Arctic top predators, their principal food sources and estimated population sizes.

Species	Habitat	Principal food source	Population size	Reference
Fulmar (<i>Fulmarus glacialis</i>)	Pelagic, surface	Cephalopods, epipelagic fish, pteropods, floating carrion	15 000 000–30 000 000	BirdLife International 2012b
Spectacled eider (<i>Somateria fischeri</i>)	Coastal, pelagobenthic	Benthos, crustaceans, molluscs	330 000–390 000	BirdLife International 2012c
Little auk (<i>Alle alle</i>)	Coastal, pelagic	Pelagic crustaceans, copepods	16 000 000–36 000 000	BirdLife International 2012a
Ringed seal (<i>Phoca hispida</i>)	Coastal, pelagobenthic, 0–100 m	Polar cod, demersal fish, large crustaceans	2 500 000	Miyazaki 2002
Bearded seal (<i>Erignathus barbatus</i>)	Coastal, benthic, 0–100 m	Demersal fish, crabs, shrimps, urchins	Unknown	Kovacs 2002
Greenland seal (<i>Phoca groenlandica</i>)	Pelagic, 0–100 m	Pelagic fish	8 000 000	Kovacs 2008
Walrus (<i>Odobenus rosmarus</i>)	Benthic, 0–50 m	Large bivalves, gastropods, shrimps	Unknown	Lowry et al. 2008
Minke whale (<i>Balaenoptera acutorostrata</i>)	Pelagic, 0–200 m	Large pelagic crustaceans, pteropods, pelagic fish	182 000	Reilly et al. 2008a
Bowhead (<i>Balaena mysticetus</i>)	Pelagic	Pelagic crustaceans, copepods	> 10 000	Reilly et al. 2012
Eastern North Pacific grey whale (<i>Eschrichtius robustus</i>)	Pelagic	Benthos, amphipods	15 000–22 000	Reilly et al. 2008b
Beluga whale (<i>Delphinapterus leucas</i>)	Coastal, pelagic, estuary	Coastal and pelagic fish, crustaceans, cephalopods	> 150 000	Jefferson et al. 2012

competition from temperate species that are expanding northward, e.g., Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) (Renaud et al. 2012) and Atlantic mackerel (*Scomber scombrus*) (Berge et al. 2015), and increased predation from species formerly unable to access them in areas of extensive sea-ice cover, such as killer whales (*Orcinus orca*) (Higdon & Ferguson 2009), gannets following northward move of herring and mackerel (Symon et al. 2005), and fish-eating whales that are getting more abundant in the Pacific Arctic region (Grebmeier 2012; Moore et al. 2014). Also, an increase in temperate and sub-Arctic fish migration is predicted to lead to a decrease in prey quality, since they are less lipid-rich than Arctic species (Symon et al. 2005; Hop & Gjøsæter 2013). Additionally, increased risks of disease and contaminants may also become an issue (Kovacs & Lydersen 2008).

Changes in species distribution ranges mediated by temperature

Temperature has a direct impact on metabolic and physiological processes as well as on the behaviour of individual organisms (Duarte 2007; O'Connor et al. 2007). It may influence growth, survival, reproduction, phenology and recruitment success of particular species (Lewis 1996; Walther et al. 2002; Lewis 2005; Herbert et al. 2007). Therefore, spatial distributions of organisms will likely change because of differential survival and recruitment of pelagic larval stages with varying water temperatures (Sirenko & Kolutin 1992; Blanchard et al. 2010; Grebmeier 2012). Changes in phenology can lead to a decoupling of the dynamics between predator and prey that will further alter current trophic relations and communities. Some species time their reproductive efforts to match the spring algal bloom (Falk-Petersen et al. 2009), e.g., females of the copepod *Calanus glacialis* utilize the spring pulse of ice algae to initiate reproduction, allowing their young to feed on the phytoplankton bloom that occurs after the breakup (Søreide et al. 2010). Along with temperature rise and sea-ice reduction, an increase in small-sized phytoplankton cells is predicted (Li et al. 2009) as well as a decrease in individual body size coupled with an increase in proportion of juveniles (Daufresne et al. 2009). At the population level, a shift of species may be observed, e.g., large, lipid-rich zooplankton species, such as *C. glacialis* and *C. hyperboreus* are being replaced by the smaller boreal and lipid-poorer species *C. finmarchicus* (Falk-Petersen et al. 2006).

Sea-water temperature rise and warmer Atlantic and Pacific waters advected northward also represent a threat to Arctic biodiversity and may further change trophic

relationships and food-web structure. These changes will facilitate open-water adapted species and boreal species to expand northward and ice-adapted species to retract in range (e.g., Sirenko & Gagaev 2007; Hollowed et al. 2013), which may lead to local extinctions, especially in the case of sea-ice dependent fauna (Clarke & Harris 2003). Changes have already been observed, including a northward distributional shift of fish and invertebrates in the Bering Sea (Mueter & Litzow 2008) and in the North Atlantic (Wienerroither et al. 2011), penetration of Pacific clams into the Chukchi Sea (Sirenko & Gagaev 2007), reoccurrence of Atlantic mussels in Svalbard (Berge et al. 2005), and Pacific zooplankton northward movement into the Beaufort Sea (Nelson et al. 2009). Also, an increase in year-round resident species may occur, e.g., grey whales that usually migrate south may stay in the Bering and Chukchi seas longer because of expanded open-water feeding areas and warmer water temperature (Moore & Huntington 2008).

Sea-ice gradient: scenarios and trends

Since sea-ice retreat is probably the most critical of expected consequences of climate warming for the Arctic marine ecosystems, in this review three regional ecosystem case studies are used to conceptualize possible changes in food-web structure and efficiency along a sea-ice gradient: the seasonally ice-free Barents Sea and Chukchi Sea, the loose ice pack PF and MIZ and the permanently ice-covered High Arctic (Table 2, Fig. 2a, b). In general, the described scenarios refer to current or possible future conditions on the shelves. The Barents and Chukchi seas were chosen as two case studies as

Table 2 Number of food-web studies undertaken in the Arctic by area. Data were collected using the search terms “Arctic” and “marine” and “food web” on the Web of Science. Studies that examined the relationship between two or more trophic levels were retained. Reviews and modelling with no in situ studies were excluded.

Area	Number of studies
Barents Sea	18
Bering Sea	17
Beaufort Sea	44
Canadian Arctic	69
Central Arctic Ocean	7
Chukchi Sea	16
Greenland Sea	23
Labrador Sea	61
Laptev Sea	1
Svalbard	45
White Sea	1
Yermak Plateau	2
Total	304

the food webs and associated trophic relations there are relatively well-studied (e.g., Iken et al. 2010; Feder et al. 2011; Renaud et al. 2011; Dunton et al. 2012; Grebmeier 2012; Kędra et al. 2012; Nelson et al. 2014; Table 2, Fig. 2). PF and MIZ are highly productive zones, which are likely to change their locations, extents and features as the ice edge retreats from the coast and continental shelves (Fig. 2). Arctic deep-sea regions represent a large part of the Arctic Ocean susceptible to change due to fast sea-ice retreat, yet studies of deep benthic food webs are scarce (Bergmann et al. 2009; Iken et al. 2010; van Oevelen et al. 2011; Table 2). In all three case studies, the scale and the extent of response to climate change and sea-ice retreat remain largely unknown.

Arctic shelf: seasonally ice-free—Barents and Chukchi seas

Many Arctic shelf systems are characterized by high benthic biomass and production especially in areas of inflow of Atlantic or Pacific nutrient-rich water masses, and along the PF (Carmack & Wassmann 2006; Grebmeier, Cooper et al. 2006; Renaud, Morata et al. 2008; Fig. 2a). On the south-eastern Chukchi Sea shelf, primary production can exceed $430 \text{ g C m}^{-2} \text{ y}^{-1}$ (Springer et al. 1996; Sakshaug 2004; Lee et al. 2007); the Barents Sea has an estimated overall average annual primary productivity of about $100 \text{ g C m}^{-2} \text{ y}^{-1}$ and up to $300 \text{ g C m}^{-2} \text{ y}^{-1}$ in shallow banks (Sakshaug et al. 2009). Typically, about 44–67% of primary production in the Barents Sea reaches the seafloor (Wassmann, Reigstad et al. 2006; Wassmann, Slagstad et al. 2006) while it is up to 70% in the Chukchi Sea (Walsh et al. 1989). Unlike the Chukchi Sea, the Barents Sea supports immense fisheries and a high density of cetaceans. Pelagic foraging piscivores and nesting seabirds are twice as abundant in the Barents Sea than in the Chukchi Sea (Hunt et al. 2013). In the Barents Sea, seasonally resident cetaceans are four to five times more abundant than in the Chukchi Sea. On the other hand, the density of pinnipeds and benthic-foraging whale species in the Chukchi is twice that of the Barents Sea, indicative of the Chukchi Sea being more of a benthic-driven system than the Barents Sea (Hunt et al. 2013). Indeed, Chukchi soft sediment infaunal and epifaunal communities are among the most productive in the world, reaching up to $50\text{--}100 \text{ g C m}^{-2}$ or up to ca. $4 \text{ kg wet wt m}^{-2}$ (Grebmeier et al. 1988; Grebmeier, Overland et al. 2006; Feder et al. 2007), while in the most productive areas of shallow banks in the Barents Sea the benthic fauna reaches up to 30 g C m^{-2} or $1.5 \text{ kg wet wt m}^{-2}$ (Kędra et al. 2013).

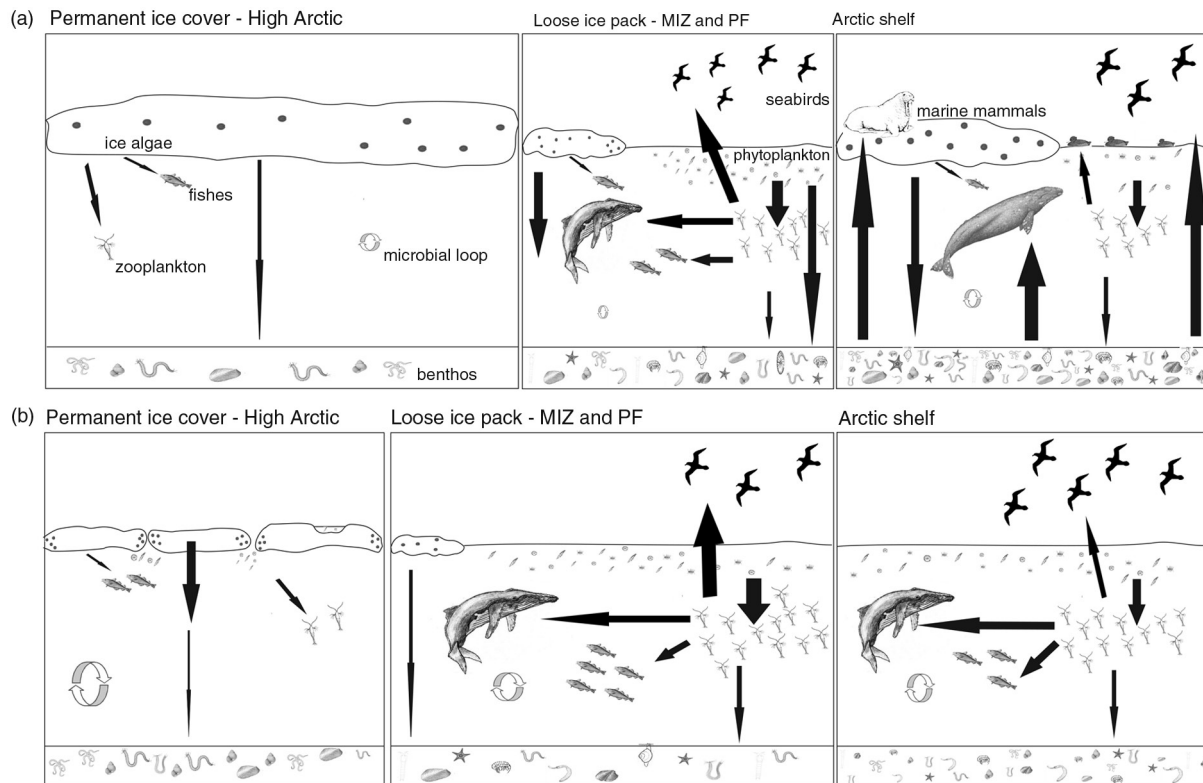


Fig. 2 (a) Current and (b) predicted food-web scenarios for the Arctic shelf, Marginal Ice Zone (MIZ) and Polar Front (PF), and the High Arctic with permanent ice cover. The size of the picture frame for (b) reflects the predicted changes of relative contribution of each area.

The ice edge is retreating northwards and, in the near future, ice-free summers and seasonal ice cover in winter may become typical for the shelf seas (Fig. 2b). Increases in primary production and phytoplankton biomass are predicted, as well as have been measured, as a consequence of sea-ice retreat and temperature rise (Gradinger 1995; Arrigo et al. 2008; Arrigo & van Dijken 2011; Wassmann & Reigstad 2011). Moreover, increased advection of Atlantic and Pacific waters into the Arctic Basin in the last decade (Walczowski & Piechura 2006; Woodgate et al. 2006; Piechura & Walczowski 2009; Woodgate et al. 2010; Walczowski et al. 2012) resulted in a 30% local increase of total primary productivity due to a greater proportion of smaller boreal planktonic species (Leu et al. 2011). Apart from quantitative changes in primary production, the quality and seasonality of primary production are expected to change because of the earlier onset of ice melt. Various stages of the reproductive cycle or increased activity of some Arctic benthic animals are timed to coincide with peak periods of organic matter deposition (Blake 1993; Renaud et al. 2007), so any change in seasonality, quantity or quality of food input may create a mismatch with faunal reproductive

cycles (Renaud, Carroll et al. 2008). A shift from a benthic-oriented ecosystem with relatively low zooplankton stocks and strong pelagic–benthic coupling to a system dominated by pelagic food webs has already occurred in the northern Bering Sea in 1970s and 1980s (Overland & Stabeno 2004; Grebmeier, Overland et al. 2006) and benthic productivity has been decreasing over the past two decades in the northern Bering and southern Chukchi seas (Moore et al. 2003; Grebmeier, Overland et al. 2006; Grebmeier 2012).

Loose ice pack—MIZ and PF

A significant feature of the recent (2007–2012) decrease in ice extent has been the retreat of the ice edge away from the coast and continental shelves. One of the most obvious impacts has been the northward expansion and widening of the MIZ, a dynamic and biologically active band of sea-ice cover adjacent to the open ocean (Strong & Rigor 2013). MIZ width is a fundamental feature for polar ecosystem functioning and climate dynamics (Wadhams 2000). It is an interfacial region that forms at the boundary of open and frozen ocean and

protects the stable morphology of the inner ice from wave penetration (Squire 2007). In the MIZ, interactions between sea-ice and the open sea result in modification of the properties of the ice compared to areas deeper within the pack (Weeks 2010). Significant forcing that impacts the sea ice in the MIZ results in varying surface roughness (Gupta et al. 2014), which affects prevalent physical and biological processes in the MIZ, such as wave dynamics (Wadhams et al. 1988; Squire et al. 1995), heat (Perovich et al. 1989), salt fluxes (McPhee et al. 2008) and floe size distribution (Lu et al. 2008). It can also create potential habitats for organisms inhabiting the ocean–ice system (e.g., Arctic cod [Fortier et al. 2006]). Properties of the MIZ relative to neighbouring ice pack can markedly affect the carbon cycle and behaviour of microorganisms and top-level predators (Dunbar & Leventer 1987; Arrigo et al. 2012). The MIZ has been a long-standing feature in many Arctic shelf seas, like in the Bering, Chukchi and Barents seas, but is a relatively new phenomenon in higher latitude regions such as the deep Beaufort Sea and Canada Basin (Shimada et al. 2006). The MIZ is advancing poleward into regions where sea ice has become increasingly younger and thinner at the beginning of the annual melt (Strong & Rigor 2013). At the time of minimum sea-ice extent in September, the sea-ice edge is located over the deep Arctic Ocean, exposing large areas of previously permanently ice-covered waters, and MIZ-type conditions are becoming more prevalent in the High Arctic with the advancement of climate change.

Loss of sea ice will likely change the amount and characteristics of primary production in the MIZ (Bluhm & Gradinger 2008; Fig. 2b). Increased summer sea-ice melt will increase the overall extent of the MIZ over the shelves and lead to increased primary productivity (Anderson & Kaltin 2001). However, export fluxes largely depend on the coupling processes in the water column, including grazing, and therefore may not increase with warmer temperatures, especially in deep areas (Forest et al. 2010). Even if primary production increases, the fate of export fluxes will be different on Arctic shelves and over the deep Arctic Ocean (Lalande et al. 2014). It is likely that particulate organic carbon export will remain low above the central basins unless additional nutrients are supplied to surface waters (Codispoti et al. 2013; Lalande et al. 2014). Decreased export of diatoms, and dominance of coccolithophores were observed in Fram Strait during the warm period of 2005–07 (Bauerfeind et al. 2009; Lalande et al. 2013). Warmer water temperature also resulted in lower export fluxes of smaller zooplankton faecal pellets due to a shift in zooplankton community composition towards small-sized zooplankton

species or a shift in phytoplankton composition that affected grazing and faecal pellet production (Lalande et al. 2013). However, over the shelves, increased primary productivity will likely supply more food to pelagic and benthic consumers, while the low-productivity zone of the multi-year sea ice would shrink (Bluhm & Gradinger 2008). Sea-ice retreat off the shelves may result in upwelling of nutrients or planktonic prey from the basins onto the shelves (Carmack et al. 2004). Based on the inorganic carbon availability, Anderson & Kaltin (2001) proposed a possible increase of up to 50 g C m^{-2} integrated over the upper 100 m of the water column across the Eurasian Basin, mainly as a result of ice loss. Nevertheless, it is the availability of nutrients, mainly nitrogen and phosphorous, that ultimately determines the total amount of primary productivity possible in any given ocean (Codispoti et al. 2013).

With reduced ice cover, ice-edge algal blooms will be displaced progressively northwards. Although benthic communities will still receive high-quality food in the short term, if the sea-ice edge retreats past the shelf break, shelf communities will no longer benefit from this early season food source (Renaud, Carroll et al. 2008) which would result in increased food input to slope and deep-sea communities (Carmack & Chapman 2003). Since it is likely that at least a part of deep-sea fauna originates from shelf species and Arctic shelf and deep-sea taxa largely overlap (Bluhm, Ambrose et al. 2011), some shelf species would be able to dwell in the deep sea. If shelf species were unable to leave the slopes or survive in slope or deep-sea habitats, many Arctic shelf–benthos taxa could become locally extinct (Renaud, Carroll et al. 2008). Changes in under-ice community structure were noticed in the Eurasian Basin in geographically close sampling locations collected within short time intervals. Habitat partitioning between sympagic and pelagic species can be abrupt, creating small-scale patterns in the surface layer community according to sea-ice habitat conditions. The difference in ice coverage was accurately mirrored by a conspicuous dominance of the ice-associated amphipod *Apherusa glacialis* in ice-covered waters, versus a dominance of the pelagic amphipod *Themisto libellula* in the surface community of ice-free waters (Koszteyn et al. 1995; Hop & Pavlova 2008; David et al. 2015).

Fronts are regions characterized by narrow bands of horizontal gradients in temperature, salinity, density and biological properties that separate broader areas of different vertical structure (Mann & Lazier 1996; Belkin et al. 2003). In the Barents Sea, the PF separates warmer, more saline Atlantic waters in the south from colder, less saline Arctic water in the north (Loeng 1991). Fronts can

play a role in setting surface layer properties by restratifying the surface layer (Timmermans & Winsor 2013) and thereby enhancing primary production. Fronts are known to support elevated biomasses of phytoplankton (Iverson et al. 1979), planktonic organisms (Basedow et al. 2014) and hyper-benthic communities (Dewicke et al. 2002) as well as bird and mammal aggregations (Bluhm et al. 2007). However, a recent study of the PF in the Barents Sea found no stimulatory effect on this front on primary production, and this result is attributed to this front being weak in terms of density (Erga et al. 2014). A related study found high secondary production at the PF, but also in surrounding waters (Basedow et al. 2014). Along with sea temperature rise and increased advection of Atlantic or Pacific waters into the Arctic Ocean, characteristics and location of PF are likely to change, influencing energy transfer to higher trophic levels. Northward displacement of the PF in the Barents Sea was predicted from coupled biophysical model for a B2 Intergovernmental Panel on Climate Change scenario (Huse & Ellingsen 2008). Simulations showed that PF displacement in the Barents Sea had an impact on the distribution and spawning of capelin (*Mallotus villosus*). The model predicted increased production and large inter-annual variability in the Barents Sea, characteristic for the MIZ (Wassmann et al. 2010).

Permanent ice cover—high Arctic

We have only limited knowledge of the energy flow and trophic structure of Arctic deep-sea regions. Very little is known about the linkages of the seasonal production pulse to the deep-sea communities in the High Arctic or even about the deep-sea communities themselves. Therefore, many of the assumptions made for shelf Arctic systems may not be valid for the central Arctic. The few available studies from the central Arctic report extremely low species richness and biomass (Kröncke 1994, 1998) for meiofaunal (Vanreusel et al. 2000) and macrofaunal taxa (Kröncke 1994, 1998; Clough et al. 1997; Deubel 2000; Bluhm et al. 2005; Bluhm, Ambrose et al. 2011), as well as a decrease in diversity with increasing water depth (Kröncke et al. 1998). Primary productivity in the central Arctic is limited by light and nutrients. Constrained by light, sea-ice algal primary production occurs only from May to August and may be further restricted by ice thickness and snow cover (Rysgaard et al. 2001; Nicolaus et al. 2012). Nutrient supply on the other hand is constrained by stratification (Bourgain & Gascard 2011) and may not be sufficient in the central Arctic (Tremblay et al. 2008). Estimated average primary production in the ice-covered central Arctic is low, on the order of 1 to

25 g C m⁻² y⁻¹ (Wheeler et al. 1997; Wassmann et al. 2010), with ice algae production contributing from 0 to 80% (Gosselin et al. 1997; Wassmann et al. 2008). Bauerfeind et al. (2009) suggested very efficient processing of carbon within the water column, with <10% of primary production reaching the seafloor in the deep sea (Fram Strait). Low primary production and export flux result in low abundance of suspension feeders in the deep basins (Kröncke et al. 1998) and a dominance of deposit feeders (van Oevelen et al. 2011). However, suspension feeders in the deep sea are known to utilize re-suspended material and directly compete with deposit feeders on the scarce food available (Lampitt et al. 1993; Iken et al. 2001). Although most benthic species in the deep sea seem to be able to cope with refractory material (van Oevelen et al. 2011), fresh phytodetritus may also arrive to the seafloor and support suspension feeders and surface deposit feeders such as cumaceans (Iken et al. 2005). Also, Boetius et al. (2013) reported fast response to *Melosira* falls of opportunistic deep-sea megafauna species, such as the holothurians *Kolga hyalina* and *Elpidia heckeri*, and the ophiurid *Ophiostriatius striatus*. Increased sediment respiration rates showed that sediment bacteria also profited from this ice algae deposition (Boetius et al. 2013). However, infauna were probably unable to utilize ice algae as infaunal burrows and tubes were rarely seen in the under-water video footage, although they are common in other deep-sea basins with seasonally sedimenting phytoplankton blooms (Boetius et al. 2013). In the Arctic deep-sea plains, benthic communities are constrained by strong seasonality and limited food supply (Iken et al. 2005); ice algae production related to permanent sea-ice cover and export fluxes of organic matter to the seafloor are therefore important in these ecosystems. Benthic trophic pathways in the deep Arctic Ocean are longer than on the shelf region or in the temperate deep sea owing to the continuous recycling and thus isotopic enrichment of food particles in the benthic system, while a more direct link to fresh phytodetritus exists in the pelagic system (Iken et al. 2005; Bergmann et al. 2009).

In the past, the central Arctic Ocean has been covered with multi-year ice, but the marked decline in multi-year ice (Maslanik et al. 2011) suggests that the region could be ice-free by the summer of 2040 (Polyakov et al. 2010). Moreover, according to the latest publications, the central Arctic Ocean is no longer covered with multi-year ice (Polyakov et al. 2012) while the remnant multi-year sea ice occurs along the north-west flank of the Canadian Arctic Archipelago, where it can drift southwards, out over the Southern Beaufort Sea and northwards (Barber et al. 2009). If we assume that areas formerly covered

with thick multi-year ice will have a thinner ice cover, permitting higher primary production, we can project a higher annual primary production level due to light availability, provided nutrients are available, which may not be the case in the basins (Codispoti et al. 2013; Matrai et al. 2013). A massive under-ice bloom was reported recently from consolidated ice pack in the northern Chukchi Sea, with phytoplankton biomass beneath the ice being about fourfold greater than in open water (Arrigo et al. 2012). Similar massive blooms might be widespread in the Arctic Ocean, in relation to the lower nutrient levels available. More work is needed to determine the extent to which such blooms are controlled by thinning sea ice and proliferating melt pond fractions and how they affect marine ecosystems.

Although higher light penetration will promote ice algal growth, low level of nutrients available and progressing climate warming may also reduce the algal growing season through increased thermal or haline stratification, limiting mixing and upward nutrient transport resulting in smaller export flux to the seafloor (Carmack & Wassmann 2006; Slagstad et al. 2011). In addition, if zooplankton abundance increases as warmer Atlantic and Pacific waters are transported into the Arctic Ocean (Hirche & Kosobokova 2007), the grazing pressure will increase, leading to increased retention of organic carbon in the water column. Some studies suggest that the flux of ice algae and ice-related particulate organic matter will decrease along with sea-ice retreat and loss of multi-year ice (Forest et al. 2010). This may lead to decreased carbon deposition at the deep seafloor to already food-limited fauna, but these shifts are not expected to be rapid (van Oevelen et al. 2011). Yet, the lack of reliable baseline information makes predictions difficult and identifying change nearly impossible (Wassmann et al. 2011).

Gaps and recommendations

Despite numerous recent studies (Table 2, Fig. 1), major gaps remain in the knowledge of general processes governing biodiversity, food-web structure, trophic transfer efficiency and functioning of Arctic ecosystems. Since different regions of the Arctic have received varying levels of scientific attention (Table 2, Fig. 1), these recommendations may not apply to the whole Arctic and should be treated as more general statements. Given that these processes are not yet clearly quantified, any attempt to project changes that may occur in Arctic food webs in the future, such as that suggested in this review, should be taken cautiously. Most predictions are qualitative and biased towards conditions on the shelves, while quantitative ones remain scarce (but see Zhang et al. 2010;

Popova et al. 2012; Slagstad et al. 2011). Since a lot of changes in the Arctic food webs are expected to be driven by a shift from decreasing sea-ice algae and an increase in pelagic production, observational, experimental and modelling approaches of the present-day coupling of these two production pathways in food webs should first be implemented, and subsequently combining different scientific methods will allow for the establishment of projection methodologies for Arctic ecosystems.

Large-scale studies of food webs across Arctic regions highlighting inherent differences among regions are still lacking. Although deep-sea areas are still under-sampled because of the difficulty in accessing field sites, and a consistent sampling design does not exist Arctic-wide, the lack of sampling is not the main issue. Throughout the years data on the response of different benthic communities to climate change and on food webs have increased from multiple projects. These include HAUSGARTEN, the Alfred Wegener Institute's long-term monitoring programme in Fram Strait (Soltwedel et al. 2005), with data over 10 years, and the Distributed Biological Observatory (DBO), an international initiative in the Pacific Arctic (Grebmeier et al. 2010), with data over 30 years, including time series from Long-term Census of the Arctic (RUSALCA) programme. While efforts to sample the Arctic Ocean must and will continue, a primary ambition should be to gather, combine and analyse existing information. Such efforts have been undertaken recently regarding Arctic biodiversity (e.g., Bluhm, Ambrose et al. 2011; Gill et al. 2011; Piepenburg et al. 2011), food sources and trophic interactions, e.g., the Pacific Marine Arctic Regional Synthesis project (PacMARS), although consistent data on food webs (sensu species interactions) are still missing. Similar-format databases should be established, centralized and made easily accessible to scientists at the international level, in order to explore the issues mentioned in this review, such as the PacMARS effort. Then, to promote further consistency of data collection, a standardized data sampling protocol should be implemented when possible to facilitate data gathering and data set use. Designated sampling stations should be sampled throughout months and years to monitor seasonal and long-term changes in biodiversity (Gill et al. 2011). Apart from species identity, functional lifestyle and life-cycle traits should be recorded, which would allow detecting and monitoring changes in ecosystem functioning (Cadotte et al. 2011).

To complement field sampling and database design, empirical manipulations to be performed in situ, in several places in the Arctic, should be encouraged. Such studies should address quantitative aspects of the impact of global warming on food-web length and components,

including primary production rates, grazing rates and growth rates at higher trophic levels, in order to estimate changes in trophic transfer efficiency in Arctic food webs. Studies of diets relative to availability of different foods are also critical to food-web analyses, especially to predicting response to changing conditions. In situ and laboratory experiments could be complemented by use of numerical modelling. Trophic network modelling methods that are widely used in other ecosystems could be implemented in the Arctic to understand food-web structure, the effects of external threats (e.g., increased fisheries pressure, invasive species) on food-web dynamics, and to quantify energy transfers between trophic levels, in conjunction with empirical work (e.g., van Oevelen et al. 2011). Results can be subsequently used to fuel models (e.g., provide nutrient–phytoplankton–zooplankton model parameters). Since data are still lacking, this could be achieved by using well-established pre-designed software able to deal with missing parameters such as Ecopath (Pauly et al. 2000), especially for fishery scenarios, and the linear inverse model package LIM in the R statistical software package (van Oevelen et al. 2010). These models have the advantage of including both pelagic and benthic compartments and are able to quantify the strength of pelagic–benthic coupling. Although such models have been implemented for some Arctic regions (e.g., Trites et al. 1999; Dommasnes et al. 2001; Pedersen & Zeller 2001; Aydin et al. 2002; Whitehouse et al. 2014), they need to be updated, integrated and compared, especially after the recent environmental changes that have occurred in the Arctic. Stability analysis methods can also be coupled with the mass-balance modelling framework to provide insights into Arctic food-web structure and intrinsic properties (Neutel et al. 2002). Such methods may comprise analyses of stable-states of population or community dynamics, and analyses of food-web properties through determination of eigenvectors, resilience and persistence levels, and equilibrium shifts. At the theoretical level, population, metapopulation, community and metacommunity dynamic models can be implemented to understand how intra- and interspecific interactions and connectivity affect diversity at different spatial scales, such as between the different Arctic regions and the surrounding oceans (Carr et al. 2011; Hardy et al. 2011). Predicted ice melt and changing hydrodynamics may alter connectivity between distant Arctic populations, in turn affecting community composition and food-web structure. Such advances could provide valuable contributions to predicting future trends of biodiversity and food-web structure in the Arctic.

Statistical modelling, particularly quantification of species–environment relationships at large scales, should

be assessed once data are pooled across Arctic regions. The statistical methods developed to date and applied to different biological organisms are an efficient means to disentangle the effects of environmental gradients (both in space and time) on community structure (Dray et al. 2012). Even though these methods are often based on species, they can be applied to functional groups to assess trait–environment relationships, reinforcing the need to monitor species traits during field sampling. Since environmental changes in the Arctic may affect species traits, the whole ecosystem functioning may be altered, and studying functional traits is a good way to assess ecosystem functioning and trophic transfer efficiency (McGill et al. 2006; Cadotte et al. 2011).

Conclusions: winners and losers

Arctic marine ecosystems are currently subjected to accelerating climate warming and fast progressing sea-ice retreat. Although our knowledge of ecosystem functioning and processes still has significant gaps, and the scale and magnitude of climate change remain largely unknown, some qualitative predictions on the fate of Arctic marine food webs are possible. In very general terms, among the “winners” will likely be boreal species as their populations tend to follow increasing sea temperature by shifting their ranges northward (and likely losing ground in the south), and pelagic species, mainly zooplankton, whose abundance and biomass may increase with increasing water column primary production related to more and earlier open water over the Arctic shelves. Pelagic feeding animals, like some fish, marine mammals and seabirds may consequently increase in abundance. Species classified as generalists are more likely to adapt to new conditions than specialists.

Groups that will likely be among the “losers” include Arctic species, especially those that are ice-dependent, as they will be most strongly affected by rising temperatures and diminishing habitat. Benthic species may decrease in biomass with increased pelagic grazing and recycling in the water column, which may lead to reduced amount or quality of organic matter settling from the water column to the seafloor. This will affect benthic feeding marine mammals and seabirds, whose foraging areas will become less productive and prey less available. Food webs will likely lengthen at the low trophic levels, lowering trophic transfer efficiency and thereby lowering the percentage of primary production that reaches top predators. Since many species at the base of the Arctic food webs are sea-ice dependent, the stability of food webs will likely be negatively affected in areas where trophic redundancy is low. Collaborative multidisciplinary research is necessary

if we are to fully understand the processes and linkages between Arctic marine environments and their associated food webs in the face of a changing North.

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