

Wells Stromberg
FISH464 AA
18 March 2019

Benthic-pelagic decoupling and walrus responses to a warming Arctic

Introduction

Global climate change is warming the Arctic. Alongside rising temperatures, sea ice is retreating, covering less of the ocean. Because the uncovered ocean is darker in color than the ice and snow, it absorbs more solar radiation, a quality known as albedo, causing a positive feedback effect to amplify the rate of melting sea ice (Arrigo et al. 2008). The loss of ice presents obvious potential problems for a variety of Arctic animals that depend on it as a habitat for birthing, nursing, and caring for young, and for hunting, but sea ice serves other important roles in the ecosystem. In addition to depriving animals of habitat, the loss of sea ice has the potential to drastically shift the dynamics of the Arctic food web, as photosynthetic algae in the sea ice is responsible for significant primary production in the Arctic ecosystem (Wassmann and Reigstad 2011). The unique ecosystem dynamics of the Arctic mean that much of the energy from the initial production bloom falls to the seafloor on continental shelves, nourishing a significant benthic community (Young et al. 2017). With limited sea ice, more primary production comes from phytoplankton, which favors a pelagic community instead (Overland and Stabeno 2004). This major transition, from a benthic-dominated to a pelagic-dominated ecosystem, has the potential to severely impact the walrus (*Odobenus rosmarus*), a highly specialized benthic predator (Fay 1982). In the face of retreating habitat and reduced prey availability, walruses have been found to change their habitat, moving north with the ice and more frequently utilizing land for resting (Beatty et al. 2016). In addition, walruses have been found to increasingly utilize other food sources to compensate for their reduced benthic food supply (Lowry and Fay 1984).

Benthic Ecosystem Ecology

The Arctic Ocean is very deep in the central basin, but nearer to the coasts of the surrounding land masses, it is primarily composed of shallower continental shelves (Kryukova et

al. 2014). These continental shelf areas support thriving benthic ecosystems, although the same is not true of the Arctic Basin, as it is too deep for benthic predators to feed. In the marginal ice zone where annual ice melts and reforms seasonally, sympagic algae trapped in brine channels in sea ice during the dark Arctic winter begin to photosynthesize in the spring when the sunlight returns and the ice melts (Piepenburg 2005). Unlike in more temperate oceans, bacterial degradation of the algae is minimal in the cold Arctic waters, and zooplankton grazing is also limited during the initial primary production bloom of the season (Young et al. 2017). Much of the energy generated by this early primary production falls to the benthos, providing the necessary nutrients to sustain the communities living on the seafloor. Significant nutrients are also brought to the benthos of the Arctic continental shelves by deep currents, especially currents from the Pacific ocean into the Bering and Chukchi seas. Highly saline, cold water near the bottom of the Chukchi sea indicate the presence of these deep currents, and low carbon:nitrogen ratios in the benthos of that region indicate deposition of carbon, representing a source of energy, from the currents (Young et al. 2017). The flow rate of these currents is faster than the rate of sinking of ice algae, further indicating the importance of their contribution of nutrients to the benthic environment (Piepenburg 2005). Although these nutrients fall to the seafloor, they do not remain there. A variety of invertebrates living in the benthos consume the falling algae, and are in turn eaten by benthic predators like walruses, bearded seals (*Erignathus barbatus*), and some seabirds. This series of interactions make the ice algae and benthos important foundations for the greater Arctic food web (Arrigo et al. 2008). The energy contributions of sympagic algae can be tracked with a 25 carbon lipid molecule referred to as IP₂₅, which is produced only by those algae, and remains detectable and unchanged through multiple trophic links of the food web. The molecule is highly prevalent in benthic organisms, indicating their dependence on the ice algae that falls to them as an energy source (Brown and Belt 2011). But the energy contributions of the algae are critical to the food web and ecosystem beyond the benthos. Even in polar bears (*Ursus maritimus*), the apex predator of the Arctic food web, fatty acid analysis from liver samples discovered significant amounts of IP₂₅ and other ice algae-associated lipids. The samples were taken in winter, long after ice algae have finished photosynthesizing for the season, revealing the continued importance of carbon from ice algae to the entire Arctic food web

throughout the year (Brown et al. 2018). The complex pathways of energy and nutrient exchange between algae, the benthos, and animals in the water column is referred to as benthic-pelagic coupling, and is a key characteristic of the Arctic ecosystem (Piepenburg 2005).

Although sea ice appears superficially to be a barren and abiotic factor in the Arctic landscape, the primary production contributions of ice-associated algae provide a critical foundation for sustaining the entire Arctic food web, from benthic invertebrates to apex predators.

Sympagic algae provides important contributions to the nutrient flow of the Arctic marine ecosystem, but it is not the only source of primary production. Phytoplankton suspended in the water column are also capable of photosynthesis, although their primary production is limited early in the season by sea ice cover. The initial bloom of primary productivity is associated with algae, but after the initial ice melt, when the algae has settled to the benthos, pelagic phytoplankton continue to photosynthesize in the water column (Wassmann and Reigstad 2011). At this later point in the season, when the water has warmed slightly, zooplankton become much more active, consuming the phytoplankton before they settle to the benthos and keeping that energy within the water column. These plankton sustain higher trophic links of the pelagic food web, which includes many species of fish, ringed seals (*Phoca hispida*), narwhals (*Monodon monoceros*) and fish-eating seabirds (Piepenburg 2005). This pathway of energy transfer is similar to that found in more temperate waters, which are less benthic-dominated than the Arctic ocean (Overland and Stabeno 2004).

The complex ecosystems of the highly productive continental shelf regions of the Arctic ocean are nourished by contributions of both sympagic algae and pelagic phytoplankton. The benthic-pelagic coupling, a key distinguishing feature of the Arctic marine ecosystem, forms the basis of the food web that connects every animal living in the Arctic.

Climate Change Effects on Benthic-Pelagic Coupling

Climate change in the Arctic is beginning to shift the delicate balance between the closely related benthic and pelagic ecosystems, which is referred to as benthic-pelagic decoupling (Piepenburg 2005). Because the Arctic food web has relatively few trophic links, the ecosystem is particularly sensitive to disruptions, meaning one change may easily disrupt multiple trophic

levels or species (Arrigo et al. 2008). Historically, Arctic waters have been benthic-dominated, while subarctic waters, like most of the world's temperate oceans, have been pelagic-dominated (Grebmeier et al. 2006). However, the line dividing the two types of ecosystem has been moving north as seas warm due to global climate change. In the Bering sea, the total biomass of the pelagic-feeding walleye pollock (*Gadus chalcogrammus*) has increased more than 400% since 1978, while the abundance of benthic-feeding fish that previously dominated the region has suffered over the same period, clearly indicating the encroachment of pelagic ecosystems into the Arctic (Overland and Stabeno 2004). Fifteen years of time series data on oxygen uptake by the seafloor sediment, a measurable indicator of carbon supply to the seafloor and general benthic activity, show a decrease from 40 mmol oxygen taken up per square meter of seafloor per day to 15 mmol (Grebmeier et al. 2006). Clearly, the advancing pelagic ecosystem does not merely represent an overall increase in productivity of the Arctic marine environment, but instead a shift of energy that was previously utilized by the now-declining benthic ecosystem.

The reasons for benthic-pelagic decoupling are readily apparent based on the dynamics that make the Arctic a benthic-dominated region in the first place. This condition depends on specific timing of algal and phytoplankton blooms to sustain both benthic and pelagic food webs, as described above. As the oceans warm, ice melts earlier in the year, but the photoperiod is constant. The necessary focused pulse of algal primary productivity is impossible when the ice melts and releases the algae before the sun has reached the Arctic in sufficient intensity to sustain photosynthesis, or when the ice does not extend to an area at all (Wassmann and Reigstad 2011). This timing mismatch severely limits the food supply settling to the benthos. The warmer waters also encourage earlier zooplankton grazing, so more of the algae is consumed in the water column before it can reach the benthos (Piepenburg 2005). The combination of reduced overall algal primary production and increased grazing severely limits the carbon deposited into the benthos from sympagic sources, although the limited sedimentation, combined with fluvial transport of nutrients from Pacific waters, maintain some benthic activity (Piepenburg 2005). Due to the seasonal timing of melts, the marginal ice zone will continue to be benthic-dominated as it moves farther north (Wassmann and Reigstad 2011). However, when the marginal ice zone

retreats past the edge of the continental shelf, the benthos will be inaccessible to benthic feeders, as the Arctic Basin is too deep for benthic foraging.

While the benthic ecosystem suffers, the developing dynamics favor the pelagic ecosystem. With earlier ice melt and less overall ice coverage, more of the available sunlight is delivered to the open water, allowing phytoplankton to photosynthesize for a longer period. This may lead to an overall increase in total primary production in the Bering and Chukchi Seas, although many other changing factors complicate projections (Wassmann and Reigstad 2011). Production in the Arctic is limited by availability of sunlight, but as overall production increases, nutrients will become a limiting factor for production (Wassmann and Reigstad 2011). The Arctic ecosystem has been characterized by seasonal pulses of primary production, but as more primary production comes from phytoplankton rather than sympagic algae, the productive window will widen, making the food supply more constant for a longer period (Brown and Belt 2011; Wassmann and Reigstad 2011). The repercussions of this specific shift on the ecosystem are currently unknown. Increased water temperature is correlated with higher rates of respiration, requiring more energy for consumers, but while primary production may increase, there is no direct relationship between temperature and production (Wassmann and Reigstad 2011). This means that as temperatures continue to increase, respiration and consumption will increase as well, while the nutrients and sunlight that drive primary production will be unaffected by rising temperature. Changing ocean currents and stratification will also affect primary production. Increasing sediment runoff will increase the availability of some important nutrients, but will simultaneously decrease the availability of sunlight due to the increased turbidity. Increased ocean stratification will also decrease overall primary production (Wassmann and Reigstad 2011). These complex interactions will affect different areas of the Arctic differently, making it difficult to predict specific effects across the region, although the trend toward a pelagic-dominated ecosystem is consistently moving north.

Pacific Walrus (*Odobenus rosmarus divergens*)

The walrus is the largest Arctic resident pinniped, with males up to 3 meters in length and weighing 1200 kg, and females slightly smaller at over 2.5 meters length and 800 kg weight (Fay

1982). The species is circumpolar in distribution, but is divided into three subspecies: the Atlantic walrus (*Odobenus rosmarus rosmarus*) is found around Greenland, Svalbard, and the Canadian Archipelago; the Laptev walrus (*Odobenus rosmarus laptevi*) is found in the Laptev Sea; and the Pacific walrus (*Odobenus rosmarus divergens*) is found in the Bering and Chukchi Seas in the Pacific Arctic. This paper will focus on the Pacific walrus, which is morphologically distinguished from the other subspecies by its larger body and tusks (Fay 1982). Pacific walruses tend to follow the seasonal progression and retreat of the sea ice, spending winters in the Bering Sea. Females and young follow the receding sea ice through the Bering Strait, spending summers in the northern Chukchi Sea, while mature males often stay in the Bering Sea, hauling out on land (Fay 1982). Walrus require sea ice as a platform for calving, which occurs in May, and nursing the young calves in the subsequent months (Ray et al. 2010). They also use the sea ice as a platform for resting while foraging. When sea ice is available, walruses typically occupy thick, medium-sized floes that can support their weight, and are near leads or polynyas for access to their foraging grounds (Ray et al. 2010).

As benthic feeders, walruses require access to the seafloor. They optimally forage at depths of 50-60 meters on continental shelves, and frequently congregate in areas with high organic carbon input, as they are densest in benthic prey (Kryukova et al. 2014; Moore and Kuletz 2018). Walrus consume a variety of benthic invertebrates, which they detect in the sediment of the seafloor with their sensitive vibrissae. Soft prey are frequently sucked down whole, without chewing, while mollusks are sucked out of their shells and swallowed (Fay 1982). Bomb calorimetry measurements of dried specimens determined that the bivalves that are preferred by walrus are very calorically dense, making them an effective and efficient food source for such large animals (Young et al. 2017). While Pacific walruses overlap in range with bearded seals, another benthic-feeding pinniped, fatty acid analysis of Pacific walrus and bearded seal blubber samples indicates that they have distinct diets: different species of benthic bivalves produce novel fatty acids that are stored in the blubber, so can be traced up through the food web, and the most prevalent molecules in Pacific walruses indicate that they primarily feed on different species than bearded seals do in the same range (Budge et al. 2007). This extreme

specialization in geographic range, ice requirements, body morphology and diet leave the Pacific walrus particularly vulnerable to the effects of climate change.

Climate Change Effects on Pacific Walrus Distribution

Like many Arctic marine animals, the Pacific walrus depends on sea ice as a platform, and for its role in the food web, leaving the species susceptible to problems from climate change-associated ice loss. However, specific ice use factors make them particularly vulnerable compared to other species. Their large size means that Pacific walruses require large, thick ice floes to support their weight, and their propensity to congregate in large herds necessitates very large floes (Ray et al. 2010). These requirements mean that the time that ice is unusable for walruses is longer than the ice free period; the ice becomes too thin to support them before it disappears fully in the summer, and is initially too thin when it first appears in the winter (Kryukova et al. 2014). In addition, Pacific walruses require ice floes with access to the open water for feeding. They do not make breathing holes, but instead require leads or polynyas nearby, although their size means they can break through ice up to 20cm thick when necessary (Ray et al. 2010). Furthermore, walrus must feed on continental shelves, no deeper than 100 meters (Rausch et al. 2007). Ice that retreats past the edge of the continental shelf is no longer useful, as the walruses cannot feed in the benthos of the Arctic Basin. A statistical analysis of Pacific walrus distribution found that their preferred foraging sites correlated most strongly with available nearby ice, that the amount or quality of prey was the next strongest correlate, and distance to land was less important when ice was available (Beatty et al. 2016). The indication that walruses prefer proximity to usable ice over higher quality or more abundant prey emphasizes the importance of sea ice as a platform for foraging walruses. When necessary, walruses can haul out on land, but this presents its own challenges (Beatty et al. 2016). Land is available to haul out throughout the year, but is frequently farther from high-quality foraging areas, and while sea ice is mobile, allowing walruses to passively travel between foraging areas, land is not, so large groups of walruses rapidly deplete food supplies near the places they congregate on land (Kryukova et al. 2014). Regardless of the additional challenges, the

prevalence of land haul-outs has increased in recent years as ice has retreated, especially among the males that remain in the Bering sea during the summer (Beatty et al. 2016).

The range of walruses, particularly female and young walruses, has extended north during the summers as the sea ice retreats. Benthic-pelagic decoupling is apparent in the northern Bering Sea and the southern Chukchi Sea, which has decreased the availability of benthic prey in the region (Young et al. 2017). There is a direct correlation between increasing temperature of bottom water and decreasing abundance, biomass, and size of bivalves in the northern Bering sea, the preferred food source of Pacific walruses (Goethel et al. 2018). According to research conducted between 1998 and 2014, the effects of climate change have not significantly impacted the availability or quality of bivalves in the northern Chukchi sea as they have in communities farther south, so Pacific walruses can still follow the retreating ice and find areas to feed, but this strategy will only be effective until the ice retreats past the edge of the continental shelf or benthic-pelagic decoupling affects the northernmost foraging areas (Goethel et al. 2018). There is some data correlating abandoned pups with warm water and northward range extension (Grebmeier et al. 2006). Although inconclusive, this presents another potential area of risk to Pacific walrus populations.

Currently, Pacific walrus populations have been able to compensate for reduced sea ice extent by hauling out on land more frequently and by following the retreating ice north, but neither of these responses is a permanent solution, as depletion of benthic prey near land and continued retreat of ice past the continental shelf edge will present new problems in the coming years.

Climate Change Effects on Pacific Walrus Diet

Walruses are highly specialized predators, using their tusks, vibrissae, and the powerful suction of their mouths and throats to efficiently eat bivalves and other benthic invertebrates (Fay 1982). Benthic-pelagic decoupling presents a significant threat, as it diminishes the abundance and quality of available benthic prey (Young et al. 2017). In response to the changing ecosystem, walruses have been increasingly exploiting alternative food sources (Rausch et al. 2007). Local Inuit hunters had long reported to researchers that they sometimes found seal skins

or blubber in the stomachs of walrus they hunted, and that it happened more frequently in years when food was scarce (Fay 1960). After hunters reported that this phenomenon was consistently increasing in frequency, Lowry and Fay investigated the stomach contents of Pacific walrus hunted in the Bering and Chukchi Seas. They found seal remains in five of 364 stomachs they examined in the Bering Sea, and in five of forty-four stomachs they examined in the Chukchi Sea. The Bering Sea walrus had eaten ringed seals, bearded seals, and spotted seals (*Phoca largha*), and the Chukchi Sea walrus had eaten only ringed seals, although bearded seals and ribbon seals (*Phoca fasciata*) were also present in the region. These data showed significantly higher proportions of seal predation than had been found in previous years, beginning in 1975 and peaking in 1979, which was a year with abnormally low ice coverage (1984). As well as limiting availability of preferred benthic prey, the receding ice compressed the ranges of all Arctic ice seals in the summer of 1979, greatly increasing overlap and therefore interaction between Pacific walrus and other pinnipeds, and apparently resulting in increased predation. In addition, Lowry and Fay reported actually seeing walrus with seal remains in 1978 and 1979, for the first time in decades of walrus observations (1984). The seal remains found in walrus stomachs, and the seal remains observed around walrus, had thick blubber, indicating that the seals were healthy at the time of death. This finding suggests that the walrus acted as predators, killing the seals to eat, rather than scavenging remains of seals that died otherwise, as their body conditions would likely be worse (Lowry and Fay 1984). Other researchers anecdotally report seeing a walrus near Svalbard eating common eider (*Somateria mollissima*) ducklings, and unsuccessfully attempting to eat auks (*Alcidae*) (Gjertz 1990). Although the significance of seabirds as a food source is unknown, the combination of local ecological knowledge and stomach contents analysis strongly indicates that walrus are increasingly turning to seals as a food source to supplement dwindling benthic prey.

Changing walrus diets can also be tracked through time based on parasitic worm infection, or trichinellosis, in humans (Rausch et al. 2007). These worms are known to accumulate in predators like polar bears, but polar bear meat is traditionally cooked before human consumption, killing the parasites (Rausch et al. 2007). The first reported outbreak of trichinellosis attributed to walrus meat was in 1949; because the infection in animals is

associated with predation of large prey, not benthic invertebrates, it is likely that the infected walrus had eaten something abnormal (Fay 1960). Since 1982, nine of thirteen trichinellosis outbreaks in the Canadian Arctic were determined to come from walrus meat, which is not traditionally cooked like bear meat is (Rausch et al. 2007). The advancing prevalence of a disease associated with mammal predation in walruses provides further evidence that walruses are increasingly depending on seals as a source of food.

The benthic-pelagic decoupling taking place in northern Bering Sea and southern Chukchi Sea ecosystems presents a significant risk to the Pacific walrus as a highly specialized benthic-feeding species. While range shifts have provided temporary relief from the effects, dietary changes appear to provide an alternative solution, as walruses are increasingly taking seals as prey. While the long-term repercussions of the dietary shift are unknown, it appears to provide a new source of food and a solution to the loss of benthic food supplies.

Obligate Carnivore “Rogue” Walruses

Most walruses are benthic feeders, despite a notable increase in predation on seals. However, Inuit hunters in the Bering Strait region have reported another type of walruses, which they call rogues. These individuals are quite rare, comprising only three of the more than 3000 walruses hunted between 1952 and 1959 by a group in Alaska (Fay 1960). The rogues are solitary bulls and obligate carnivores, subsisting primarily or exclusively on vertebrate prey rather than the invertebrates more commonly eaten by walruses. Walruses that occasionally eat seals are visually identical to other walruses, distinguished only by their diet, but rogue walruses are morphologically distinct: they are lean, with exceptionally developed shoulders and flippers, and are stained an amber color by oxidized blubber on their tusks, heads, and chests. Their tusks are longer and sharper than normal walrus tusks, with different patterns of wear because they are not constantly ground down against the seafloor (Fay 1960). Traditional knowledge holds that these rogue walruses are pups that were abandoned before they were taught how to forage benthic prey normally, and survived by finding another way to hunt and feed themselves (Fay 1960). To corroborate these reports, the same Inuit avoid eating the liver whenever they kill a suspected rogue walrus, as it is said to cause a sickness comprised of headaches, nausea, and skin

peeling, the same symptoms associated with eating polar bear liver (Fay 1960). The sickness from polar bear livers is known to be caused by the toxic vitamin A concentration found in the livers; concentrations of 13,000-18,000 I.U. per gram of liver are common in polar bears.

Benthic invertebrates contain minimal vitamin A, and a typical walrus liver contains less than 500 I.U. per gram, which is consistent with their standard diet and well below toxic levels. In contrast, fresh seal blubber can contain forty to fifty I.U. of vitamin A per gram, which means that one seal could contain as many as one million I.U. in its blubber (Fay 1960). The similarity of illness caused by consumption of rogue walrus and polar bear livers strongly suggests that, as indicated by reports from hunters, a small minority of walruses subsist primarily by hunting and eating seals.

The actual abundance and impact of rogue walruses is unknown, but the limited reporting on the topic indicates that they are very rare. These special individuals, however, do indicate that walruses can survive on a diet of only seals, supporting the viability of the same dietary shift seen in the more common opportunistically carnivorous walruses.

The Future of the Pacific Walrus

Continued global climate change poses an obvious threat to the Pacific walrus. Sea ice loss is removing the very specific habitat required for walruses to mate, birth and nurse calves, and forage for their benthic prey. Sea ice loss is also limiting the contributions of sympagic algae primary production, a critical foundation of the benthic ecosystem, which, coupled with increasing water temperatures, is decreasing the abundance and quality of walrus prey organisms. In response, walruses have increasingly depended on land for hauling out, or have followed the retreating ice edge as it recedes north. Currently, both of these solutions are effective, but are not permanent solutions to the threats facing the Pacific walrus. Following the retreating ice is effective, because benthic-pelagic decoupling is less severe in the colder northern reaches of the Chukchi Sea, but this is only a temporary solution. Sea ice will continue to recede past the edge of the continental shelf, at which point the walruses will no longer be able to forage from the ice, and may be stranded far from the nearest land. Hauling out on land provides a platform when suitable ice floes are unavailable, but as benthic-pelagic decoupling

intensifies and large walrus herds continue to exploit the same grazing areas near land, the benthic prey they require will be depleted, at which point the herd will be stranded far from another source of food. This strategy has the potential to be effective over a longer period, but will likely only sustain a small population of walruses.

More encouraging for the future of the walrus species is the evidence of a dietary shift. The ability to utilize a new source of food may save the walrus as the supply of benthic invertebrates continues to dwindle, although the behavior may have negative repercussions for the seals that constitute their new prey. While predation of seals appears to be relatively rare now, it is likely to spread rapidly as the lack of benthic food becomes a more dire problem. As benthic grazing gradually becomes nonviable as a means of sustenance, the walruses that eat seals will be much more likely to survive and successfully reproduce, and will teach their offspring to do the same, increasing the frequency of the behavior. It is plausible that, for walruses to survive in a warming Arctic, the species will need to shift from exclusively benthic grazing to an opportunistic mix of benthic grazing and seal hunting, utilizing whatever food is available to them.

Walruses are undoubtedly at risk from multiple factors associated with global climate change, and the combination of very specific ice habitats and specialized morphology to exploit an energy source that is now diminishing makes them appear particularly vulnerable. However, their seeming ability to adapt to changing conditions, both in range and in diet, provide some hope for their survival in the warming and changing Arctic.

References

- Arrigo KR, van Dijken G, Pabi S (2008) Impact of a shrinking Arctic ice cover on marine primary production. *Geophys Res Lett* 35:L19603
- Beatty WS, Jay CV, Fischbach AS, Grebmeier JM, Taylor RL, Blanchard AL, Jewett SC (2016) Space use of a dominant Arctic vertebrate: effects of prey, sea ice, and land on Pacific walrus resource selection. *Biol Conserv* 203:25-32
- Brown TA, Belt ST (2012) Identification of the sea ice diatom biomarker IP25 in Arctic benthic macrofauna: direct evidence for a sea ice diatom diet in Arctic heterotrophs. *Polar Biol* 35:131-137
- Brown TA, Galicia MP, Thiemann GW, Belt ST, Yurkowski DJ, Dyck MG (2018) High contributions of sea ice derived carbon in polar bear (*Ursis maritimus*) tissue. *PLoS ONE* 13(1):e0191631
- Budge SM, Springer AM, Iverson SJ, Sheffield G (2007) Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. *Mar Ecol Prog Ser* 336:305-309
- Fay FH (1960) Carnivorous walrus and some Arctic zoonoses. *Arctic* 13(2):111-122
- Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. United States Department of the Interior Fish and Wildlife Service, Washington, D.C.
- Gjertz I (1990) Walrus predation of seabirds. *Polar Rec* 26(159):317
- Goethel CL, Grebmeier JM, Cooper LW (2018) Changes in abundance and biomass of the bivalve *Macoma calcareo* in the northern Bering Sea and the southeastern Chukchi Sea from 1998 to 2014, tracked through dynamic factor analysis models. *Deep-Sea Res Pt II* doi:10.1016/j.dsr2.2018.10.007
- Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. *Science* 311:1461-1463
- Kryukova NV, Kochnev AA, Pereverzev AA (2014) The influence of ice conditions on terrestrial haulouts of the Pacific walrus *Odobenus rosmarus divergens* Illiger, 1815 in the Gulf of Anadyr, Bering Sea. *Russ J Mar Biol* 40(1):30-35
- Lowry LF, Fay FH (1984) Seal eating by walruses in the Bering and Chukchi Seas. *Polar Biol* 3:11-18.

Moore SE, Kuletz KJ (2018) Marine birds and mammals as ecosystem sentinels in and near disturbed biological observatory regions: an abbreviated review of published accounts and recommendations for integration to ocean observatories. *Deep-Sea Res Pt II* doi:10.1016/j.dsr2.2018.09.004

Overland JE, Stabeno PJ (2004) Is the climate of the Bering Sea warming and affecting the ecosystem?. *EOS T Am Geophys Un* 85(33):309-316

Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. *Polar Biol* 28:733-755

Rausch RL, George JC, Brower HK (2007) Effect of climatic warming on the Pacific walrus, and potential modification of its helminth fauna. *J Parasitol* 93(5):1247-1251

Ray GC, Overland JE, Hufford GL (2010) Seascape as an organizing principle for evaluating walrus and seal sea-ice habitat in Beringia. *Geophys Res Lett* 37:L20504

Wassman P, Reigstad M (2011) Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography* 24(3):220-231

Young JK, Black BA, Clarke JT, Schonberg SV, Dunton KH (2017) Abundance, biomass and caloric content of Chukchi Sea bivalves and association with Pacific walrus (*Odobenus rosmarus divergens*) relative density and distribution in the northeastern Chukchi Sea. *Deep-Sea Res Pt II* 144:125-141