



Marine birds and mammals as ecosystem sentinels in and near Distributed Biological Observatory regions: An abbreviated review of published accounts and recommendations for integration to ocean observatories

Sue E. Moore^{a,*}, Kathy J. Kuletz^b

^a NOAA/Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, USA

^b US Fish and Wildlife Service, 1011 E. Tudor Rd., Anchorage, AK 99503, USA

ABSTRACT

Marine birds and mammals can act as sentinels to shifts in ocean ecosystems, due to their (i) reliance on finding aggregated prey for efficient foraging, (ii) need to respond to biophysical signals in support of successful seasonal migrations, and (iii) capacity to reflect changes in marine food webs. Here we present an abbreviated review of recent published accounts of marine bird and mammal responses to biophysical features of the ocean ecosystem in and near sampling regions of the Distributed Biological Observatory (DBO). The review is meant to provide both *context* for seabird surveys and marine mammal watches conducted in conjunction with DBO sampling and *support* for the inclusion of marine bird and mammal research, either by direct sampling or collaboration, in the protocols of other ocean observatories. The review is framed by the ocean processes imbedded in the Arctic Marine Pulses conceptual model, with the overarching goal to promote the routine integration of data on marine birds and mammals during the development of marine ecosystem models for Arctic regions.

1. Introduction

Marine birds and mammals are Upper Trophic Level (UTL) species (\geq secondary consumers) that reflect ecosystem dynamics by changes in habitat use and body condition. These species can act as sentinels to shifts in ocean ecosystems, due to their (i) reliance on finding aggregated prey for efficient foraging, (ii) need to respond to biophysical signals in support of successful seasonal migrations, and (iii) capacity to reflect changes to marine food webs and exposure to contaminants via their state of health (Moore, 2018; Moore and Gulland, 2014; Piatt et al., 2007). Tracking both ecological (extrinsic) and physiological (intrinsic) responses in UTL species can reveal fundamental changes in marine ecosystems (Fig. 1). This capacity has been described for UTL species in both northern and southern hemisphere ocean ecosystems (e.g. Sydeman et al., 2015, and references therein). In the Pacific Arctic, seabird distribution and relative abundance has been linked to ocean conditions from the Bering Sea through the Chukchi and Beaufort seas (Santora et al., 2018; Hunt et al., 2014; Gall et al., 2013; Piatt and Springer, 2003). Similarly, examples of marine mammal responses to ocean variability extend from the Bering to the Beaufort seas (Moore and Stabenho, 2015; Moore et al., 2014, and references therein).

The Distributed Biological Observatory (DBO) provides a framework to track and assess changes in the Pacific Arctic marine ecosystem across both latitudinal and longitudinal gradients (Moore and Grebmeier, 2018). Four of the original five sampling regions were

focused on 'hotspots' of benthic biomass and biodiversity on the continental shelf, with the fifth region corresponding to the dynamic environment of Barrow Canyon (Grebmeier et al., 2010). Subsequently, three regions were added to track ecosystem changes in the Beaufort Sea; two along the outer continental shelf and slope of the Alaskan Beaufort and a third located northeast of Cape Bathurst in the Canadian Beaufort Sea. These regions too were focused on areas with previous reports of relatively high benthic, epi-benthic and pelagic biomass and biodiversity (Ravelo et al., 2015; Moore and Grebmeier, 2018).

The inclusion of marine bird and mammal surveys in the standard DBO sampling protocol is meant to insure a 'top-down' view of changes in the Pacific Arctic marine ecosystem (e.g. Kuletz et al., 2018). Resulting data provide the means to directly align UTL data with standard ocean measurements in space and time. However, because the spatial and temporal scales to which UTL species respond are often dissimilar from the scales of oceanographic analysis, it is useful to review results from focused studies on these species. UTL species are generally long-lived, range broadly across ocean regions, and are highly seasonal in occurrence in the Arctic. Thus, a review of long-term datasets from a variety of research efforts (e.g. visual and acoustic surveys, satellite telemetry tracking, and body condition/diet studies) conducted in and near DBO regions can be informative. For example, visual surveys of seabirds from 1975 to 2015 in the Bering Sea showed shifts in abundance and distribution of seabirds with respect to early vs. late ice retreat (Renner et al., 2016; Hunt et al., 2018), and increased abundance

* Corresponding author.

E-mail address: sue.moore@noaa.gov (S.E. Moore).

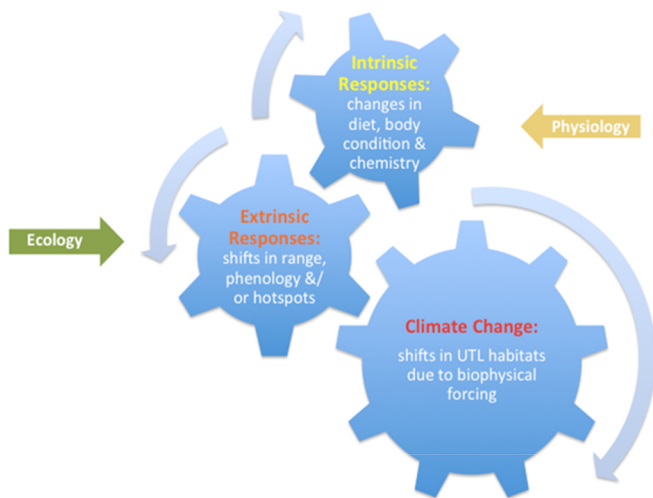


Fig. 1. Marine birds and mammals are upper trophic level (UTL) species that reflect ecosystem alterations by changes in their ecology (extrinsic) and physiology (intrinsic). Tracking both extrinsic and intrinsic responses in UTL species can reveal alterations in marine ecosystems (Moore and Stabeno, 2015; reproduced with permission).

and northerly shifts in distribution for three *Phoebastria* albatross species (Kuletz et al., 2014). Similarly, in the Beringia region, over a four-year period but with greater precision, satellite-tagged black guillemots (*Cepphus grylle*) showed close association with the marginal ice zone, with tagged birds moving in concert with seasonal ice expansion and retreat (Divoky et al., 2016).

Here we present an abbreviated review of recent published accounts of marine bird and mammal responses to biophysical variability of the ocean ecosystem in and near sampling regions of the DBO. This review is meant to provide both *context* for UTL surveys conducted in conjunction with DBO sampling and *support* for the inclusion of marine bird and mammal research, either by direct sampling or collaboration, in the protocols of other ocean observatories. The review is framed by the ocean processes imbedded in the Arctic Marine Pulses (AMP) conceptual model (Moore et al., 2016), with the overarching goal to promote the routine integration of data on marine birds and mammals during the development of models for Arctic marine ecosystems. We conclude with an overview of how the integration of marine bird and mammal data can link the DBO and AMP models, and thereby contribute to the Global Ocean Observing enterprise (Miloslavich et al., 2018).

2. Examples of UTL species' responses to ecological shifts in and near DBO regions

The DBO extends from the northern Bering to the Beaufort Sea (Fig. 2A), with sampling regions focused on continental shelf habitats (DBO regions 1–4) and continental slope, basin and canyon habitats (DBO regions 5–8; Fig. 2B). The seasonal advance and retreat of sea ice is fundamental to biophysical processes that shape the ecology of the Pacific Arctic (Grebmeier et al., 2010; Moore and Stabeno, 2015). Further, the seasonal cycle of sea ice affects ocean processes of pelagic-benthic coupling, advection and upwelling, all of which are key components of the conceptual AMP model (Moore et al., 2016). Here, we provide examples of published accounts of UTL species' responses to ecological shifts in the context of these ocean processes in and near each DBO region (Table 1). Through these examples, we aim to strengthen the linkages between research on UTL species and ocean ecosystem modeling.

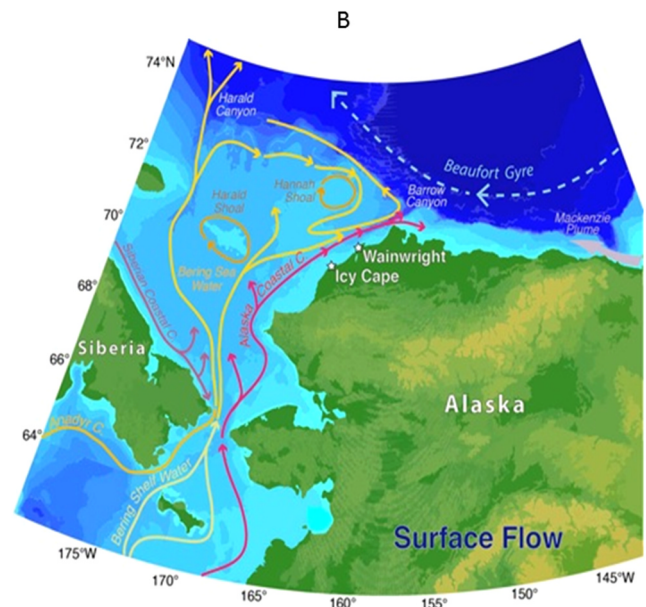
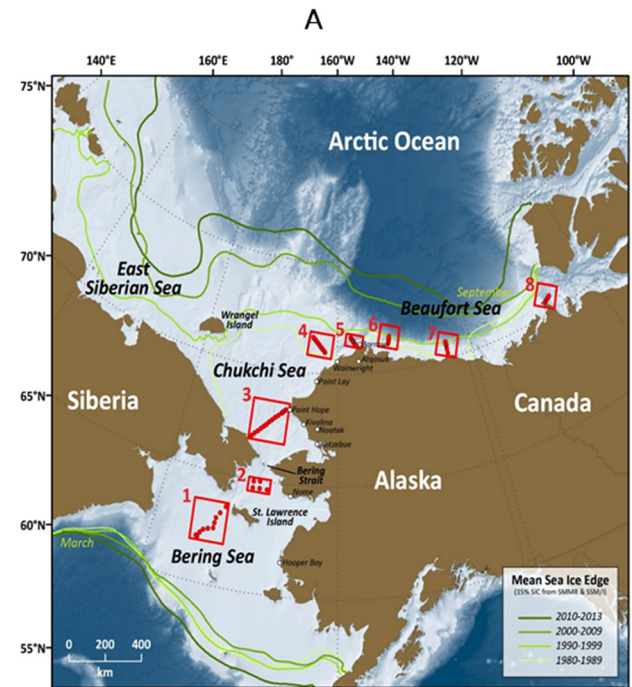


Fig. 2. The Distributed Biological Observatory (DBO) consists of eight sampling regions focused on 'hotspots' of biological productivity and biodiversity, extending from the northern Bering Sea to the Beaufort Sea (A: Moore and Grebmeier, 2018; reproduced with permission); and schematic of bathymetric features and surface currents mentioned in text (B: Wood et al., 2015; reproduced with permission).

2.1. Pelagic-benthic coupling in and near DBO regions 1–5

Pelagic-benthic coupling in the Pacific Arctic was first described in the early 1990s (Grebmeier and Barry, 1991), with the resultant 30-year record of enhanced benthic biomass and productivity providing the basis for siting DBO regions 1–4 (Grebmeier et al., 2010, 2015a, 2015b). This process is essential to trophic pathways that result in dense patches of macrofaunal prey sought by diving sea ducks (e.g. eiders), walrus (*Odobenus rosmarus*), and gray whales (*Eschrichtius robustus*), among other species. In and near DBO region 1, both eiders and

Table 1

Examples of upper trophic level (UTL) species' responses to biophysical ocean processes in and near DBO regions. (P-B = pelagic benthic).

DBO Region	Process	UTL species	Response	Reference
1	P-B Coupling	Eiders	Habitat selection	(Lovvorn et al., 2014)
		Walrus	Habitat selection	(Jay et al., 2014)
2	P-B Coupling	Gray whales	Distribution shift	(Moore et al., 2003; Coyle et al., 2007)
	Advection	Least Auklets	Forage range, energetics	(Obst et al., 1995)
		Least & Crested Auklets	Diet, productivity	(Gall et al., 2006)
				(Sheffield-Guy et al., 2009)
3	P-B Coupling	Gray whales	Distribution shift	(Moore et al., 2003)
	Advection	Gray whales	Occurrence patterns	(Bluhm et al., 2007; Kuletz et al., 2015)
		Humpback, Fin Minke whales	Occurrence patterns	(Clarke et al., 2013; Moore, 2016)
		Auklets, Shearwaters	Occurrence patterns	(Kuletz et al., 2015)
4	P-B Coupling	Gray whales	Habitat selection	(Brower et al., 2017)
		Walrus	Habitat selection	(Jay et al., 2012; Beatty et al., 2016; Young et al., 2017)
	Advection	Bowheads	Movement patterns	(Citta et al., 2017)
		Seabirds	Occurrence patterns	(Gall et al., 2013, 2017)
				(Kuletz et al., 2015; 2018)
5	P-B Coupling	Gray whales	Habitat selection	(Brower et al., 2017)
	Advection	Belugas	Occurrence patterns	(Stafford et al., 2017)
		Bowheads	Movement patterns	(Citta et al., 2015, 2017)
		Seabirds	Occurrence patterns	(Kuletz et al., 2015; 2018)
Near 6	Advection & Upwelling	Bowheads	Feeding patterns: 'Krill trap'	(Okkonen, Ashjian et al., 2011, 2010)
Near 8	Advection & Upwelling	Bowheads	Feeding patterns	(Walkusz et al., 2014)
Near 1–6	Ice edge effects	Black guillemot	Movement patterns	(Divoky et al., 2016)
	Advection	Short-tailed shearwater	Movement patterns	(Nishizawa et al., 2017)

walrus rely on dense assemblages of bivalves that correspond to areas with high organic carbon input (Grebmeier et al., 2015a, 2015b). In winter and spring, spectacled eiders (*Somateria fischeri*) congregate south of the open polynya in leads within the moving ice pack of DBO region 1, which provides critical access to benthic prey for overwintering and preparation for spring migration to breeding grounds (Petersen et al., 1999; Lovvorn et al., 2015). Both eiders and walrus feed on bivalves from the Nuculidae and Tellinidae family, with tellinid caloric biomass the strongest link to habitat selection (Lovvorn et al., 2014; Jay et al., 2014). These authors suggest that a decline in bivalves in the region, associated with sea-ice loss and the associated coupling of organic carbon from ice algae and the ice-edge phytoplankton bloom to the sea floor, could result in a loss of preferred bivalve biomass. This change in prey availability will trigger a shift in seasonal distribution, or change in diet, for species like eiders and walrus that rely on bivalves to maintain good body condition.

In and near DBO region 2 between the mid-1980s and 2002, reduced extent of gray whale distribution and decline in relative abundance coincided with a drop in abundance of ampeliscid amphipods, their primary prey (Moore et al., 2003; Coyle et al., 2007). Gray whales appeared to shift north to DBO region 3, where benthic amphipods remained abundant from the 1980s through 2012 (Grebmeier et al., 2015a; Fig. 2). Similarly, gray whale distribution is linked to benthic amphipod abundance near DBO regions 4 and 5 in the northeastern Chukchi Sea, primarily within 70 km of shore (Brower et al., 2017). Walrus also commonly occupy habitats in both DBO regions 3 and DBO 4 (Jay et al., 2012; Fig. 4), where benthic prey (comprised of bivalves, polychaetes, amphipods and tunicates) biomass was especially high (Beatty et al., 2016; Young et al., 2017).

In fall, there are also marine bird benthivores (primarily common eiders [*Somateria mollissima*] and king eiders [*S. spectabilis*] and long-tailed ducks [*Clangula hyemalis*]) in southern Hanna Shoal (DBO region 4), though their numbers relative to other marine birds is low in the offshore waters (Kuletz et al., 2015; and this volume). During summer and fall, the presence of sea ducks in the offshore DBO regions may be more representative of migratory routes between critical nearshore foraging habitats (Grebmeier et al., 2015a; Opper et al., 2009). In addition, red phalaropes (*Phalaropus fulicaria*), the most 'oceanic' of shorebirds when not breeding, are often associated with the plumes of feeding gray whales, taking advantage of benthic amphipods brought to the surface (Grebmeier and Harrison, 1992).

Phalaropes are most abundant in DBO region 4 during summer and found farther south near DBO region 3 in fall (Kuletz et al., 2015), indicative of intensive foraging in the Chukchi before migration to Pacific regions (Taylor et al., 2011).

2.2. Advection in and near DBO regions 1–5

Advection (transport of nutrients and prey by ocean currents) is an oceanographic process that has been described as key to the ecology and pelagic distribution of seabirds in the northern Bering and Chukchi seas (Piatt and Springer, 2003). In the Beaufort Sea, the importance of advection to prey delivery for bowhead whales (*Balaena mysticetus*) has been the primary focus of study (Berline et al., 2008; Ashjian et al., 2010). In and near DBO region 3, the importance of advection to zooplankton prey delivery is supported by observations of feeding gray whales that were co-located with high euphausiid biomass associated with an oceanographic front (Bluhm et al., 2007). The reliance of baleen whales on this prey stream was inferred for the now-common seasonal occurrence of humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*) and minke (*Balaenoptera acutorostrata*) whales in and near DBO region 3 (Clarke et al., 2013; Moore, 2016).

In offshore seabird communities, an ecological shift from predominately piscivorous to planktivorous seabirds in the northeastern Chukchi Sea over the last four decades coincides with an increase in the availability of large zooplankton associated with earlier sea ice retreat (Gall et al., 2017), coupled with increased advective inflow of Bering Sea Water through Bering Strait (Woodgate et al., 2015, 2018). Similarly, in the Chukchi and Beaufort seas, plankton and krill-feeding bowhead whales have increased, whereas piscivorous seals, beluga, and black guillemot chicks show evidence of reduced body condition, growth, or productivity (Harwood et al., 2015). In and near DBO region 4, the advective processes that transport large zooplankton associated with Bering Sea Water influenced the distribution and abundance of marine birds, especially planktivorous species (Gall et al., 2013).

Both surface feeding (e.g. kittiwakes, gulls) and subsurface feeding (e.g. murre, auklets, puffins) seabirds nest in some of the largest breeding aggregations in the world in the northern Bering and southern Chukchi seas, at least partly due to proximity to areas of advection and upwelling (Piatt and Springer, 2003). During the breeding season, these birds are tied to colony sites while sharing incubation and chick-feeding duties, thus their distributions tend to create a 'halo' of higher bird

density around the colony. Foraging ranges of auklets can vary greatly and the least auklets (*Aethia pusilla*) nesting on St. Lawrence Island travel farther to obtain food than do birds at other Bering Sea colonies (Obst et al., 1995). The St. Lawrence Island auklets apparently benefit from persistent oceanographic features within DBO region 2 that advect and concentrate typically high energy *Neocalanus* copepod and euphausiid prey species (Obst et al., 1995). However, the mix of prey species available in DBO region 2 can vary considerably under different spring ice and oceanographic conditions, and chick growth and fledging success for least and crested auklets (*A. cristatella*) proved sensitive to changes towards smaller prey species with low energetic value (Gall et al., 2006; Sheffield-Guy et al., 2009).

After the chick-rearing season, auklets, particularly the planktivorous crested auklets, are found in high densities hundreds of km north of colony nesting sites, with ‘hot spots’ occurring in the Hanna Shoal region (DBO region 4), nearly 600 km from the nearest colonies (Kuletz et al., 2015). Surface feeding birds (e.g. kittiwakes, gulls) also had ‘hotspots’ along the Chukchi shelf edge near Barrow Canyon (Kuletz et al., 2015; and this volume) Short-tailed shearwaters (*Ardenna tenuirostris*), which breed in the southern hemisphere and come to the Pacific Arctic to feed in the northern summer and fall, are highly concentrated in areas with high or episodic periods of advection and upwelling, such as occur around Barrow Canyon near DBO regions 5 and 6 in the western Beaufort Sea (Kuletz et al., 2015; Nishizawa et al., 2017). The advection of zooplankton in Bering Sea Water is also thought key to contrasting patterns of bowhead whale autumn movements in and near DBO region 4 (Citta et al., 2017). Whales that lingered in the central NE Chukchi Sea (presumably to feed) were associated with a strong Bering Sea Water signal, and especially with strong gradients in bottom salinity, where krill are thought to reside.

In and near DBO region 5, advection seemingly plays a role in prey delivery to both beluga (*Delphinapterus leucas*) and bowhead whales. Two populations of beluga consistently occupy Barrow Canyon and western Beaufort Sea slope habitat, where hydrographic evidence suggests advection plays a role in maintaining high abundances of Arctic cod, their primary prey (Stafford et al., 2017). The canyon, western Beaufort slope, and outer shelf are also core-use habitats for bowhead whales both for feeding and as a migration corridor, with advection key to prey delivery processes on the outer shelf (Citta et al., 2015, 2017).

2.3. Advection and upwelling in and near DBO regions 6–8

A combination of advection and episodic wind-driven upwelling events are common along the continental slope and shelf in the Beaufort Sea (Pickart et al., 2013; Walkusz et al., 2012). Advection of waters from Bering Strait and across the Chukchi shelf can transport nutrients and zooplankton into the Beaufort outer shelf and slope (Berline et al., 2008). Subsequent upwelling events can deliver both Bering-derived zooplankton and overwintering arctic-endemic species onto the Beaufort inner shelf from the deep basin. In and near DBO region 6, the number and strength of upwelling events has increased over the past 25 years, with seasonal peaks in May and November (Pickart et al., 2013). Upwelled water often contains euphausiids, which likely contributes to the now-common use of the western Beaufort Sea shelf for feeding by bowhead whales in late summer (Ashjian et al., 2010; Citta et al., 2015). A mechanistic model, called the ‘krill trap’, has been developed to explain the relationship between winds, upwelling and whale foraging for this region (Okkonen et al., 2011). The krill trap is a 2-step process whereby strong easterly winds drive upwelling and push the Alaskan Coastal Current (ACC) offshore, with the trap ‘tripped’ by a slackening of winds (or winds from the south), which allows the ACC to shift to the coast and effectively ‘trap’ krill on the western Beaufort shelf for the whales to feast upon (Ashjian et al., 2010). The resulting aggregation of feeding bowhead whales indicates to local indigenous hunters when the trap has been tripped.

Upwelling occurs all along the Beaufort Sea slope, including near and in DBO region 7, and while bowheads are commonly seen there during the fall migration, there are no correlative studies describing connections between wind-upwelling-prey aggregations-whales. In and near DBO region 8, episodic upwelling events have been linked to bowhead feeding on aggregations of calanoid copepods near Cape Bathurst in summer (Walkusz et al., 2012). The copepod aggregations there had twice the biomass and abundance, three times the caloric density, and therefore six times the energy content of contemporaneous zooplankton samples from the western Canadian Beaufort shelf.

The processes that attract whales to waters in and near DBO region 6 likely influence seabirds as well, although there have been no specific seabird studies in the region examining the links between birds and these mechanisms. In general, it is surface feeding seabirds, both piscivorous and planktivorous, that forage in DBO region 6, with hotspots of activity occurring in summer near the shelf break between DBO regions 5 and 6 (Kuletz et al., 2015). Black-legged kittiwakes and red phalaropes, two of the more abundant surface feeders in the region, had hotspots of abundance in DBO region 6 in summer (mid-June through August); both species will feed where prey are aggregated near the surface (Piatt and Springer, 2003). Large aggregations of shearwaters are also seen near DBO region 6, but farther east (DBO regions 7 and 8), there are few shearwaters offshore near the shelf edge (Kuletz et al., 2015; 2018). Possibly, these areas are too far from breeding colonies for the planktivorous auklets, and too far east for shearwaters, which begin their journey back towards the Pacific by late summer or early fall. Foraging phalaropes appear to use the area for staging prior to migration west and south through Bering Strait (Kuletz et al., 2015; Taylor et al., 2011). Although total bird density is typically very low in these easternmost DBO regions, sea ducks and waterfowl are encountered near the coast, and they have large populations in the region's coastal lagoons and nearshore waters (Fischer and Larned, 2004).

3. Discussion

This abbreviated account demonstrates the capability of UTL species to reflect ecosystem structure resulting from ocean processes in the Pacific Arctic, such as pelagic-benthic coupling, advection, and upwelling. Because UTL species reflect processes throughout the ecosystem, they are natural sentinels to shifts therein and can serve as guides to changes in these ocean processes (Moore and Stabenro, 2015; Moore et al., 2014). Both pelagic-benthic coupling and advection are key components of the conceptual AMP model for the Pacific Arctic, and case studies wherein UTL species have provided insight as to how seasonal biophysical ‘pulses’ structure lower-trophic prey fields were instrumental to its derivation (Moore et al., 2016). This top-down approach compliments the bottom-up method typically used in the construction of ecosystem models. Recognizing UTL species as sentinels to ecosystem alterations gives them a pivotal role in the development of integrated ecosystem models responsive to resource managers and local communities who seek to predict outcomes for populations of marine fishes, birds, and mammals. Indeed, leaving UTL species out of ecosystem model development results in an incomplete accounting of ocean dynamics and productivity.

While standard seabird surveys and marine mammal watches undertaken during DBO sampling provide data for direct integration with oceanographic sampling, inclusion of data from broad-scale UTL-focused research can offer insights on the capability of these species to act as sentinels to shifts in ocean processes and productivity. Collaboration among UTL and other ocean researchers will be more productive if hypotheses can be identified and approaches towards testing those questions agreed upon among investigators. At present, UTL research is often species-focused, while oceanic research is often process-focused. These approaches need to be better integrated to inform models of the Pacific Arctic marine ecosystem.

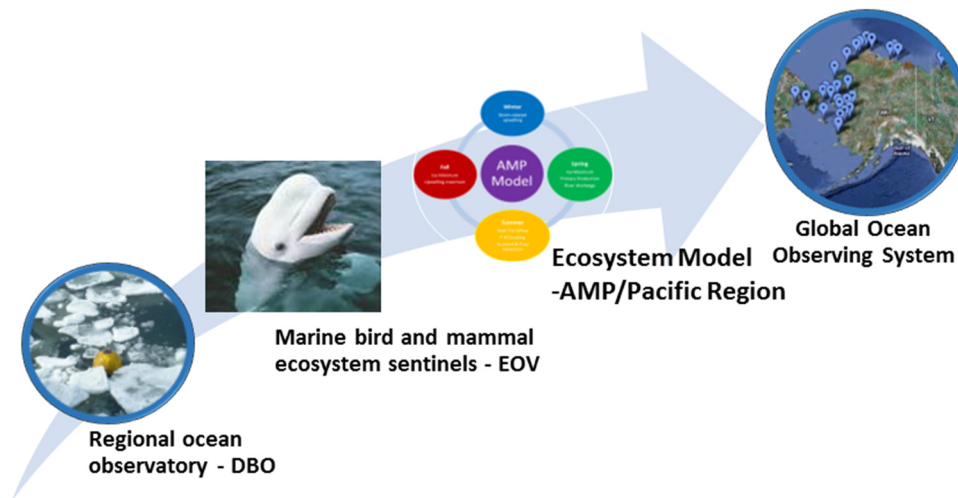


Fig. 3. Schematic diagram depicting the role of marine birds and mammals in linking the DBO to the AMP model in the Pacific region (Moore et al., 2016), and ultimately contributing to the Global Ocean Observing effort (Miloslavich et al., 2018).

4. Recommendations

This short review provides examples of how marine birds and mammals can act as sentinels to shifts in the Pacific Arctic ocean ecosystem. This capacity is germane not only to the DBO, but to all ocean observatories. Indeed, the Global Ocean Observing System (GOOS) is now advancing the goal of including data products from research on marine turtles, birds, and mammals as Essential Ocean Variables (EOVs) in the global system of ocean observatories (Miloslavich et al., 2018; www.goosocean.org/eov). Work on this goal is in the early stages, which makes this an opportune time to consider how research on marine birds and mammals in the Pacific Arctic might contribute to this global ocean observation enterprise. Three recommendations for next steps are provided below, a list which is not comprehensive but intended to initiate discussion on future directions for the DBO (Fig. 3).

4.1. Routine integration of marine bird and mammal data products, both from sampling during DBO cruises and from auxiliary studies, to ecosystem models

The AMP conceptual model aims to connect the annual cycles of sea-ice cover, pelagic-benthic coupling, advection, and upwelling in the context of ecological domains (Moore et al., 2016). While this model provides a framework for thinking about annual events in the Pacific Arctic, it will become useful only if its components can be quantified in a manner that can predict future states. Next steps towards that goal should include the integration of marine bird and mammal data products, such as species' seasonal movement patterns and body condition indices, with outcomes of biophysical models that can resolve oceanographic variability at local (ca. 10 s km/month) spatial and temporal scales. While individual observational studies do make some of these connections (e.g. Citta et al., 2015, 2017, in press), it is not routine practice. For example, a future goal of the AMP model might be to predict shifts in timing of marine bird and mammal migration, or feeding 'hotspot' locales based upon biophysical parameters. Data from bird and mammal surveys during DBO-focused cruises can provide direct correlation with concurrent regional oceanographic status, while information from telemetry, passive acoustic, and/or body condition sampling, can offer a fuller picture of how these top predators are responding to shifting ocean conditions (Moore and Gulland, 2014).

The signal provided by marine birds and mammals might be strengthened through the compilation of data by feeding clades (i.e. benthivore, planktivore, piscivore, omnivore), by foraging mode (surface feeders vs sub-surface divers), or by trophic roles as either

specialists or generalists (McTigue and Dunton, 2017). For example, a broad-scale examination of zoogeography from the Bering Sea through the Beaufort Sea identified large scale regional patterns in relative abundance among seabird feeding clades (Sigler et al., 2011). Within the more-focused region of the Chukchi Sea, seabird feeding clades showed shifts in relative abundance among oceanographic events (Gall et al., 2013) and over decades (Gall et al., 2017). In the Bering Sea, foraging mode has been used to examine seabird response to seasonal changes in hydrography (Hunt et al., 2014), prey distribution (Suryan et al., 2016), and to long-term changes in timing of sea-ice retreat (Renner et al., 2016; Hunt et al., 2018). Making these connections more comprehensive and focused on specific data products could facilitate the integration of marine bird and mammal data products into ecosystem models.

4.2. Link DBO sampling to the coast, via partnerships between conventional science practitioners and holders of Indigenous Knowledge

While the DBO was designed as an ocean observatory, establishing links to coastal research on marine birds and mammals and information from holders of Indigenous Knowledge would be a proactive step, helpful to understanding the marine system as a whole. This goal is specifically identified as a future step for the AMP model (Moore et al., 2016). Marine birds are reliant upon and responsive to changes in coastal features, as they use these areas for breeding and sometimes foraging (eiders, other waterfowl, phalaropes). Marine mammals often feed in the coastal domain (e.g. Ashjian et al., 2010; Beatty et al., 2016; Brower et al., 2017), or rely on coastal haul outs for rest and pupping (seals, walrus). Most DBO stations are too far from shore to sample coastal bird and mammal communities, especially in the Beaufort DBO regions 6, and 7. Linking DBO sampling to coastal studies could provide key information on the influence of the riverine-coastal domain to the ocean system (Carmack et al., 2015), as well as body condition and diet data for marine birds and mammals (i.e. Fig. 1: Intrinsic Responses).

Marine bird research is commonly conducted at coastal breeding colonies stretching from the northern Bering through the Chukchi Sea, with results on diet, body condition, and breeding success that could prove very relevant to the interpretation of ocean variability at DBO sites. Similarly, over 30 years of research partnerships supported by marine mammal co-management activities has resulted in a wealth of data on population status and state of health (e.g. Harwood et al., 2015; George et al., 2015). Indeed, establishing better linkages between marine mammal and ocean health was promoted as essential to tracking ecosystem changes in a rapidly changing arctic (Moore and Gulland, 2014).

Of note, the AMP model's focus on seasonal events over annual cycles may aid communication between conventional science and Indigenous Knowledge in the Pacific Arctic (Moore et al., 2016). The two approaches to observing the marine system appear to be complementary; i.e. conventional science is spatially broad (Pacific Arctic region) and time shallow (decades), while Indigenous Knowledge is spatially focused (villages) and time deep (centuries). Finding ways to better connect the two approaches could be advantageous to both.

4.3. Identification of data gaps

One of the biggest data gaps regarding trophic dynamics is the role of euphausiids in the Pacific Arctic marine ecosystem. Krill have been tracked as key trophic components in the Atlantic Arctic/Barents Sea for decades (e.g. Eriksen et al., 2017), but data are scant on the status of krill in the Pacific Arctic north of Bering Strait. Combined, the step-increase in inflow at Bering Strait since ~2000 (Woodgate et al., 2015), the influx of short-tailed shearwaters to the Chukchi (Gall et al., 2017) and now Beaufort seas (Kuletz et al., 2015; 2018), and increasingly common observations of bowhead (and sometimes gray) whales feeding on krill near Barrow (Ashjian et al., 2010; Okkonen et al., 2011), make a compelling case that the importance of krill in the system now is greater than it was 30 years ago.

Another data gap is the lack of current bird diet data for Arctic regions. Most data are old (1970s), yet much of the ecosystem has changed and many birds can be flexible in prey species, even switching between planktivorous and piscivorous foraging. However, dietary changes can have repercussions to bird's foraging distances from colonies, their body condition, productivity, and chick growth or fledging success, as was shown for black guillemots near DBO region 6 in the western Beaufort (Divoky et al., 2015). Marine mammals too seem to be flexible with regard to prey species, as exemplified by beluga and ice seals (e.g. Stafford et al., 2017; Crawford et al., 2015). One approach to filling this gap would be to have DBO studies partner with developing repositories for seabird and marine mammal diet data.

For both marine birds and mammals, the distribution and abundance patterns tracked via surveys in the pelagic realm of the DBO regions should complement colony-based (seabirds) or haulout-focused (seals, walrus) studies. There have been few studies of the large populations of planktivorous auklets that dominate colonies near DBO regions 1 and 2, or the colonies of piscivorous seabirds near DBO region 3. To fully understand how the changes being tracked in the DBO regions are affecting breeding populations, it will be necessary to link land-based with offshore studies. Similarly, changes to the Northeast Chukchi ecosystem tracked in DBO regions 4 and 5 should be linked to studies of the comparatively 'new' coastal haulouts used by walrus (Jay et al., 2012).

References

- Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E., Nicolson, C.R., Okkonen, S.R., Sherr, B.F., Sherr, E.B., Spitz, Y.H., 2010. Climate variability, oceanography, bowhead whale distribution and Inupiat subsistence whaling near Barrow, Alaska. *Arctic* 63, 179–194.
- Beatty, W.S., Jay, C.V., Fischbach, A., Grebmeier, J.M., Taylor, R.L., Blanchard, A.L., Jewett, S.C., 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.
- Berline, L., Spitz, Y.H., Ashjian, C.J., Campbell, R.G., Maslowski, W., Moore, S.E., 2008. Euphausiid transport in the western Arctic Ocean. *Mar. Ecol. Prog. Ser.* 360, 163–178.
- Bluhm, B.A., Coyle, K.O., Konar, B., Highsmith, R., 2007. High gray whale relative abundances associated with an oceanographic front in the south-central Chukchi Sea. *Deep-Sea Res.* II 54, 2919–2933.
- Brower, A.A., Ferguson, M.C., Schonberg, S.V., Jewett, S.C., Clarke, J.T., 2017. Gray whale distribution relative to benthic invertebrate biomass and abundance: north-eastern Chukchi Sea 2009–2012. *Deep-Sea Res.* II 144, 156–174. <https://doi.org/10.1016/j.dsr2.2016.12.007>.
- Carmack, E., Winsor, P., Williams, W., 2015. The contiguous panarctic Riverine Coastal Domain: a unifying concept. *Prog. Oceanogr.* 139, 13–23.
- Citta, J.J., Quakenbush, L.T., Okkonen, S.R., Druckenmiller, J.L., Maslowski, W., Clement-Kinney, J., George, J.C., Brower, H., Small, R.J., Ashjian, C.J., Harowwd, L.A., Heide-Jorgensen, M.P., 2015. Ecological characteristics of core-use areas used by Bering-Chukchi-Beaufort (BCB) bowhead Whales, 2006–2012. *Prog. Oceanogr.* 136, 201–222.
- Citta, J.J., Okkonen, S.R., Quakenbush, L.T., Maslowski, W., Osinski, R., George, J.C., Small, R.J., Brower Jr., H., Heide-Jorgensen, M.P., Harwood, L.A., 2017. Oceanographic characteristics associated with autumn movements of bowhead whales in the Chukchi Sea (published online). *Deep-Sea Res.* II. <https://doi.org/10.1016/j.dsr2.2017.03.009>.
- Clarke, J., Stafford, K., Moore, S.E., Rone, B., Aerts, L., Crance, J., 2013. Subarctic cetaceans in the southern Chukchi Sea: evidence of recovery or response to a changing ecosystem. *Oceanography* 26, 136–149. <https://doi.org/10.5670/oceanog.2013.81>.
- Coyle, K.O., Bluhm, B., Konar, B., Blanchard, A., Highsmith, R.C., 2007. Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002–2003. *Deep-Sea Res.* II 54, 2906–2918.
- Crawford, J.A., Quakenbush, L.T., Citta, J.J., 2015. A comparison of ringed and bearded seal diet, condition and productivity between historical (1975–1984) and recent (2003–2012) periods in the Alaskan Bering and Chukchi seas. *Prog. Oceanogr.* 136, 133–150.
- Divoky, G.J., Lukacs, P.M., Druckenmiller, M.L., 2015. Effects of recent decreases in arctic sea ice on an ice-associated marine bird. *Prog. Oceanogr.* 136, 151–161.
- Divoky, G.J., Douglas, D.C., Stenhouse, I.J., 2016. Arctic sea ice a major determinant in Mandt's black guillemot movement and distribution during non-breeding season. *Biol. Lett.* 12, 0160275. <https://doi.org/10.1098/rsbl.2016.0275>.
- Eriksen, E., Skjoldal, H.R., Gjøsæter, Primicerio, R., 2017. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Prog. Oceanogr.* 151, 206–226.
- Fischer, J.B., Larned, W.W., 2004. Summer distribution of marine birds in the Western Beaufort Sea. *Arctic* 57 (2), 43–159.
- Gall, A.E., Roby, D.D., Irons, D.B., Rose, I.C., 2006. Inter-annual variation in diet and nest survival of plankton feeding auklets on St. Lawrence Island, Alaska. *Mar. Ecol. Prog. Ser.* 308, 279–291.
- Gall, A.E., Day, R.H., Weingartner, T.J., 2013. Structure and variability of the marine-bird community in the northeastern Chukchi Sea. *Cont. Shelf Res.* 67, 96–115.
- Gall, A.E., Morgan, T.C., Day, R.H., Kuletz, K.J., 2017. Ecological shift from piscivorous to planktivorous seabirds in the Chukchi Sea, 1975–2012. *Polar Biol.* 61–78. <https://doi.org/10.1007/s00300-016-1924-z>.
- George, J.C., Druckenmiller, M.L., Laidre, K.L., Suydam, R., Person, B., 2015. Bowhead whale body condition and links to summer sea ice and upwelling in the Beaufort Sea. *Prog. Oceanogr.* 136, 250–262.
- Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. *J. Mar. Syst.* 2, 495–518.
- Grebmeier, J.M., Harrison, N.M., 1992. Seabird feeding on benthic amphipods facilitated by gray whale activity in the northern Bering Sea. *Mar. Ecol. Prog. Ser.* 80, 125–133.
- Grebmeier, J.M., Moore, S.E., Overland, J.E., Frey, K.E., Gradinger, R., 2010. Biological response to recent Pacific Arctic sea ice retreats. *EOS* 91 (18), 161–162.
- Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., et al., 2015a. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Prog. Oceanogr.* 136, 92–114.
- Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Denisenko, S.G., Iken, K., Kedra, M., Serratos, C., 2015b. Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 program. *Oceanography* 23, 116–133.
- Harwood, L.A., Smith, T.G., George, J.C., Sandstrom, S.J., Walkusz, W., Divoky, G.J., 2015. Change in the Beaufort Sea ecosystem: diverging trends in body condition and/or production in five marine vertebrate species. *Prog. Oceanogr.* 136, 263–273. <https://doi.org/10.1016/j.pocan.2015.05.003>.
- Hunt Jr., G.L., Renner, M., Kuletz, K.J., 2014. Seasonal variation in the cross-shelf distribution of seabirds in the Southeastern Bering Sea. *Deep-Sea Res.* II 109, 266–281.
- Hunt Jr., G.L., Renner, M., Kuletz, K.J., Salo, S., Eisner, L., Ressler, P., Ladd, C., Santora, J.A., 2018. Timing of sea-ice-retreat affects the distribution of seabirds and their prey in the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.* 593, 209–230.
- Jay, C.V., Fischbach, A.S., Kochnev, A.A., 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Mar. Ecol. Prog. Ser.* 468, 1–13.
- Jay, C.V., Grebmeier, J.M., Fischbach, A.S., McDonald, T.L., Cooper, L.W., Hornsby, F., 2014. Pacific walrus (*Odobenus rosmarus divergens*) resource selection in the northern Bering Sea. *PLOS One* 9 (4), e93035.
- Kuletz, K.J., Renner, M., Labunski, E.A., Hunt Jr., G.L., 2014. Changes in the distribution and abundance of Albatrosses in the Eastern Bering Sea: 1975–2010. *Deep-Sea Res.* II 109, 282–292.
- Kuletz, K.J., Ferguson, M.C., Hurley, B., Gall, A.E., Labunski, E.A., Morgan, T.C., 2015. Seasonal spatial patterns in seabird and marine mammal distribution in the eastern Chukchi and western Beaufort seas: identifying biologically important pelagic areas. *Prog. Oceanogr.* 136, 175–200.
- Kuletz, K.J., Cushing, D.A., Osnas, E.E., Labunski, E.A., Gall, A.E., Morgan, T.C., 2018. Seabird species composition, distribution, and abundance within the Distributed Biological Observatory array of the Pacific Arctic, 2007–2015.
- Lovvorn, J.R., Anderson, E.M., Rocha, A.R., Larned, W.W., Grebmeier, J.M., Cooper, L.W., Kolts, J.M., North, C.A., 2014. Variable wind, pack ice, and prey dispersion affect the long-term adequacy of protected areas for an Arctic sea duck. *Ecol. Appl.* 24, 396–412.
- Lovvorn, J.R., Rocha, A.R., Jewett, S.C., Dasher, D., Oppel, S., Powell, A.N., 2015. Limits to benthic feeding by eiders in a vital Arctic migration corridor due to localized prey and changing sea ice. *Prog. Oceanogr.* 136, 162–174.
- McTigue, N.D., Dunton, K.H., 2017. Trophodynamics of the Hanna Shoal ecosystem (Chukchi Sea, Alaska): connection multiple end-members to a rich food web. *Deep-Sea Res.* II 144, 175–189.

- Miloslavich, P., Bax, N.J., Simmons, S.E., Klein, E., Appeltans, W., Aburto-Oropeza, O., Garcia, M.A., Battne, S.D., Benedetti-Cercchi, L., Checkley Jr., D.M., Chiba, S., Duffy, J.E., Dunn, D.C., Fischer, A., Gunn, J., Kudela, R., Marsac, F., Muller-Karger, F.E., Obura, D., Shin, Y.-J., 2018. Essential ocean variables for global sustained observations of biodiversity in a dynamic ecosystem changes. *Glob. Change Biol.* <https://doi.org/10.1111/gcb.14108>.
- Moore, S.E., 2018. Climate change. In: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), *The Encyclopedia of Marine Mammals*, 3rd edition. Academic Press, San Diego, CA.
- Moore, S.E., Grebmeier, J.M., 2018. The Distributed Biological Observatory: linking physics to biology in the Pacific Arctic region. *Arctic* 71 (Suppl. 1), 1–7. <https://doi.org/10.14430/arctic4606>.
- Moore, S.E., Gulland, F.M.D., 2014. Linking marine mammal health and ecology in the 'new normal' Arctic. *Ocean Coast. Manag.* 102, 55–57.
- Moore, S.E., Stabeno, P.J., 2015. Synthesis of Arctic research (SOAR) in marine ecosystems of the Pacific Arctic. *Prog. Oceanogr.* 136, 1–11.
- Moore, S.E., Grebmeier, J.M., Davies, J.R., 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. *Can. J. Zool.* 81, 734–742.
- Moore, S.E., Logerwell, E., Eisner, L., Farley, E., Harwood, L., Kuletz, K., Lovvorn, J., Murphy, J., Quakenbush, L., 2014. Marine fishes, birds and mammals as sentinels of ecosystem variability and reorganization in the Pacific Arctic region. In: Grebmeier, J., Maslowski, W. (Eds.), *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*. Springer, Dordrecht, pp. 337–392.
- Moore, S.E., Stabeno, P.J., Grebmeier, J.M., Okkonen, S., 2016. The Arctic Marine Pulses (AMP) Model: linking temporal processes to contiguous ecological domains in the Pacific Arctic (published online). *Deep-Sea Res. II*. <https://doi.org/10.1016/j.dsr2.2016.10.1011>.
- Nishizawa, B., Matsuno, K., Labunski, E.A., Kuletz, K.J., Yamaguchi, A., Watanuki, Y., 2017. Seasonal distribution of short-tailed shearwaters and their prey in the Bering and Chukchi Seas. *Biogeosciences* 14, 1–12. <https://doi.org/10.5194/bg-14-1-2017>.
- Obst, B.S., Russell, R.W., Hunt, G.L., Eppley, Z.A., Harrison, N.M., 1995. Foraging radii and energetics of Least Auklets (*Aethia pusilla*) breeding on three Bering Sea islands. *Physiol. Zool.* 68, 647–672.
- Okkonen, S.R., Ashjian, C.J., Campbell, R.G., Clarke, J.T., Moore, S.E., Taylor, K.D., 2011. Satellite observations of circulation features associated with a bowhead whale 'hot-spot' near Barrow, Alaska. *Remote Sens. Environ.* 115, 2168–2174.
- Oppel, S., Lynne Dickson, D., Powell, A.N., 2009. International importance of the eastern Chukchi Sea as a staging area for migrating king eiders. *Polar Biol.* 32, 775–783.
- Petersen, M.R., Larned, W.W., Douglas, D.D., 1999. At-sea distribution of Spectacled Eiders: a 120-year-old mystery resolved. *Auk* 116, 1009–1020.
- Piatt, J., Sydeman, W., Wiese, F., 2007. Introduction: a modern role for seabirds as indicators. In: *Seabirds as indicators of marine ecosystems*. Mar. Ecol. Prog. Ser. 353, 199–209.
- Piatt, J.F., Springer, A.M., 2003. Advection, pelagic food webs and the biogeography of seabirds in Beringia. *Mar. Ornithol.* 31, 141–154.
- Pickart, R.S., Schulze, L.M., Moore, G.W.K., Charette, M.A., Arrigo, K.R., van Dijken, G., Danielson, S.L., 2013. Long-term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. *Deep-Sea Res. I* 79, 106–121.
- Ravelo, A.M., Konar, B., Bluhm, B.A., 2015. Spatial variability of epibenthic communities on the Alaska Beaufort Shelf. *Polar Biol.* <https://doi.org/10.1007/s00300-015-1741-9>.
- Renner, M., Salo, S., Eisner, L., Ressler, P., Ladd, C., Kuletz, K., Santora, J., Piatt, J., Drew, G., Hunt Jr., G.L., 2016. Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea. *Biol. Lett.* 12, 20160276. <https://doi.org/10.1098/rsbl.2016.0276>.
- Santora, J.A., Eisner, L.B., Kuletz, K.J., Ladd, C., Renner, M., Hunt Jr., G.L., 2018. Biogeography of seabirds within a high-latitude ecosystem: use of a data assimilative ocean model to assess impacts of mesoscale oceanography. *J. Mar. Syst.* 178, 38–51. <https://doi.org/10.1016/j.jmarsys.2017.10.006>.
- Sheffield-Guy, L.M., Roby, D.D., Gall, A.E., Irons, D.B., Rose, I.C., 2009. The influence of diet and ocean conditions on productivity of auklets on St. Lawrence Island, Alaska. *Mar. Ornithol.* 37, 227–236.
- Sigler, M.F., Renner, M., Danielson, S.L., Eisner, L.B., Lauth, R.R., Kuletz, K.J., Logerwell, E.A., Hunt Jr., G.L., 2011. Fluxes, fins, and feathers: relationships among the Bering, Chukchi, and Beaufort Seas in a time of climate change. *Oceanography* 24 (3), 250–265.
- Stafford, K.M., Ferguson, M.C., Hauser, D.W., Okkonen, S.R., Berchok, C.L., Citta, J.J., Clarke, J.T., Garland, E.C., Jones, J., Suydam, R.S., 2017. Beluga whales in the western Beaufort Sea: current state of knowledge on timing, distribution, habitat use and environmental drivers. *Deep-Sea Res. II*. <https://doi.org/10.1016/j.dsr2.2016.11.017>. (published online).
- Suryan, R.M., Kuletz, K.J., Parker-Stetter, S.L., Ressler, P.H., Renner, M., Horne, J.K., Farley, E.V., Labunski, E.A., 2016. Temporal shifts in seabird populations and spatial coherence with prey in the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.* 549, 199–215.
- Sydeman, W.J., Poloczanska, E., Reed, T.E., Thompson, S.A., 2015. Climate change and marine vertebrates. *Science* 350, 772–776.
- Taylor, A.R., Lancot, R.B., Powell, A.N., Kendall, S.J., Nigro, D.A., 2011. Residence time and movements of post-breeding shorebirds on the northern coast of Alaska. *Condor* 113 (4), 779–794.
- Walkusz, W., Williams, W.J., Harwood, L.A., Moore, S.E., Stewart, B.E., Kwasniewski, S., 2012. Composition, biomass and energetic content of biota in the vicinity of feeding bowhead whales (*Balaena mysticetus*) in the Cape Bathurst upwelling region (south eastern Beaufort Sea). *Deep-Sea Res. I* 69, 25–35.
- Wood, K.R., Bond, N.A., Danielson, S.L., Overland, J.E., Salo, S.A., Stabeno, P.J., Whitefield, J., 2015. A decade of environmental change in the Pacific Arctic region. *Prog. Oceanogr.* 136, 12–31.
- Woodgate, 2018. Increases in the Pacific inflow to the Arctic from 1990 to 2015, and insights into seasonal trends and driving mechanisms from year-round Bering Strait mooring data. *Prog. Oceanogr.* 160, 124–154.
- Woodgate, R.A., Stafford, K.M., Prah, F.G., 2015. A synthesis of year-round interdisciplinary mooring measurements in Bering Strait (1990–2014) and the RUSALCA years (2004–2011). *Oceanography* 28, 39–59.
- Young, J.K., Black, R.A., Clarke, J.T., Schonberg, S.V., Dunton, K.H., 2017. Abundance, biomass and caloric content of Chukchi Sea bivalves and association with Pacific walrus (*Odobenus rosmarus divergens*) relative density and distribution in the north-eastern Chukchi Sea. *Deep-Sea Res. II* 144, 125–141.