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REGIONAL VARIABILITY IN FOOD AVAILABILITY FOR ARCTIC MARINE MAMMALS

Bodil A. Bluhm[1] and Rolf Gradinger

University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Institute of Marine Science,
245 O'Neill Building, Fairbanks, Alaska 99775 USA

Abstract. This review provides an overview of prey preferences of seven core Arctic marine mammal species (AMM) and four non-core species on a pan-Arctic scale with regional examples. Arctic marine mammal species exploit prey resources close to the sea ice, in the water column, and at the sea floor, including lipid-rich pelagic and benthic crustaceans and pelagic and ice-associated schooling fishes such as capelin and Arctic cod. Prey preferred by individual species range from cephalopods and benthic bivalves to Greenland halibut. A few AMM are very prey-, habitat-, and/or depth-specific (e.g., walrus, polar bear), while others are rather opportunistic and, therefore, likely less vulnerable to change (e.g., beluga, bearded seal). In the second section, we review prey distribution patterns and current biomass hotspots in the three major physical realms (sea ice, water column, and seafloor), highlighting relations to environmental parameters such as advection patterns and the sea ice regime. The third part of the contribution presents examples of documented changes in AMM prey distribution and biomass and, subsequently, suggests three potential scenarios of large-scale biotic change, based on published observations and predictions of environmental change. These scenarios discuss (1) increased pelagic primary and, hence, secondary production, particularly in the central Arctic, during open-water conditions in the summer (based on surplus nutrients currently unutilized); (2) reduced benthic and pelagic biomass in coastal/shelf areas (due to increased river runoff and, hence, changed salinity and turbidity conditions); and (3) increased pelagic grazing and recycling in open-water conditions at the expense of the current tight benthic–pelagic coupling in part of the ice-covered shelf regions (due to increased pelagic consumption vs. vertical flux). Should those scenarios hold true, pelagic-feeding and generalist AMM might be advantaged, while the range for benthic shelf-feeding, ice-dependent AMM such as walrus would decrease. New pelagic feeding grounds may open up to AMM and subarctic marine mammal species in the High Arctic basins while nearshore waters might provide less abundant food in the future.

Key words: Arctic; benthos; climate change; food availability; marine mammal; plankton; prey; sea ice; seal; whale.

Introduction

The physical and chemical settings of Arctic seas provide the framework for the structure of marine food webs, which support Arctic marine mammals (AMM) as top consumers. Unique features specific to the Arctic influencing habitat suitability and prey availability include the seasonal and permanent sea ice cover, the extreme seasonal variability of light and primary production and their consequences, the interannual and decadal climate variations, and the polar amplification of recent climate change (Walsh 2008). The focus area of this paper includes the deep central Arctic Basin, consisting of two major sub-basins (the Eurasian Basin and the Amerasian Basin) and the surrounding shallow continental shelves, occupying approximately 53% of the Arctic Ocean. The shelves vary in width, with narrow extents along part of the Beaufort Sea and Canadian Archipelago coastlines and wide shelves everywhere else. The shelves are the locations at which currently most of the annual ice formation and melt occurs and where AMM spend most of their time. Freshwater runoff from major river systems influences the Arctic hydrography and chemistry, contributing sediment, organic material, and inorganic nutrients to the shelves. Annual sea ice dominates on the shelves while unique multiyear sea ice covers the Arctic deep-sea basins (Wadhams 2000). The complex bathymetric and hydrographic structure of the Arctic basins and shelves influence their use by AMM as summarized by Laidre et al. (2008).

Large parts of the Arctic, in particular the shelves, are inhabited by AMM for at least part of the year (Laidre et al. 2008, Moore and Huntington 2008). During their feeding periods, AMM require energy hot spots to forage efficiently (e.g., Piatt and Methven 1992) and to build up reserves to sustain their metabolism and potentially produce a calf or pup during fasting periods. Caloric density at AMM feeding sites, therefore, appears

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[1] E-mail: bluhm@ims.uaf.edu

to be at least as important as prey species choice per se (Darling et al. 1998). Some migratory AMM specifically select subarctic or Arctic latitudes for their foraging period (Laidre et al. 2008). Feeding can occur throughout the year (e.g., male polar bear), primarily in the summer (e.g., gray whale; Nerini 1984), or primarily outside the summer (e.g., narwhal; Laidre and Heide-Jørgensen 2005). Whatever the selected site or time period, AMM foraging areas are selected because of certain, typically high, levels of primary and/or secondary production at the trophic levels of phytoplankton through fishes (e.g., Bradstreet and Cross 1982, Piatt and Mathven 1992).

This review aims at providing an overview of AMM prey preferences and prey distribution patterns and current biomass hotspots, organized by the three major physical realms: sea ice, water column, and seafloor. Examples of observed changes in AMM prey distribution and biomass are presented and potential biotic change scenarios suggested, based on published observations and predictions of environmental change. We propose these scenarios to provide insights into possible linkages between environmental changes and effects and caution the reader that settings on local or regional scales might have different effects than those described. This paper tightly links to Walsh (2008), which describes the climatic conditions by which AMM prey species are framed, and Laidre et al. (2008), which reviews habitat utilization of AMM species and quantifies their sensitivity to climate-induced habitat change.

Prey Preferences

Here we summarize the main prey items at different Arctic foraging sites for seven Arctic core and four subarctic (non-core) AMMs (Moore and Huntington 2008), while acknowledging bias introduced by differences in digestion rates of different prey. The information is presented, albeit admittedly incomplete, in short paragraphs organized by core and non-core AMM species and in the form of two tables, one on major prey by species (Table 1) and one on energy content of major prey items (Table 2). We will use the term Arctic cod for *Boreogadus saida* (see Plate 1) and polar cod for *Arctogadus glacialis*, according to the fish name list used by the American Fisheries Society.

Core Arctic marine mammals

Bowhead whale (Balaena mysticetus).—Most information on bowhead whale feeding ecology comes from the Alaskan and Canadian Arctic. Bowhead whales primarily feed on zooplankton, mostly crustaceans such as copepods, euphausids, and hyperiid amphipods (Lowry et al. 2004), all of which have especially high lipid and therefore caloric content (Percy and Fife 1980; Table 2). Feeding behavior may be consistent within size cohorts and diving abilities of age classes (Finley 2000). Juvenile bowheads tend to feed on large swarming zooplankton such as mysids or euphausids or on the very small copepods *Pseudocalanus* and *Limnocalanus*, while adults prefer large *Calanus glacialis* and *C. hyperboreus* in offshore areas (Lowry et al. 2004). Less common food items such as mysids, fish, and isopods were more frequent in smaller whales in the Alaskan Beaufort Sea, although this difference was not statistically significant compared to bigger whales ($n = 32$). No differences between size classes or sexes were found in a large sample of bowhead whale stomachs in the Alaskan Beaufort Sea ($n = 242$; Lowry et al. 2004). On occasion, bowheads may feed on benthic prey, as indicated by mud plumes and stomach contents. Epibenthic prey includes mysids and cumaceans.

In the Alaskan Beaufort Sea, a large fraction of whales feed throughout the fall with regional differences regarding the major prey, such as a higher fraction of copepods in fall-hunted animals from Kaktovik, whereas fall-hunted whales from Barrow consumed more euphausids and hyperiid amphipods (Lowry et al. 2004). A substantial sample size covering 1969–2000 indicates that feeding during the spring migration is opportunistic, but may be more common than previously appreciated. Major feeding areas are known from the western and eastern Beaufort and Chukchi Seas (Lowry et al. 2004) and off Baffin Island (Finley 1990), where whales primarily fed on copepods. Stable isotope studies suggest that the Chukchi-Beaufort Sea stock may also be feeding in the Bering Sea and that habitat selection patterns were consistent over a three-year period (Hoekstra et al. 2002). Little is known about the foraging grounds of the Svalbard and Okhotsk bowhead stocks (Shelden and Rugh 1995).

Beluga (Delphinapterus leucas).—The North Atlantic Marine Mammal Commission (NAMMCO 2004) recently summarized beluga prey spectrum findings from various foraging grounds. *Boreogadus saida* dominated beluga whale diet in Greenland, the Canadian High Arctic, Russian waters, and waters around Svalbard. *Arctogadus glacialis* and whitefish (Coregonidae) were similarly common in the Upernavik area in Greenland and in Russian waters, respectively. Other items found in stomachs in Greenland-caught belugas included squid beaks, redfish (*Sebastes marinus*), Greenland halibut (*Reinhardtius hippoglossoides*), and the decapod *Pandalus borealis*. Belugas preyed largely upon salmon in the Okhotsk Sea (Sobolevskii 1983) and on saffron cod and other fishes as well as shrimps and octopus in Norton and Kotzebue Sounds (Seaman et al. 1982). In the St. Lawrence River and Hudson Bay, stomach contents were dominated by capelin, but also included sand lance, Atlantic cod, tomcod, and benthic invertebrates such as crustaceans and polychaetes (NAMMCO 2004).

Ice type and distribution may influence beluga feeding patterns (Seaman et al. 1982), but prey species distribution also appears to affect seasonal movement patterns. Spring prey in migrating belugas in the Chukchi Sea was dominated by Arctic cod, shrimps, and octopus, while summer foods in the coastal northern Bering and southern Chukchi Seas included saffron cod, sculpins, herring, smelt, capelin, salmon, and char (Seaman et al. 1982). However, foraging occurred to a large extent in the wintering grounds rather than at the shallow estuarine summer sites in belugas off west Greenland (NAMMCO 2004). Shallow murky areas with relatively warm temperatures and mollusk, crustacean, and fish bottom fauna are generally often occupied by females and their young.

Narwhal (Monodon monoceros).—Studies of narwhal stomach contents in the Canadian Arctic, off west Greenland, and in Russian waters revealed that Arctic and polar cod, squid, in particular *Gonatus fabricii*, and Greenland halibut were the primary prey items of narwhals during the summer (e.g., Finley and Gibb 1982, $n = 73$; Laidre and Heide-Jørgensen 2005, $n = 121$). Less prevalent were redfish, snail fish, and crustaceans (Baffin Island; Finley and Gibb 1982). Fall and winter prey were dominated by Greenland halibut and squid (Laidre and Heide-Jørgensen 2005). The deep-water fishes indicate the deep-diving capability of narwhals. Laidre and Heide-Jørgensen (2005) reported that stomachs taken off west Greenland contained considerably more and fresher food during the winter than stomachs sampled in the summer. Similarly, Finley and Gibb (1982) observed little feeding during later summer in the Canadian Arctic fjords and suggest that summering areas may not primarily be inhabited based on their prey availability.

Walrus (Odobenus rosmarus).—Walrus primarily feed on benthic bivalves, but stomachs of some walrus also included a variety of other benthic invertebrates from all major phyla and over 60 genera (e.g., Fay et al. 1984). Food items other than clams were suggested to only be consumed opportunistically while clams were preferred, although later digestion experiments indicated that differential digestion probably exaggerates the importance of bivalves in walrus' diet to some extent (Sheffield et al. 2001). In the Bering Sea, the clams *Mya truncata*, *Serripes groenlandicus* (see Plate 1), and *Macoma* spp. dominated stomach contents as well as benthic communities in which feeding pits and furrows of walrus were studied (Oliver et al. 1983). In the Foxe Basin, Northwest Territories, stomach contents were also dominated by the clam *Mya truncata*, and the same species was dominant in Atlantic walrus feces around Svalbard (e.g., Fisher and Steward 1997). *Mya truncata*, *Hiatella arctica*, and *Serripes groenlandicus* were dominant prey in Young Sound, east Greenland (Born et al. 2003). Other bivalves, holothurians, and polychaetes contributed most of the remaining share in the Canadian study (Fisher and Steward 1997). Occasionally, ringed seals, bearded seals, seabirds, and squid have been reported from walrus stomachs.

For east Greenland waters, a male 1200-kg walrus consumed on average 2576 kJ per dive (53.2 bivalves), and consumption in Alaskan waters was estimated at 6 bivalves/minute (Oliver et al. 1983). Some authors found that probably all soft parts of the bivalves were consumed, while others suggested that primarily the exposed tissue parts such as foot and siphon are taken (Sheffield et al. 2001).

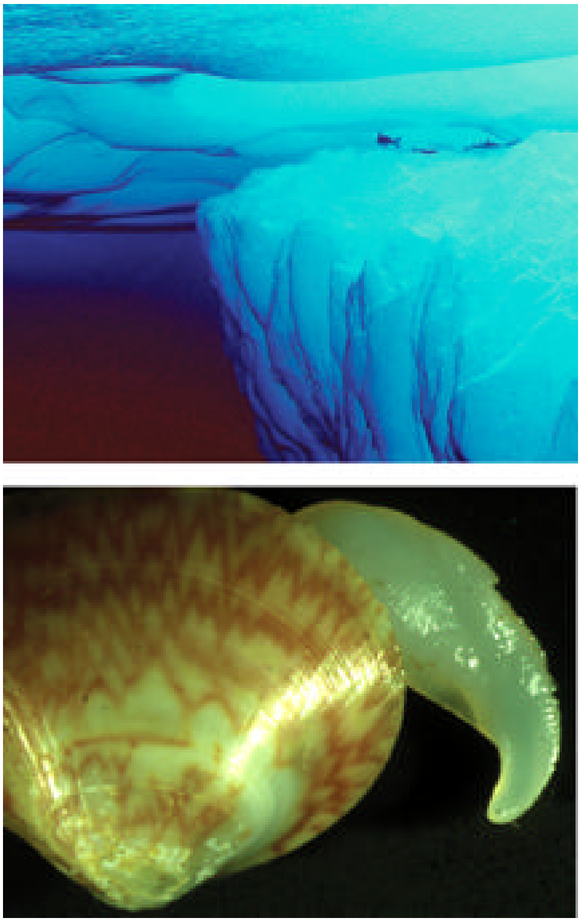

PLATE 1. Common prey organisms of Arctic marine mammals: (top) Arctic cod, *Boreogadus saida*, and (bottom) an example of benthic clam species, *Serripes groenlandicus*. Photo credits: cod, Katrin Iken; clam, B. Bluhm.

Bearded seal (Erignathus barbatus).—Bearded seals have been characterized as foraging generalists that prey on pelagic and demersal fishes as well as a wide range of infaunal and epifaunal invertebrates. The relative contribution of prey species varied between and within geographic areas and seasons (Antonelis et al. 1994). In a Bering Sea study, bearded seals primarily fed at the seafloor, where they consumed bivalves, crabs, and shimps, but few fishes, similar to findings from a southern Chukchi Sea study (Lowry et al. 1980*b*). Other invertebrates from seals taken around Svalbard include shrimps and whelks (Hjelset et al. 1999). In contrast, near St. Matthew Island, in the Bering Sea, 78 bearded seal stomachs were dominated by fishes, especially capelin, cod species, and eelpouts (Antonelis et al. 1994); snow crab, clams, snails, and amphipods were prevalent among the invertebrates in that study. Fish

TABLE 1. Primary prey and feeding areas of Arctic marine mammals.

Species and major feeding area	Feeding habits	Primary prey items	Trophic level	Reference
Core Arctic marine mammals				
Bowhead whale				
Chukchi and Beaufort Seas	shallow, pelagic, (hyperbenthic)	copepods, euphausids, mysids	3.2†	Lowry et al. (2004)
West Greenland, Baffin Bay	shallow, pelagic, (hyperbenthic)	copepods, euphausids, mysids	3.2†	Finley (2000)
Beluga whale				
Greenland, Russia	shallow, deep, pelagic, benthic	Arctic and polar cod, whitefish	4.0†	NAMMCO (2004)
Arctic Canada, Svalbard	shallow, deep, pelagic	Arctic cod	4.0†	NAMMCO (2004), Seaman et al. (1982)
Bering and Chukchi Seas	shallow, pelagic, benthic	saffron cod, shrimps	4.0†	NAMMCO (2004)
Hudson Bay, St. Lawrence Island	shallow, deep, pelagic, benthic	capelin, sand-lance, benthic invertebrates	4.0†	NAMMCO (2004)
Narwhal				
Baffin Bay, Canadian Archipelago, Russian waters	shallow, deep, pelagic, benthic	Arctic and polar cod, *Gonatus* sp. (su), Greenland halibut, squid (fall–wi)	4.2†	Finley and Gibb (1982), Laidre and Heide-Jørgensen (2005)
Walrus				
Bering and Chucki Seas	shallow, benthic	*Mya truncata, Macoma* spp., *Serripes groenlandicus*	3.4†	Fay et al. (1984)
Northwest Territories, Svalbard, Franz Josef Land	shallow, benthic	*Mya* spp.	3.4†	Gjertz and Wiig (1992), Fisher and Steward (1997)
Northeast Greenland	shallow, benthic	*Mya truncata, Hiatella arctica, Serripes groenlandicus*	3.4†	Born et al. (2003)
Bearded seal				
Bering and Chukchi Seas	shallow, benthic, pelagic	bivalves, crabs, shrimps	3.4†	Lowry et al. (1980*a*)
St. Matthew Island	shallow, benthic, pelagic	capelin, gadids, eelpouts, crustaceans	3.4†	Antonelis et al. (1994)
Canadian Arctic, Kara and Barents Seas, Svalbard	shallow, benthic, pelagic	various fishes, crustaceans	3.4†	Hjelset et al. (1999)
Ringed seal				
White, Barents, and Kara Seas, Greenland, Baffin Bay	shallow, pelagic, (hyperbenthic)	Arctic cod, mysids, shrimps, euphausids, amphipods	3.8,† 4.5‡	Siegstad et al. (1998)
Northern Bering	shallow, pelagic, hyperbenthic	saffron cod (su), Arctic cod (wi)	3.8,† 4.5‡	Lowry et al. (1980*b*)
Southern Chukchi Seas	shallow, pelagic	shrimps (su), Arctic cod (wi)	3.8,† 4.5‡	Lowry et al. (1980*b*)
Beaufort Sea	shallow, pelagic	hyperiid amphipods, euphausids (su), Arctic cod (wi)	3.8,† 4.5‡	Lowry et al. (1980*b*)
Polar bear				
Canada, Barents Sea	shallow, deep, pelagic, hyperbenthic	ringed seal, bearded seal, harp seal	5.5‡	Derocher et al. (2002)
Non-core Arctic marine mammals				
Gray whale				
Northern Bering, Chukchi Sea	shallow, benthic, (pelagic?)	Ampeliscid amphipods, other invertebrates	3.3†	Nerini (1984)
Kodiak Island	hyperbenthic	cumaceans	3.3†	Moore et al. (2007)
Vancouver Island	shallow, benthic, pelagic	mysids, crab larvae, herring eggs, polychaetes	3.3†	Darling et al. (1998)
Spotted seal				
Bering Sea	shallow, pelagic, (hyperbenthic)	pollock, capelin, Arctic and saffron cod, herring, zoarcids, octopus (spring); salmon (fall)	4.0†	Lowry et al. (2000)
Chukchi Sea	shallow, pelagic, (hyperbenthic)	herring, saffron cod, smelt, Arctic cod	4.0†	Lowry et al. (1980*a*)
Ribbon seal				
Bering Sea	shallow, pelagic	pollock, Arctic cod	3.8†	Frost and Lowry (1980, 1986)
Harp seal				
Norwegian coast	shallow, pelagic, hyperbenthic	gadoid, Atlantic herring, capelin	3.8†	Haug et al. (1991)

TABLE 1. Continued.

Species and major feeding area	Feeding habits	Primary prey items	Trophic level	Reference
Barents Sea	shallow, pelagic	*Parathemisto libellula*, shrimps, euphausids	3.8†	Nilssen et al. (1991)
Gulf of St. Lawrence	shallow, pelagic, hyperbenthic	capelin, Atlantic cod	3.8†	Stenson et al. (1997)
Newfoundland	shallow, pelagic	Arctic cod, capelin	3.8†	Stenson et al. (1997)
Greenland Sea	shallow, pelagic	*Parathemisto, Gonatus fabricii*, Arctic cod, capelin	3.8†	Haug et al. (2004)

Notes: Information in parentheses in the "Feeding habits" column indicates less common feeding habits. Information without parentheses indicates common feeding habits. Trophic level values are taken from Pauly et al. (1998) (indicated by a dagger) and Hobson et al. (2002) (indicated by a double dagger). Abbreviations are: su, summer; wi, winter.

were also major prey items for bearded seals in the Kara and Barents Seas, in the Canadian High Arctic, and in the Svalbard area (Hjelset et al. 1999). Like other researchers, these investigators expressed uncertainty about the degree of selective feeding because of sampling biases.

Diets were similar between genders in two Bering Sea studies (Lowry et al. 1980*b*, Antonelis et al. 1994). Contradictory results were published about age class-specific prey selection: Lowry et al. (1980*b*) found that young bearded seals preyed upon shrimps, crabs, and fish while adults preferred clams; no age-specific differences were found in the mainly fish-eating bearded seals near St. Matthew Island (Antonelis et al. 1994).

Ringed seal (Phoca hispida).—Studies from various Arctic areas showed considerable regional and seasonal variability in ringed seal primary prey. In Northwest and East Greenland *Boreogadus saida* and *Arctogadus glacialis* were the most dominant prey items, while seals in central West Greenland mainly preyed upon pelagic amphipods (*Parathemisto* spp.), capelin, redfish, and squid, while capelin was the most important prey item in southwest Greenland (Siegstad et al. 1998). In the northern Bering and southern Chucki Seas (U.S. sector),

TABLE 2. Energy value of major Arctic marine mammal prey items.

Species	Phylum or order	Energy content	Realm	Area	Reference
Aglantha digitale†	Cnidaria	4.7–5.0 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Autolytus spp.	Polychaeta	5.4–5.9 kcal/mg AFDM	benthic	Frobisher Bay, Canada	Percy and Fife (1980)
Clione limacina	Gastropoda	5.6–6.5 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Calanus glacialis/ hyperboreus	Copepoda	7.2–7.9 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Macoma calcarea	Bivalvia	4.3–6.3 kJ/g DM	benthic	Bering Sea (with shell)	Lovvorn et al. (2003)
Gonatus sp.	Cephalopoda	6.9 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Mesidotea sabini†	Isopoda	4.6 kcal/mg AFDM	benthic	Frobisher Bay, Canada	Percy and Fife (1980)
Parathemisto libellula	Amphipoda	5.2–6.6 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Anonyx nugax	Amphipoda	5.9–6.4 kcal/mg AFDM	benthic	Frobisher Bay, Canada	Percy and Fife (1980)
Thysanoessa inermis	Euphausiacea	5.3–6.6 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Pandalus borealis	Decapoda	4.8 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Boreogadus saida	Pisces	4.4 kJ/g WM	all realms	Newfoundland and Labrador	Lawson et al. (1998)
Gadus morhua	Pisces	4.2 kJ/g WM	demersal	Newfoundland and Labrador	Lawson et al. (1998)
Theragra chalcogramma (age 0)	Pisces	5.8 kcal/g AFDM	pelagic (to demersal)	Bering Sea	Perez (1994)
Clupea harengus	Pisces	9.4 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Mallotus villosus	Pisces	8.4 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Reinhardtius hippoglossoides	Pisces	5.5 kJ/g WM	demersal	Newfoundland and Labrador	Lawson et al. (1998)

Notes: The Frobisher Bay samples were collected from late July to mid-September. Abbreviations are: AFDM, ash-free dry mass; DM, dry mass; WM, wet mass.

† Other abundant species rarely preyed upon, given for comparison.

saffron cod dominated stomach contents in spring/summer, while the shrimps *Pandalus* spp., *Eualus* spp., *Lebbeus polaris*, and *Crangon septemspinosa* dominated in the north-central Bering, the hyperiid amphipod *Parathemisto libellula* in the central Beaufort Sea, and the euphausid *Thysanoessa* spp. in the Barrow area (Lowry et al. 1980*a*; total number of stomachs = 299). Similar prey taxa were preferred in Svalbard: Arctic cod, shrimps (*Pandalus borealis*), euphausids (*Thysanoessa inermis*), and amphipods (*Themisto libellula*) (Weslawski et al. 1994). A seasonal shift towards a dominance of Arctic cod was observed in the northern Bering, Chukchi, and Beaufort Seas in the winter, similar to findings from the Kara Sea and Novaya Zemlya (Lowry et al. 1980*a*). In other areas, saffron cod, smelt, and herring dominated the winter diet (Sea of Okhotsk), whereas no seasonality was found in yet other areas, where euphausids, amphipods, shrimps, mysids, Arctic cod, and other fishes were consumed throughout the year (e.g., northern Labrador and southwest Baffin). Age-specific differences in diet were found in some areas and included a smaller fraction of cod in pups than in adults in the northeast Bering and southeast Chukchi Seas and a decline of crustacean consumption with age in the Canadian Arctic. Based on energetic value and amounts consumed, Lowry et al. (1980*a*) concluded that species occurring in high densities or swarms were of particular importance for ringed seals.

Polar bear (Ursus maritimus).—Polar bears prey primarily on ringed seals, bearded seals, and harp seals (e.g., Derocher et al. [2002]). Based on 135 observations in Svalbard and the western Barents Sea, ringed seals were the dominant prey numerically (63%), while bearded seals contributed the highest biomass (55%). Prey composition was suggested to depend on the area a bear roamed for prey, with more ringed seals taken by near-shore bears on land-fast ice and more bearded and harp seals taken by off-shore bears (Mauritzen et al. 2003). Occasional opportunistic prey items include other marine mammals such as beluga whales, walrus, and narwhals as well as marine birds and even reindeer (references in Derocher et al. [2002]). Polar bears also opportunistically scavenge, for example in Barrow Alaska, where bears take advantage of subsistence-harvested bowhead whale carcasses (C. George, *personal communication*).

Non-core species

Gray whale (Eschrichtius robustus).—Throughout their feeding grounds in the northern Bering and Chukchi Seas and offshore Kodiak and Vancouver Islands, eastern North Pacific gray whales prey on a variety of invertebrates, ranging from benthic amphipods, polychaetes, cumaceans, and bivalves to pelagic mysids, herring eggs, and crab larvae (e.g., Nerini 1984, Darling et al. 1998). Dietary analysis indicated that ampeliscid amphipods, tube-building benthic crustaceans, are, or were, the primary prey item of gray whales in some northern feeding grounds, in particular the Chirikov Basin in the northern Bering Sea. Pelagic feeding has so far been reported less frequently from the northern feeding areas than from Vancouver Island (Darling et al. 1998), although some evidence for pelagic feeding is emerging. Overall, the taxonomic composition of the available prey per se may be less relevant than the energy density in gray whale feeding sites (Darling et al. 1998). Some authors attributed recent mortality events of gray whales to limited food supply in the northern feeding grounds, but other factors such as disease may also have played a role.

Spotted or Largha seal (Phoca largha).—The prey spectrum of spotted seals in the Bering Sea is dominated by pelagic fishes, but also includes invertebrates such as shrimp, crabs, and octopus (Sobolevskii 1996, Lowry et al. 2000). Spring foods included walleye pollock and zoarcids in the central Bering Sea and capelin, pollock, and herring in the southeast Bering Sea; Arctic cod was important prey in the northern Bering Sea, while octopus played an important role in the Gulf of Anadyr and Karaginsky Bay. In the fall, herring, saffron cod, and salmon were dominant prey (Lowry et al. 2000). In the Chukchi Sea, 41 spotted seals stomachs primarily contained herring (Lowry et al. 1980*b*), but saffron cod, smelt, Arctic cod, and capelin were also found in seals from the Chukchi Sea (Sobolevskii 1996). Spotted seals mostly utilized small to medium sized fishes as prey (Lowry et al. 1980*b*), e.g., two Bering Sea spotted seals primarily ate pollock with a mean fork length of 10.9 cm. In the Russian sector of the Bering Sea, young seals heavily depended upon crustaceans and octopus in the summer (Sobolevskii 1996).

Ribbon seal (Phoca fasciata).—Little has been published on the feeding ecology of ribbon seals. Walleye pollock and Arctic cod otoliths dominated digestive tracts of 61 ribbon seals from the south-central and northern Bering Sea, respectively (Frost and Lowry 1980). From concurrent trawls, these authors concluded that ribbon seals selected against sculpins and capelin in the central and northern Bering and preferred large Arctic cod to small ones. While pollock of all sizes were preyed upon in this study, ribbon seals primarily ate small pollock (mean 11.2 cm fork length) in a later study from the Bering Sea (Frost and Lowry 1986).

Harp seal (Phoca groenlandica).—The North Atlantic-wide-distributed harp seal preys on both pelagic and demersal fishes and pelagic invertebrates. Stomach contents of 369 harp seals in coastal waters of northern Norway were dominated by a variety of near-bottom fishes such as gadoids and energy-rich pelagic shoaling fish such as Atlantic herring and capelin (Haug et al. 1991). Shrimps and squid were present in stomachs, but less prevalent. Dominant prey species varied between years, areas, and age classes; for example, saithe was eaten by older seals off northern Norway, while Norway pout was consumed by younger seals. In the Barents Sea, the pelagic amphipod *Parathemisto libellula* dominated the diets of 22 harp seals by abundance and mass, and the shrimp *Pandalus borealis*, euphausids *Thysanoessa* spp., and fishes contributed the remaining 25% (Nilssen et al. 1991). In the Greenland Sea, pelagic amphipods (*Parathemisto*), the squid *Gonatus fabricii*, Arctic cod, and capelin combined constituted 63–99% of the observed diet biomass with the amphipod dominating in the summer (Haug et al. 2004). Arctic cod and capelin were the major prey species off eastern Newfoundland, while capelin and Atlantic cod were most important in the Gulf of St. Lawrence (Stenson et al. 1997).

Conclusion

In summary, AMM exploit a wide range of pelagic and benthic invertebrate and vertebrate food resources, ranging from small copepods to large fishes and other mammals. Some AMM or at least some populations are very prey-, habitat-, and/or depth-specific (e.g., walrus, polar bear) while others are more opportunistic (e.g., beluga, bearded seal). It is apparent that prey occurring in high densities and/or with high caloric values are preferred. The distribution and biomass of the various prey items is ultimately linked to the productivity of the Arctic marine food webs, which varies on temporal and regional scales.

Arctic Marine Food Webs

The occurrence of marine mammals in the Arctic is patchy due to variations in both physical and biological (prey) characteristics. The differences in water depth, ice cover, and hydrography (Walsh 2008) cause considerable differences in the rate of primary production and food web structure between different Arctic shelves and in particular between the shelves and the Arctic deep sea. Consequently, prey availability and use of that prey will largely depend on the physical settings of the habitat of any given AMM species (Laidre et al. 2008, Walsh 2008). Below we outline the general biological characteristics of the three major physical realms (sea ice, pelagic, and benthic) in the Arctic Seas and discuss their current relevance for the nutrition of Arctic marine mammals. This information will also be used as a platform to discuss the impacts of ongoing and future environmental changes in the Arctic marine environment on AMM.

Sea ice communities and food web

Sea ice, formed by freezing of seawater, is a key component in structuring polar environments in general (Gradinger 2002, Sakshaug 2004). In addition to its important role as a platform for marine mammals (Laidre et al. 2008) and birds, sea ice serves as a habitat for a unique, highly specialized community of bacteria, algae, protozoans, and metazoans, which contribute to the biogeochemical cycles of polar seas (Horner 1985, Gradinger 2002).

Two major types of Arctic sea ice can be distinguished, depending on location and ice age (Wadhams 2000). Fast ice is attached to land and forms ice sheets in coastal areas, where it may grow either annually or for several years. Pack ice consists of separate ice floes of varying sizes (ranging from a centimeter to a kilometer in scale), drifting on the surface of the ocean with wind and currents. The sea ice cover in the Arctic shows distinct seasonal patterns driven by the yearly melt and ice formation cycle, with maximum ice extent in March (average 15.7×10^6 km^2) and minimum extent in September (average 9.3×10^6 km^2; period 1979–1987) (Wadhams 2000). Most of the annual sea ice formation occurs on the shelves, while the central Arctic Ocean remains ice-covered by multiyear pack ice even in summer. The accumulation of snow is not well studied but a thickness of $\sim$40 cm may accumulate over winter and starts to melt (depending on latitude) in May/June (Gradinger 2002).

On average, ice thickness increases from areas with mainly first-year ice (e.g., Russian Arctic: thickness $<$2 m) to areas with multiyear ice cover (central Arctic) to a maximum north of Greenland (thickness 7–8 m) (Wadhams 2000). Recent observations indicate a substantial reduction in the ice thickness by 0.5–1.5 m in various parts of the Arctic, parallel to a loss of ice extent by $\sim$2–3% per decade (ACIA 2004).

The biology related to sea ice is largely controlled by its physical and chemical properties (e.g., Gradinger 2002), mainly light availability and nutrient supplies. The biota is found inside the sea ice in pockets and channels of brine between the ice crystals or is attached to the underside of the fast and pack ice. So far, more than 200 diatom species (mainly pennate taxa) and more than 70 species of flagellates are described from Arctic sea ice (Horner 1985). Ice algae contribute 4–26% to total primary production in seasonally ice-covered waters and more than 50% in the permanently ice-covered central Arctic (Gosselin et al. 1997, Sakshaug 2004; Fig. 1). Overall, absolute production rates of organic carbon were below 10 g C/yr. The organic matter produced within the sea ice serves as the base for the sympagic (ice-associated) food web including protozoans and metazoans, e.g., ciliates, rotifers, copepods, copepod nauplii, nematodes, turbellarians, and, in fast ice, larvae of benthic polychaetes and gastropods (Horner 1985). Meiofauna abundances decrease from the nearshore fast ice (up to 350 000 animals/m^2) to the deep-sea basin by about three orders of magnitude (Gradinger and Bluhm 2005, Gradinger et al. 2005). Although a variety of ice meiofauna and meroplanktic larvae consume ice algae, only a minor fraction ($<$10%) of the ice algal production is consumed by sea ice metazoans (Gradinger et al. 2005).

Gammaridean amphipods, the dominant macrofaunal taxon in the Arctic under-ice habitat, are the best-studied consumers of ice algal production in all parts of the Arctic (e.g., Gradinger and Bluhm 2004). Several

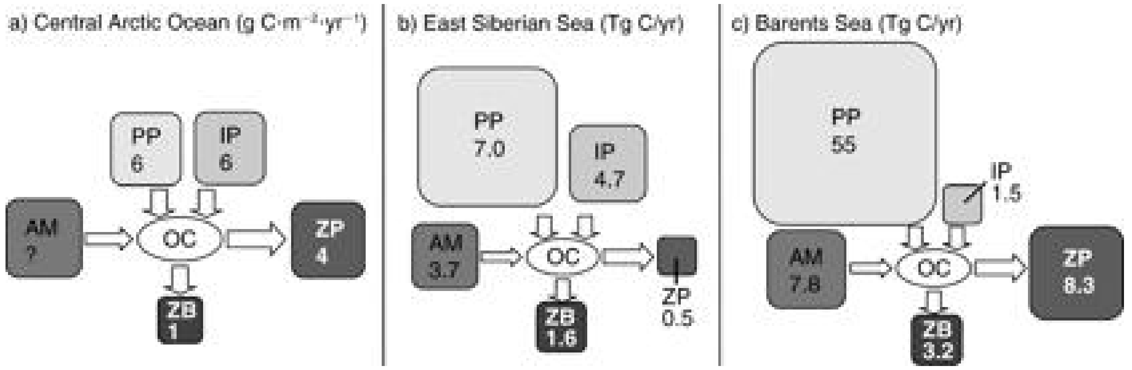

FIG. 1. Yearly production estimates for phytoplankton (PP), ice algae (IP), allochthonous material (AM), zooplankton (ZP), and zoobenthos (ZB) contributing to the organic-carbon pool (OC) for three different Arctic regions: (a) central Arctic Ocean (from Gosselin et al. 1997 [PP, IP], Klages et al. 2004 [ZB], and Mumm et al. 1998 [ZP]), (b) East Siberian Sea (Petrova et al. 2004), and (c) Barents Sea (Vetrov and Romankevich 2004). Units used correspond to those in the original data sources. This schematic depicts only rough estimates to emphasize the different sizes of the boxes in each region.

species of amphipods (e.g., *Gammarus wilkiztkii*, *Apherusa glacialis*, *Onisimus* spp.) are endemic to the multiyear sea ice cover and exploit the ice cover year-round, while benthic species such as *Onisimus litoralis* are common in nearshore seasonal ice regimes (Bradstreet and Cross 1982). Under-ice amphipods occur in abundances of 1–1000 individuals/m^2 in coastal areas and with, on average, 1–40 individuals/m^2 in offshore pack ice (Gradinger and Bluhm 2004). These under-ice amphipods are an important food source for Arctic diving birds and Arctic cod (*Boreogadus saida*) (Bradstreet and Cross 1982) and thereby provide the link from the food web within the sea ice to the more accessible open water below.

Arctic cod are frequently observed in close association with fast ice and pack ice year-round, and use the ice both for protection against potential predators and as a feeding habitat, ingesting under-amphipods and zooplankton (Gradinger and Bluhm 2004). In ice-free areas or conditions, Arctic cod is a pelagic species, but may also be found near the bottom in shallow shelves. Arctic cod can occur in small groups in protected seawater wedges within the offshore pack ice or form dense swarms of several million fish. This northernmost distributed gadid is the crucial link between the sea ice food web and AMM, in particular ringed seals, ribbon seals, and narwhals (e.g., Siegstad et al. 1998; Table 1) in that it "concentrates mg-sized particles into energy packets large enough to be eaten efficiently by seals, whales and birds" (Welch et al. 1992:351). In Lancaster Sound, Canada, alone, AMM and birds consume ~148 000 Mg/yr (metric tons per year) of Arctic cod (Welch et al. 1992).

Pelagic communities and food web

Much like those occurring in the ice, biological processes in the water column are mainly controlled by abiotic forcing. Seasonal fluctuation of light and ice melting and formation regularly alter growth conditions for phytoplankton. In early spring, increasing light and ice melt enhance water column stability; as a result phytoplankton blooms form in the marginal ice zones (MIZ) before algal growth occurs in the adjacent open ocean. These substantial MIZ algal blooms, which move across the shelves with the sea ice retreat, make up 50% of the total primary production in Arctic waters (Sakshaug 2004).

Total primary production rates in the Arctic can exceed values of >100 g C·m^{-2}·yr^{-1} on the shelves of the Barents, Chukchi, and Bering Seas (Sakshaug 2004). The highest production values are encountered on the Bering Shelf, where values are close to 5 g C·m^{-2}·d^{-1} or >500 g C·m^{-2}·yr^{-1} and are among the highest in the world's oceans. These very high rates reflect the high nutrient concentrations that allow the buildup of substantial phytoplankton biomass while Arctic shelves with lower nutrient availability (e.g., northern Barents Sea, East Siberian Sea, Kara Sea) exhibit much lower production values (15–70 g C/m^2; Sakshaug 2004). Primary production rates in the central Arctic Basin are one order of magnitude (<20 g C·m^{-2}·yr^{-1}) lower than on the shelves (Gosselin et al. 1997, Sakshaug 2004; Fig. 1). Within the ice pack, enhanced primary production rates were found in polynyas around Greenland, where yearly primary production estimates range between 20 and 50 g C/m^2.

In certain areas, the microbial food web plays an important role in the Arctic, based on locally very high concentrations of dissolved organic carbon (e.g., Sherr and Sherr 2003). From the perspective of AMM however, larger size classes, mainly herbivorous mesozooplankton, such as copepods and euphausiids, and fish are the most significant prey items within the water column. For example, the adults of some of the biomass-dominating marine Arctic copepod species, such as *Calanus glacialis* and *C. hyperboreus*, reach sizes larger than 1 mm. The Arctic pelagic herbivores adapted their life cycles to deal with the seasonally pulsed food supply (Hagen and Auel 2001). The storage of large amounts of lipids in form of either waxesters or triglycerids for either winter survival or spring reproduction (Hagen and Auel 2001) makes these copepods a rich food source for higher trophic levels from fish to AMM, among those in particular the bowhead whale (Tables 1 and 2). These copepods contribute the largest fraction to Arctic mesozooplankton biomass (Mumm et al. 1998). Besides copepods, typical Arctic zooplankton includes amphipods, chaetognaths, larvaceans, hydro- and scyphomedusae, and pelagic snails (Hopcroft et al. 2005). The biomass of Arctic mesozooplankton can exceed the phytoplankton biomass and shows a steep decline north of approximately 83° N from values of 8 g dry mass/m^2 in the Greenland Sea to $\sim$1 g dry mass/m^2 in the High Arctic Nansen and Makarov Basins (Mumm et al. 1998). Similar latitudinal trends are obvious for the zooplankton productivity, as exemplified in Fig. 1.

Several of the dominant zooplankton taxa are linked in their occurrence to the Arctic hydrographical regime. The lipid-rich calanoid copepod species *Calanus glacialis* is endemic to polar waters, while *C. finmarchicus* is found in the Atlantic domain and, e.g., *Neocalanus cristatus* in the Pacific domain (Hopcroft et al. 2005). Similarly, the herbivorous euphausiid *Thysanoessa inermis* is abundant in the sectors influenced by Atlantic water and *T. longicauda* and *T. raschii* in Bering Sea water. Fluctuations or long-term changes in the large-scale hydrographical regimes will consequently alter the species spectra in the inflow shelves, which carry Atlantic and Pacific species, respectively. On a smaller scale, regional hydrographical processes, specifically freshwater runoff and consequent salinity changes, influence zooplankton composition and biomass, in particular on the shelves with large rivers (e.g., Deubel et al. 2003). For example, decreasing total zooplankton abundance and increasing contribution of smaller freshwater taxa were observed along a decreasing salinity gradient in the Lena River delta.

The food spectrum of copepods and euphausiids includes phytoplankton and microzooplankton but varies from species to species with actual ingestion rates frequently relating to the abundance of the prey (Hagen and Auel 2001). Depending on the availability of food and the abundance of mesozooplankton, their yearly grazing rates range between 1 and >18 g C/m^2 (Sakshaug 2004) and zooplankton production shows similar variability (Fig. 1). Increased primary productivity rates in specific regions such as marginal ice zones can sustain high densitites of mesozooplankton, which attract higher trophic levels such as plankton feeding birds and baleen whales (Bradstreet and Cross 1982).

Major AMM nekton prey include capelin, herring, walleye pollock, and squid (Table 1). In the southeastern Bering Sea walleye pollock is the single most abundant fish, and variations in its stock, therefore, percolate through the whole food web (Wepestad et al. 2000). Fish stock size is highly variable and, along with distribution, may be influenced by temperature. Walleye pollock, for example, currently a subarctic species, is dispersed across the Bering Sea shelf and even north of Bering Strait in warm but not in cold years and spends most time above 2°C, while Arctic cod inhabits areas of consistently colder waters (Wyllie-Echeverria and Wooster 1998). In the Atlantic sector of the Arctic, the distribution of forage fishes such as herring and capelin is influenced by climatic conditions in any given year (e.g., Loeng 1989). For example, capelin, a very energy-dense fish relative to walleye pollock (Table 2), was distributed more easterly and northerly in warm than in cold years in the Barents Sea. Adult capelin fed in both Atlantic and Arctic water masses in the Barents Sea with a preference for temperatures between −1°C and +2°C. Feeding area and growth were related, probably a function of temperature, with warmer temperatures and faster growth in southern areas. In the northwest Atlantic, the large capelin schools formed during the spawning season also make up a significant contribution of the diet of commercial fishes, marine mammals, and seabirds. Less is known about the pelagic fishes of the High Arctic shelves and Arctic deep sea. In a three-year study in the Beaufort Sea, Arctic cod (more on this species in *Sea ice communities and food web*), capelin, and liparids dominated epipelagic catches in coastal waters, with the 0+ age class being most abundant (Jarvela and Thorsteinson 1999). During approximately 15 pelagic dives of a remotely operated vehicle across the Canada Basin, few pelagic fishes were observed (R. Hopcroft, *personal communication*).

Among the squids, *Gonatus fabricii* is the most abundant species in Arctic and subarctic waters of the North Atlantic, where *Gonatus* predators apparently take advantage of aggregations of inactive females at their spawning sites (e.g., Bjørke 2001). While *Gonatus* juveniles inhabit the upper water column, the short-lived adults roam depths >400 m, where they are preyed upon by narwhals (Laidre and Heide-Jørgensen 2005), belugas, and other deep-diving mammals such as sperm whales, northern bottlenose whales, and long-finned pilot whales (Bjørke 2001). In the Bering Sea, where *Berrytheuthis magister* is the predominant squid species, squid are preyed upon by some mammals such as northern fur seals (Arkhipin et al. 1995).

Arctic benthic communities and food web

Major environmental determinants of Arctic benthic community structure include food supply, which largely originates in the surface waters and is highly seasonal in the Arctic, substrate type and grain size, salinity, temperature, and, in shallow water, ice scouring (Klages et al. 2004, Piepenburg 2005). Densities of sedimenting particles and their nutritional values range vastly from the nutrient-rich waters of the northern Bering, Chukchi, and Barents Seas to the oligotrophic deep waters of the Arctic Basins (Klages et al. 2004). Settling food particles add to the soft sediments predominating the Arctic and the grain size of these sediments, along with above-listed factors, determines faunal community composition (Grebmeier et al. 2006*a*). Exceptions to the soft bottoms in the Arctic are local accumulations of boulders, nearshore coastal regions, canyons, and High Arctic islands and Arctic fjords. In near-shore areas, benthic biomass and diversity intermittently decline due to ice scour, resulting in a patchwork of different successional stages (Piepenburg 2005). In addition, nearshore areas are under the influence of freshwater runoff, in particular the Laptev, Kara, and Beaufort Seas (Jørgensen et al. 1999, Deubel et al. 2003). Low numbers of euryhaline and brackish-water benthic species, some particularly well-adapted to high sedimentation rates (e.g., *Portlandia arctica*), dominated the shelf regions in estuaries (Deubel et al. 2003), where benthic biomass can be lower than under fully marine conditions (Jørgensen et al. 1999).

Arctic marine mammals prey on benthic species from the size classes macrofauna (mostly infaunal; >1 mm) to megafauna (large enough to be seen on seafloor images; mostly epifaunal). Benthic bacteria and meiofauna (<1 mm) are therefore excluded from this review. Arctic macrofauna is dominated, like most soft-bottom fauna in the world's oceans, by polychaetes, bivalve mollusks, and crustaceans, in particular amphipods, both on the Arctic shelves and in the central deep sea (e.g., Klages et al. 2004, Grebmeier et al. 2006*a*). Important macrofauna AMM prey species include bivalves taken by walrus, *Macoma* spp. and *Mya truncata*, and benthic amphipods utilized by gray whales and bearded seals (Table 1). Enhanced primary production at frontal systems, polynyas, and along the ice edge result in enriched benthic biomass with high water column productivity related to high benthic infaunal biomass in tightly coupled systems such as the Bering/Chukchi Seas. Benthic biomass is particularly high in the northern Bering Sea (~24 g C/m^2), the southern Chukchi Sea (~40–50 g C/m^2), and in the Gulf of Anadyr (~30 g C/m^2; Grebmeier et al. 2006*a*). In contrast, benthic infauna communities are depleted in biomass on the less productive Alaskan Beaufort Sea shelf (~4 g C/m^2) and in the eastern Chukchi Sea under influence of the nutrient-poor Alaska Coastal Current water (<10 g C/m^2; Grebmeier et al. 2006*a*). On the river-influenced Russian interior shelves, strong gradients of estuarine to fully marine conditions result in benthic biomass gradients (Deubel et al. 2003).

Arctic epibenthic communities include taxa with long life spans (several years to decades) and often slow growth rates such as echinoderms, crabs, and demersal fishes. These communities account for >25% of the overall benthic community respiration and, due to their often large size, contribute significantly to overall benthic biomass despite their patchy occurrence (Piepenburg 2005). At most locations studied, ophiuroids dominated the epibenthic megafauna with locally several hundred individuals per square meter. Other conspicuous epibenthic faunal elements, in varying abundances, included sea urchins, sponges, sea cucumbers, sea stars, crabs, and bryozoans (Piepenburg 2005). With the exception of crabs, shrimps, and molluscs, heavily calcified taxa tend to have little nutritional value (Table 2) and are rarely found on the AMM prey list. Several epifaunal organism groups are highly mobile and play an important role in the redistribution of pelagic carbon partitioned to the benthos and in organic carbon mineralization (Piepenburg 2005).

Benthic or demersal fishes preyed upon by AMM include mostly gadids, redfishes, and Greenland halibut (Table 1). Off Greenland, the demersal fish assemblage is dominated by Atlantic cod, golden and deep sea redfish, American plaice, Atlantic wolfish, and starry skate, although all underwent dramatic declines in abundance, biomass, and/or individual fish size from 1982 to 1996 (Rätz 1999). Greenland halibut, a major prey species of narwhals in Baffin Bay (Laidre and Heide-Jørgensen 2005), ranked 12th in average catch statistics off Greenland from 1982 to 1996 (Rätz 1999). Common and commercially fished demersal fishes in the eastern Bering Sea include Pacific cod, Greenland halibut (or turbot), yellowfin sole, arrowtooth flounder, and other flatfishes (Witherell 2000), a group which in that area does not seem to be among the preferred AMM prey items (Table 1). In High Arctic regions, benthic marine fishes have been poorly studied. Nevertheless, local subsistence fishing has a long tradition along the Arctic coasts and Barrow's native population, for example, is reporting more salmon catches in recent years (C. George, *personal communication*). In the northeastern Chukchi Sea, gadids made up 69–83% of the fishes in trawls in 1990 and 1991; cottids, pleuronectids, and zoarcids contributed much of the remaining catches (Barber et al. 1997). Two species of sculpin were dominant in the southern and northwestern Chukchi Sea in 2004, followed by Bering flounder and Arctic cod (C. W. Mecklenburg, B. A. Sheiko, D. L. Stein, N. V. Chernova, and B. A. Holladay, *unpublished manuscript*). Gadids and sculpins were dominant in a few bottom trawls in the Chirikov Basin in 2003 (R. Highsmith, C. O. Coyle, B. A. Bluhm, and B. Konar, *unpublished data*). The potential distribution and stock size changes in a warming Arctic climate may prompt more interest in Arctic fishes in the future.

Cryo-pelagic–benthic coupling

Coupling processes and interdependencies between ecosystem components are of great significance in the Arctic and are, therefore, stressed again here. The sea ice and pelagic and benthic realms are inherently linked through sedimentation of particles, animal migrations, life cycles, and direct food web interactions. The quantity and quality of particles produced in the sea ice or water column and settling out to the sea floor depend on nutrient availability and overall primary production in the water column, water stratification and mixed layer, midwater grazing rates, and bacterial degradation (Klages et al. 2004). If primary production is high in regions of high nutrient availability and zooplankton grazing is simultaneously low, coupling between the ice and/or pelagic and the benthic systems is tight, resulting in high benthic biomass (Grebmeier et al. 2006*a*). In a latitudinal comparison of energy flow partitioning, the benthic system received more energy in Arctic vs. temperate and tropical systems, although there are significant differences within the Arctic. A prime example for tight pelagic–benthic coupling can be found in the northern Bering and southern Chukchi Seas (Grebmeier et al. 2006*a*). Sediment trap measurements in the 1980s indicate that total particulate organic carbon (POC) flux in the northern Bering Sea is extremely high (253–654 mg $C \cdot m^{-2} \cdot d^{-1}$) and low C/N ratios of organic material in the sediment traps (4.9–7.4) indicate that fresh organic matter is reaching the benthic community. The latter utilizes the carbon directly and efficiently as indicated by a match of the mean vertical carbon flux (501 mg $C \cdot m^{-2} \cdot d^{-1}$) and the estimated organic carbon utilization at the seafloor (464 mg $C \cdot m^{-2} \cdot d^{-1}$; Grebmeier et al. 2006*a*). The high carbon flux is driven by high primary production, which was estimated at 250–300 g C/m^2 for the summer months or ~2 g $C \cdot m^{-2} \cdot d^{-1}$. Those high production areas serve as feeding grounds for the bottom-feeding Pacific walrus, California gray whale, diving birds, and surface-feeding seabirds associated with feeding mammals (e.g., Oliver et al. 1983). In recent years, evidence is accumulating that change is underway, with less tight pelagic–benthic coupling and locally changing benthic biomass (Grebmeier et al. 2006*b*; see *Recent changes and fluctuations in Arctic marine food webs*).

RECENT CHANGES AND FLUCTUATIONS IN ARCTIC MARINE FOOD WEBS

The described characteristics of the ice, pelagic, and benthic realms provide a diverse spectrum of feeding habitats and prey communities for AMM. Variability and changes in environmental conditions (Walsh 2008) likely have different consequences for different trophic levels and species within them (Laidre et al. 2008). The growing concern about the potential impact of Arctic warming on the marine ecosystem stimulated major new large-scale biological climate studies and is one of the topics of the ongoing International Polar Year (IPY) 2007–2008. While Arctic systems have been described as well adapted or resilient to some degree of climate variation because of the frequent natural disturbances (Piepenburg 2005), the magnitude of change expected in this century makes the Arctic system vulnerable to climate change (ACIA 2004). It should be noted, however, that large changes are not necessarily (only) driven by climate. Arctic ecosystems are also impacted by high loads of pollutants and human exploitation (including harvest of fish and AMM), which have caused changes in Arctic food webs (e.g., AMAP 2003). The difficulty in documenting solid causal relationships between climate and biological populations lies in several factors, most importantly, the scarcity of long-term time series. Also, the best studied (sub-)arctic regions, the southern Bering and Barents Seas, are those that have undergone major climate variability, but are at the same time the most heavily exploited Arctic areas in terms of historic whaling, past and present fisheries, and/or oil and gas exploration.

Here we present examples of documented changes, attributed to climate variability or change, in subarctic and Arctic biological communities on a range of trophic levels. Examples will have a focus on subarctic regions, as biological investigations in the High Arctic have been too rare for analyses of interdecadal variabilities. Our current understanding of the High Arctic provides evidence for the close linkages between environment and marine food webs, but long-term time series are largely missing. Sporadic observations from the Central Arctic indicate substantial changes might be occurring already with the loss of sea ice and its attributed flora and fauna (Melnikov et al. 2001). Even today in the era of Arctic warming (ACIA 2004), no unified pan-Arctic long-term monitoring plan has been implemented to follow changes in the High Arctic marine food web composition and biomass. National programs, however, are underway, and so are efforts attempting to connect those in the framework of the IPY.

Pacific (sub-)arctic

A growing body of evidence suggests that regime shifts and long-term climate changes in the Bering and Chukchi Seas are coincident with alterations in biological regimes (Schumacher et al. 2003, Grebmeier et al. 2006*b*). Regime shifts are dynamic and can oscillate. The co-occurring biological changes can serve as model scenario indicators for effects of long-term climate change. The best understood example for climate-driven variability is the Bering Seas regime shift complex. The regime shift in 1997 had various effects on sea surface temperature, the extent of sea ice, and wind forcing of ocean currents in the Bering Sea. Since then, several coccolithophorid blooms have occurred in the Bering Sea and were intermittently thought to replace the previously occurring summer flagellate community (Schuhmacher et al. 2003). As a result, profound effects on consumer abundance and feeding types and on biogeochemical cycling were observed. As an example, zooplankton communities in the Bering Sea changed from crustacean-dominated communities to an increase in gelatinous plankton, which has since decreased again. The prey items of the dominant jellyfish species in the late 1990s and early 2000s, *Chrysaora melanaster*, includes euphausids, copepods, and amphipods, as well as juvenile pollock and, hence, overlaps with that of some Arctic marine mammals.

Shifts in fish and benthic community composition also occurred in recent decades (Hamazaki et al. 2005). In the heavily fished southeastern Bering Sea, flatfish and general groundfish biomass was higher in 1980–2000 than in 1960–1980. Catch per unit effort of total benthic epifauna (in particular crabs and sea stars) and fish (in particular flatfishes) increased from 1976 to 2002 in Norton Sound and from 1976 to 1998 in Kotzebue Sound. In contrast, a decrease in benthic infauna biomass and sediment oxygen uptake was observed south of St. Lawrence Island on the Bering Sea shelf (Grebmeier et al. 2006*b*). Here, the changes in the bivalve population composition by the late 1980s affected benthic predators, such as the spectacled eider, that heavily use this feeding ground. Between 1986 and 1988, ampeliscid amphipod biomass and production in the Chirikov Basin (northern Bering Sea) declined by ~20%, and by 2002–2003 production had further declined to ~50% of the highest value in 1986 (Coyle et al., *in press*). It is not fully resolved to what extent climate or whale predation is responsible for this decline. Indications for climate-related shifts in Arctic community composition are also evident from benthic studies in this region: Recent sampling in the Chukchi Sea suggests northern range extensions of some mobile epifauna species with climate warming as the suspected cause (B. Sirenko, B. A. Bluhm, and K. Iken, *unpublished manuscript*).

Arctic marine mammals have been used to understand long-term trends in ecosystem productivity in this region. The $\delta^{13}C$ stable isotope ratios in bowhead whale baleens support the hypothesis that the productivity of the Bering Sea declined by ~30–40% over the time period 1966–1997 (Schell 2000). Besides food web changes, ranges of AMMs might have changed as recent acoustic and visual observations documented temporally extended stays of gray whales in the Chukchi Sea all the way up to Barrow, potentially a consequence of warming trends (Moore et al. 2006).

Atlantic (sub-)Arctic

The variable inflow of comparatively warm North Atlantic water into the Barents Sea drives the variability of environmental conditions and of fish larval and zooplankton biomass in this area (e.g., Dalpadado et al. 2003). The North Atlantic Oscillation is thought to have an effect on the distribution and biomass of North Atlantic zooplankton. Over the last two decades the Barents Sea zooplankton biomass has undergone large changes with overall higher plankton biomass in relatively warm years such as 1994 than in cold years such as 1986. The biomass of the dominant copepod species, *Calanus finmarchicus*, was tightly linked to the supply of Atlantic water into the Barents Sea. With warming North Atlantic waters and stronger inflow into the Arctic, "warm-year" conditions may become prevalent in the future and extend northward. Zooplankton stock and growth fluctuations affect pelagic planktivorous fish such as capelin and herring, prey items of ringed seals and other AMM (Siegstad et al. 1998). More directly, a climate-related shift from large lipid-rich Arctic copepod species (Table 2) to smaller North Atlantic taxa might reduce the nutritional quality of the food present in areas affected by warming.

Similar linkages between warming and climate-related changes in benthic invertebrate and fish biomass and composition have already been observed in the Barents Sea half a century ago. Warming in the Barents Sea in the first half of the 20th century resulted in the restoration of the cod stock on Bear Island Bank after the species' practical absence for about four decades (Blacker 1957). Blacker also observed that several Atlantic indicator species had a northward range extension from 75° N to 78° N since 1878, apparently as a consequence of increased inflow of warm North Atlantic water. By 1978–1981, Dyer et al. (1984) noted that the same indicator species had further increased their temperature ranges in the same study region. In addition Arctic and Atlantic species overlapped more extensively in their ranges in the 1970s relative to the 1950s. Kiyko and Pogrebov (1997:330), in their analysis of pollution effects, observed decreases in polychaete biomass in the Barents and Kara Seas in the early 1990s relative to the 1920–1930s as well as a "redistribution of some organism groups." Although these authors interpret these changes as sampling effects and "natural population fluctuations," an analysis of these range changes in relation to climatic conditions still needs to be done.

Potential future scenarios for Arctic marine food webs

The Arctic Ocean will be, and to some extent already is, exposed to tremendous changes in the environmental boundary conditions, including loss of summer sea ice, increasing temperatures, and alterations in the precipitation and river runoff patterns (ACIA 2004, Walsh 2008). Detailed biological consequences of such changes on a species level are difficult to predict, as biological systems might react in unprecedented ways as learned from the described shifts between crustaceans and jellyfish in the Bering Sea. Here we describe three scenarios that, therefore, should be considered as thought experiments, providing inspiration to discuss possible effects on the Arctic marine food web and their implications for AMM and to pose related hypotheses. The underlying assumptions for the scenarios are based on published results from the literature described in the sections before; the scenarios themselves are, from our perspective, likely but not prognostic, each taking into account a particular set of parameters. We restricted ourselves to alterations outlined within the ACIA (2004) framework that assumes only slight modifications of the current Arctic Ocean hydrography; we excluded major alterations such as a potential loss of the Arctic halocline (Walsh 2008) and its subsequent impacts.

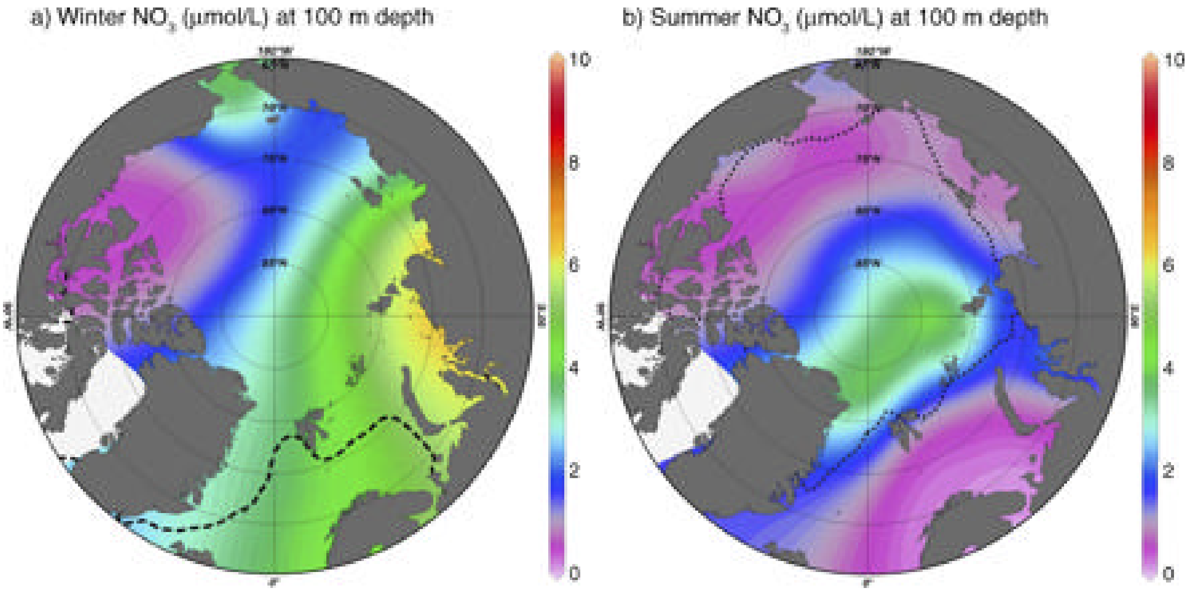

FIG. 2. (a) Winter and (b) summer nitrate concentration in the Arctic seas based on Colony and Timokhov (2001). Note that the data for winter are sparse (for details, see Colony and Timokhov [2001]). The dashed line indicates the long-term mean ice extent (concentration >50%) for (a) March and (b) September. The nutrient reservoir over the Central Arctic in the summer (blue and green areas) could support additional new primary production in an ice-free Arctic Ocean.

Changes in sea ice cover and resulting primary production.—The loss of summer sea ice cover will have immediate consequences for ice-dependent AMM. Examples include reduced reproductive success and survival chances of polar bears and the loss of insulation from snow and interruption of nursing in ringed seals due to early breakup (Kelly 2001, Laidre et al. 2008). The loss of the ice-based food web and the associated food sources such as amphipods and Arctic cod (Gradinger and Bluhm 2004) would additionally negatively impact the ice seals. For the Pacific walrus, the retreat of spring sea ice beyond the Arctic shelves into the deep basins will make ice no longer a resting and reproduction environment that is within the reach of their benthic prey (depth limit approximately 100 m; Kelly 2001).

On a broader ecosystem scale, the loss of sea ice will likely change the amount and characteristics of primary production in the Arctic seas. Several researchers (e.g., Anderson and Kaltin 2001) have proposed that the increased summer ice melt will increase the overall extent of marginal ice zones and lead to increased primary productivity in these regions. Increased primary productivity would supply more food for pelagic and benthic consumers, while the low productivity zone of the multiyear sea ice (MYI) would shrink. Also, ice retreat off the shelves may result in upwelling of nutrients or prey from the basins (Carmack et al. 2004). Based on the inorganic carbon availability, Anderson and Kaltin (2001) proposed an increase of up to 50 g C/m^2 integrated over the upper 100 m of the water column across the Arctic, mainly as a result of ice loss. Ultimately, however, nutrient availability, mainly nitrogen and phosphorous, determines the total amount of primary productivity possible in any given ocean.

Hence, we estimated the potential for increased primary productivity in the Arctic based on nutrient concentration data from the "Hydrochemical Atlas of the Arctic Ocean" (Colony and Timokhov 2001), which summarizes hydrographical and chemical data from drift ice stations and ship-based expeditions from 1948 to 2000. We selected nitrate concentration data from within the euphotic zone (10-m depth) to address the question of whether the removal of sea ice, and thus the increase in solar radiation in the water column, could indeed support an increase in primary production or whether the current nutrient resources are already completely consumed by phytoplankton growth. The large-scale nutrient regime in winter (Fig. 2a) shows three major features: (1) the oligotrophic Beaufort Gyre in the Canadian Basin, (2) the higher nutrient concentrations in the Transpolar Drift regime, and (3) the inflow of nutrients through the Bering Strait, the North Atlantic, and rivers on the Arctic shelves. The summer distribution (Fig. 2b), in contrast, shows a reduction of nitrate in the region south of approximately 80° N as a consequence of phytoplankton blooms in the dynamic marginal ice zones. North of 80° N, an area that currently overlaps with the MYI zone (Walsh 2008), summer nutrient concentrations remain higher, i.e., they are not completely utilized by phytoplankton. Based on the provided gridded data set, we calculated a mean nitrate summer concentration of 3.2 µmol NO$_3$ north of 80° N and of 0.8 µmol NO$_3$ between 70° and 80° N.

Assuming a typical phytoplankton C/N ratio of 7, the mean summer concentration of approximately 3.2 μmol NO_3 in the central Arctic would allow for an additional new production of 270 mg C/m^3 or 13 g C/m^2 (assuming a relatively shallow 50-m euphotic zone as typical for marginal ice zones, e.g., Sakshaug 2004) (Fig. 2b). This estimate is within the same order of magnitude as the current production estimates for the central Arctic Ocean (Gosselin et al. 1997), which according to our scenario would, hence, roughly be doubled. Similarly noteworthy is that the current nutrient regime would not allow for a substantial change in total primary productivity in the coastal and shelf regions using our assumptions.

In reality, total primary production will also depend on seasonal stratification, river runoff (see *Increased river runoff changes nearshore biological communities*), etc. Ice receding from the shelves could facilitate upwelling along the shelf breaks (Carmack et al. 2004), which in turn may support higher primary production on the shelves than suggested in our scenario that assumed constant nutrient concentrations. Nevertheless, we consider it reasonable to assume a primary production increase in the central Arctic Transpolar Drift system. Currently little of the Transpolar Drift system and the area north of 80° N is utilized by AMM (Laidre et al. 2008), but this might change under the outlined scenario. The fate of the above-described increased production at very high latitudes will depend on the food web structure. Currently, subarctic and Arctic pelagic and benthic communities (including AMMs) successfully exploit the seasonal ice systems of the Arctic shelves. Increased primary production in the Central Arctic might lead to higher biomass of zooplankton and/or benthos, depending on the reworking and sedimentation patterns. The great water depths in the Central Arctic will make remineralization of the majority of the production in the water column very likely, similar to current conditions in the Central Arctic (Fig. 1). From the perspective of AMM, benthic feeders such as gray whale and walrus will remain unable to exploit the Arctic basins because they are well beyond their diving depths. Pelagic feeders such as bowhead, fin, minke, and blue whales, in contrast, might be able to use the increased productivity. The question of whether jellyfish rather than (or in addition to) crustaceous zooplankton would increase in relative importance in subarctic and Arctic food webs, as documented in the Bering Sea and elsewhere, is open. Jellyfish and other gelatinous zooplankton are an integral part of the current High Arctic food web (Hopcroft et al. 2005) but have low caloric value for higher trophic levels (Table 2). Their increase would likely not lead to better feeding conditions for AMMs.

Increased river runoff changes nearshore biological communities.—A second scenario revolves around the potential effects of the observed and predicted increase in river runoff in the Arctic (ACIA 2004). Total freshwater inflow into the Arctic Ocean is on the order of 4523 km^3/yr (R-ArcticNet, *available online*)[2] and increased by ~7% from 1936 to 1999, with the potential for further increase with Arctic warming (ACIA 2004).

Increased freshwater discharge acts on biological communities through three major pathways (besides addition of organic dissolved matter): (1) nutrient transport, (2) turbidity, and (3) inflow of low salinity water (Pivovarov et al. 2003). All three effects can act on the levels of species richness, community composition, productivity, and biomass, and although these effects are tightly coupled, we will evaluate their current significance separately for clarity of the argument.

1) Arctic river runoffs differ in the amount of inorganic nutrients, both macro- and micronutrients. The injected macronutrients are consumed by phytoplankton within the river estuaries, as exemplified for both the Kara and the Beaufort Seas (e.g., Pivovarov et al. 2003). Additional nutrient input to the nearshore waters through either higher freshwater input (through changes in the hydrological cycle) or higher nutrient concentrations in the freshwater (through changes in the terrestrial environment; ACIA 2004) could increase the current productivity in coastal and estuarine areas, but this might be counteracted by the impact of decreased salinities and increased turbidity.

2) Increased river runoff, with its high levels of suspended inorganic material, will increase nearshore sedimentation and turbidity, which reduces light transmission for algae and can clog filtration apparatuses of filter-feeding animals (Thrush et al. 2004). Certain Arctic cumacean and bivalve species, e.g., *Portlandia arctica*, can endure high sedimentation rates (Syvitski et al. 1989) while many other species cannot. High turbidity reduces the capability of visual predators to find prey. Increased land use in the Arctic over the next decades due to resource exploitation and climate change has the potential to further increase the sediment load and impact the marine food web.

3) Increased freshwater discharge would likely result in larger areas inhabited by euryhaline and brackish-water species relative to marine species compared to the current situation. In general, species richness is related to salinity, with high numbers of species in fully marine and true freshwater conditions and the lowest number of species around 5–7 practical salinity units (PSU; Remane 1958; Fig. 3). Brackish-water species occur at a salinity range from close to 0 to ~20 PSU, but are not very numerous.

The structuring effect of freshwater runoff, with all features combined, on the biomass, productivity, and community composition of Arctic phytoplankton, zooplankton, and benthic taxa is reasonably well documented and outlined here, although some results are

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[2] ⟨http://www.r-arcticnet.sr.unh.edu⟩

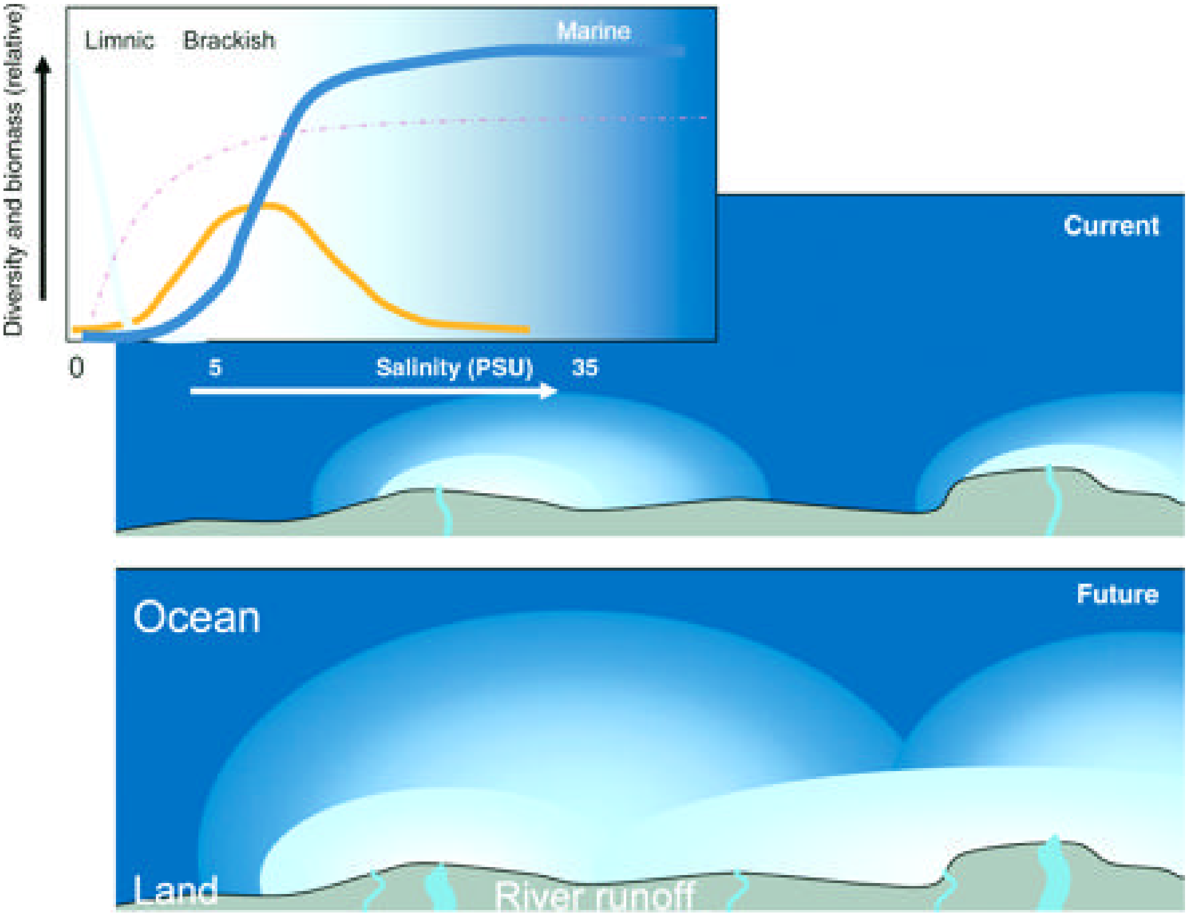

Fig. 3. Schematic representation of surface water salinity gradients in Arctic estuaries. Increased river runoff will decrease salinity over a broader area (indicated by light blue colors) in the nearshore Arctic Seas. This might lead to decreased diversity and biomass of the pelagic and benthic prey taxa of Arctic marine mammals. The relationship between water salinity and species diversity for freshwater (light blue line), brackish-water (orange line), and marine species (dark blue line), and biomass (pink line) is based on Remane (1953). For details see *Potential future scenarios…: Increased river run-off…*.

conflicting (Parsons et al. 1988, Deubel et al. 2003, Udalov et al. 2005).

In the pelagic realm, freshwater taxa currently dominate in the river mouths of the large Siberian rivers, and highest biomass was associated with the marine realm, where large copepods (*Calanus glacialis*) dominated the zooplankton (Deubel et al. 2003). In the near-mouth zone of an estuary in the White Sea, the concentration of suspended matter was higher than in the intermediate and marine zones, and the highest phytoplankton concentrations were observed in the marine zone, whereas the lowest occurred in the near-mouth zone (Dolotov et al. 2002). Similarly, minimum algal biomass (0.3 μg chlorophyll *a*/L) occurred close to the mouth of the estuary of Chesterfield Inlet in the Canadian Arctic, and maximum biomass (1.9 μg chlorophyll *a*/L) was observed near the estuary head (Roff et al. 1979). In the MacKenzie River estuary, the planktonic community near the river mouth experienced high dissolved organic carbon pools, high bacterial activity, and high amphipod biomass, while the more productive offshore community consisted of copepods, medusae, and ctenophores (Parsons et al. 1988).

Benthic infaunal species richness, biomass, and Shannon-Wiener diversity increased with salinity in the Kara Sea (e.g., Deubel et al. 2003). Arctic estuaries are dominated by few benthic species, as is typical for areas with large fluctuations in environmental conditions, such as the euryhaline polychaetes *Prionospio cirrifera* and *Marenzelleria arctica*, the cumacean *Diastylis* cf. *glabra*, and the bivalve *Portlandia* cf. *arctica* (Denisenko et al. 1999, Jørgensen et al. 1999). The biomass of micro- and macrozoobenthos also decreased with salinity in a White Sea estuary, whereas that of the meiozoobenthos increased in association with dramatic community composition changes: At salinity values <10 PSU, the proportion of nematodes dropped from 86% to 50% by abundance, while ostracods increased to up to 45% of the total abundance of meiobenthos (Udalov et al. 2005). Nematode and harpacticoid densities and biomass dropped dramatically below salinities of 3 PSU. These studies suggest that diversity and biomass in Arctic

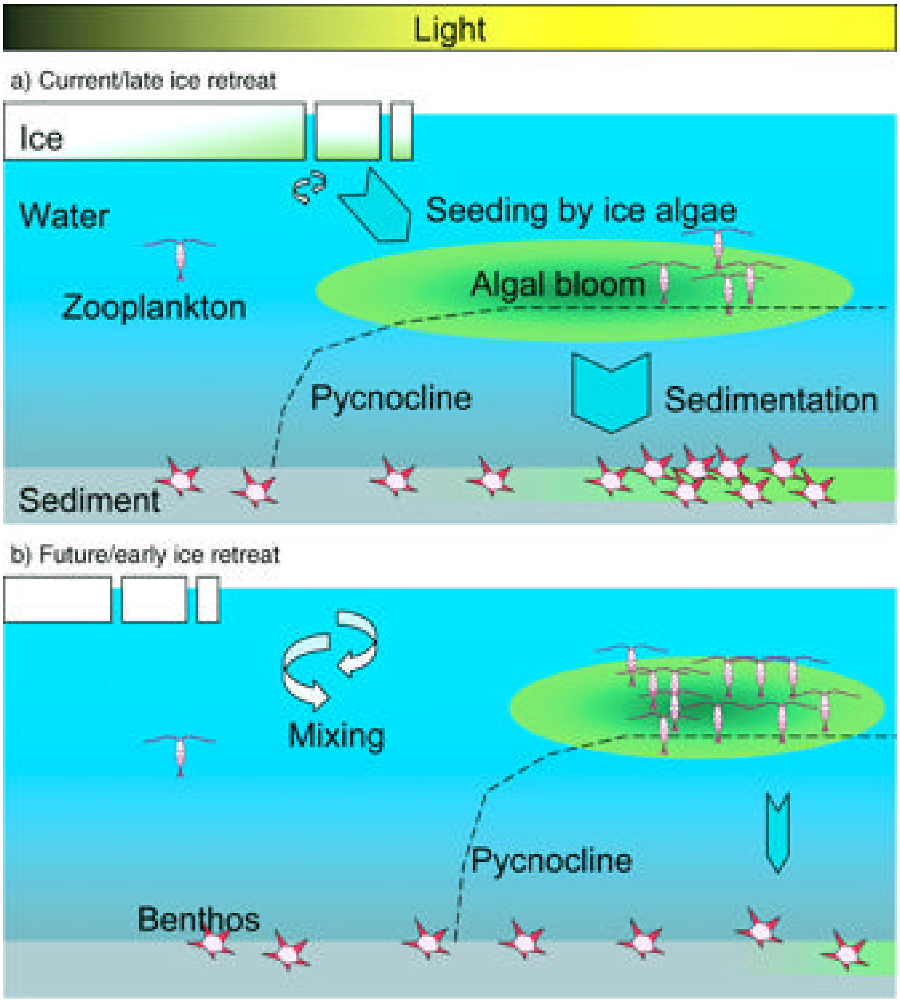

FIG. 4. Schematic representation of seasonal cycle of marine production in current/late ice retreat (a) and future/early ice retreat conditions (b). Early ice retreat allows for stronger wind mixing and causes later formation of the seasonal pycnocline. The delayed phytoplankton bloom is consumed by zooplankton, while, under current conditions on several Arctic shelves, it largely sinks directly to the sea floor, sustaining high benthic biomass.

estuaries often, but not always, covary along a salinity gradient with increasing biomass from the freshwater to the marine conditions and a diversity minimum at salinities of ~5 PSU (Fig. 3).

Applying the described relationships to the future situation for AMM, increased river runoff may be more likely to cause reduced rather than constant or increased benthic biomass and diversity, which would put benthic-feeding AMM at a disadvantage in the nearshore freshwater to brackish-water areas. Some studies suggest that reduced biomass may also be the trend in a fresher future pelagic realm. The total biological changes associated with the salinity gradient might cause AMM to prefer areas further offshore than they currently occupy, which could be harmful for the subsistence hunting activities of coastal Arctic communities.

Changes in cryo-pelagic–benthic coupling.—The extent of cryo-pelagic–benthic coupling varies in the Arctic, from regimes in which most of the primary production is consumed by pelagic zooplankton to regions with substantial flux to the seafloor and resulting high benthic biomass and production (Fig. 1; Piepenburg 2005, Grebmeier et al. 2006*a*). Two conceptual primary production scenarios have been suggested that relate to ice cover and may, therefore, have predictive value. In years of abundant sea ice (and, thereby, cold surface waters), herbivorous zooplankton is less abundant early in the season and has little grazing impact on the ice algal and marginal ice zone blooms (e.g., Carroll and Carroll 2003). As a result, primary production occurring in these well-stratified conditions is largely exported to the benthic community and can support a biomass-rich benthic community and benthic-dominated food web including bottom-feeding mammals and birds (Grebmeier et al. 2006*a*). In years or areas with less ice, in contrast, an open water and later-occurring phytoplankton bloom dominates over sea ice-related blooms. With zooplankton further along in their life cycles at this time and water temperatures slightly warmer, these phytoplankton blooms may be efficiently grazed by abundant zooplankton (Carroll and Carroll 2003; Fig. 4), which in turn are capable of supporting pelagic larval and juvenile fishes. The increased pelagic carbon utilization and recycling would result in a reduced flux of more refractory carbon to the seafloor.

These two contrasting scenarios imply that the ongoing trend of declining sea ice, earlier ice melt, and increased water temperatures in the Arctic (ACIA 2004) would make the pelagic food web-dominated scenario both more common and occur over a geographically larger area. The increased consumption of pelagic primary production by pelagic herbivores enhancing planktivorous fish abundance would increase the prey concentrations for pelagic-feeding AMM such as bowhead whales. Reduced carbon input to the benthic environment could have the reverse effect for benthic-feeding AMM such as walrus. Arctic marine mammal species currently flexible in their feeding mode and capable of utilizing both pelagic and benthic prey, e.g., bearded seals, may be less affected by the proposed alterations of the food web structure. In the extreme case of all benthic-feeding AMM species switching to pelagic feeding, if so capable, resource competition might be intensified.

Closing Remarks

Two if not all three of the suggested scenarios, although somewhat hypothetical at this point, propose higher pelagic rather than benthic prey availability to AMM in the future. Should these assumptions hold true, some AMM populations would need to adjust their feeding habits and/or location and timing of migrations for populations to maintain their current population levels. Several AMM (Table 1) are apparently capable of feeding in the pelagic and benthic realms within the same or in different geographic areas, e.g., bearded seals and gray whales. Other species, such as the walrus, may be less capable of changing to a different feeding mode and/or location and may hence be more vulnerable to changing conditions (Laidre et al. 2008). Besides changing food availability, the capability of shifting prey items and realms will ultimately depend on the trophic plasticity of AMM species with respect to their functional morphology, enzymatic and diving physiology, and foraging behavioral spectrum.

Our compilation shows that, for certain areas and species, sufficient information is now available on major prey selection patterns to produce pan-Arctic resource selection functions and preferred habitat models for AMM. Such approaches are underway for cetaceans on a worldwide scale and for selected vertebrate species on regional scales. These modeling efforts should be linked to historic data sets as currently compiled for cetaceans by the History of Marine Animal Population project and others in order to address effects of environmental change and human impact on a stronger data basis.

It should be noted that the various effects of environmental changes will occur simultaneously, which may provoke unpredicted and unprecedented developments. As pointed out previously, other changes that are not directly related to Arctic warming also influence AMM, but are not included in this paper. In our view, only holistic ecosystem monitoring approaches, combining ocean-observing systems and AMM and prey distribution and biomass surveys with modeling efforts, will provide the tools to detect, predict, and evaluate changes in the next decades.

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APPENDIX

A bibliographic list of additional sources (*Ecological Archives* A018-016-A1).