



Developing an observational design for epibenthos and fish assemblages in the Chukchi Sea



K. Iken^{a,*}, F. Mueter^a, J.M. Grebmeier^b, L.W. Cooper^b, S.L. Danielson^a, B.A. Bluhm^c

^a College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA

^b University of Maryland Center for Environmental Science, Solomons, MD, USA

^c Department of Arctic and Marine Biology, UiT – the Arctic University of Norway, Tromsø, Norway

ARTICLE INFO

Keywords:

Arctic
Observing system
Biomass
Diversity

ABSTRACT

In light of ongoing, and accelerating, environmental changes in the Pacific sector of the Arctic Ocean, the ability to track subsequent changes over time in various marine ecosystem components has become a major research goal. The high logistical efforts and costs associated with arctic work demand the prudent use of existing resources for the most comprehensive information gain. Here, we compare the information that can be gained for epibenthic invertebrate and for demersal fish assemblages reflecting coverage on two different spatial scales: a broader spatial coverage from the Arctic Marine Biodiversity Observing Network (AMBON, 67 stations total), and the spatial coverage from a subset of these stations (14 stations) that reflect two standard transect lines of the Distributed Biological Observatory (DBO). Multivariate cluster analysis was used to discern community similarity patterns in epibenthic invertebrate and fish communities. The 14 stations reflecting the two DBO lines captured about 57% of the epibenthic species richness that was observed through the larger-scale AMBON coverage, with a higher percentage on the more southern DBO3 than the northern DBO4 line. For demersal fishes, both DBO lines captured 88% of the richness from the larger AMBON spatial coverage. The epifaunal assemblage clustered along the south-north and the inshore-offshore axes of the overall study region. Of these, the southern DBO3 line well represented the regional (southern) epifaunal assemblage structure, while the northern DBO4 line only captured a small number of the distinct assemblage clusters. The demersal fish assemblage displayed little spatial structure with only one coastal and one offshore cluster. Again, this structure was well represented by the southern DBO3 line but less by the northern DBO4 line. We propose that extending the coverage of the DBO4 line in the northern Chukchi Sea farther inshore and offshore would result in better representation of the overall northern Chukchi epifaunal and fish assemblages. In addition, the multi-annual stability of epifaunal and, to a lesser extent also fish assemblages, suggests that these components may not need to be sampled on an annual basis and sampling every 2–3 years could still provide sufficient understanding of long-term changes. Sampling these assemblages every few years from a larger region such as covered by the AMBON project would create the larger-scale context that is important in spatial planning of long-term observing.

1. Introduction

High levels of biodiversity promote ecosystem productivity and stability and secure the multiple functions and services the oceans provide (Palumbi et al., 2009; Duffy et al., 2017). Essential ecosystem services of the Arctic Ocean for humans include climate regulation from regional to global scales (Overland and Wang, 2010), food and traditional lifestyle for indigenous peoples, untapped reservoirs of natural oil and gas resources, new shipping routes, growing tourism (Hall and Saarinen, 2010), and potential new fisheries as subarctic species expand

into Arctic waters (Christiansen et al., 2014; Hollowed et al., 2013). More diverse systems are thought to have higher resilience to perturbations and more potential for recovery and reversibility after they are affected, compared to less diverse systems (e.g. Sala and Knowlton, 2006; Worm et al., 2006; Palumbi et al., 2009). Thus, biodiversity can be used as a gauge of ecosystem status and a “common master variable”, linking ocean management, conservation, and development interests (Duffy et al., 2013). Yet, biodiversity as a cornerstone of long-term observing systems in the marine realm is still in its infancy compared with physical observing programs.

* Corresponding author.

E-mail address: kbiken@alaska.edu (K. Iken).

<https://doi.org/10.1016/j.dsr2.2018.11.005>

One of the world's oceans in need of increased ocean observing is the Arctic. The ongoing and rapidly increasing drastic changes in the Arctic marine physical environment such as the loss of sea-ice cover and changes in heat budget are projected to elicit significant responses in the marine biological system (Wassmann et al., 2011). Both the ecological significance of the Arctic marine ecosystems, the increasing interest in resource use in the Arctic as well as the global biodiversity loss and its negative influence on ecosystem services (Worm et al., 2006; Cobb et al., 2014; Miller and Ruiz, 2014) spur efforts to develop and maintain observation programs of physical and biological changes. It is well understood that long-term observations of the Arctic (and other) marine ecosystems are needed to create an understanding of natural fluctuations on seasonal to interannual time scales so that long-term, unidirectional responses due to climate warming or other causes can be differentiated (Magurran et al., 2010). However, the logistically and financially intense fieldwork in the Arctic demands a prudent approach to the optimization of resources and collaborative approaches in developing marine observing networks.

Both national and international efforts are underway in the Arctic to implement long-term observational programs that capture variability or trends not only in the physical environment but also the biological system (e.g. Soltwedel et al., 2005, 2013; Michalsen et al., 2013; Moore and Grebmeier, 2018). Most of these observing systems have a focus on seabed fauna as a long-term indicator of changes from climatic processes or anthropogenic influences. For example, the arctic deep-sea HAUSGARTEN observatory in Fram Strait has measured benthic processes since 1999, measuring faster than expected responses to environmental variation (Soltwedel et al., 2016). On the European Arctic Barents Sea shelf, the assessment of epibenthos as part of annual fish trawl surveys is starting to provide long-term records that allow the assessment of responses to trawling impacts and shifts in dominant water masses (Jørgensen et al., 2014, 2015). Within the Pacific Arctic, two of the currently ongoing observational programs that link variability or trends in the physical environment with the biological system are the Distributed Biological Observatory (DBO) and the Arctic Marine Biodiversity Observing Network (AMBON). The goal of the DBO is to repeatedly (from seasonally to annually) sample regions of persistently high benthic biomass “hotspots” that are representative of the tight pelagic-benthic coupling and short food webs of many arctic shelf systems (Grebmeier et al., 2010; Moore and Grebmeier, 2018). Core measurements of the DBO program include physical and chemical properties of the water column and sediments; the species composition, abundance and biomass of phytoplankton, zooplankton and macrobenthos; and the abundance and distribution of seabirds and marine mammals, with only occasional epibenthic and fish trawling efforts. DBO sampling is currently implemented as an international collaboration of six countries (USA, Canada, Japan, Korea, China, Russia) along cross-shelf transects in the Bering and Chukchi seas, and with new implementations of shelf to upper slope transects also in the Beaufort Sea and the Atlantic sector (Barents Sea and Fram Strait).

The AMBON program is part of a US national effort to develop prototypes for marine observing networks that focus on biodiversity (Duffy et al., 2013). Biodiversity measures are at the core of the AMBON program, which engages in a monitoring approach of ecosystem components from microbes to whales. The ecosystem components monitored include temperature, salinity and nutrient concentrations; microbial and phytoplankton composition and microalgal biomass (as chlorophyll *a*); zooplankton, meiobenthos, macrobenthos, epibenthos and demersal fish composition, biodiversity, biomass and abundance; as well as seabird and marine mammal distribution along observational transects. The strategy of the AMBON project is to continue spatial coverage of previous observational programs to take advantage of existing knowledge and to create or extend much-needed time series. Only long-term, decadal-scale datasets provide the basis for distinguishing natural (stochastic) variability and regular cycles from gradual or abrupt directional changes driven by climate change and

other human influences, e.g. chronic pollution or oil spills. For example, a 40-year time series on macrobenthos in the Chukchi Sea allowed detection of decadal changes in this system (Grebmeier et al., 2015b). Similarly, a 60-year time series on zooplankton in the Chukchi Sea detected significant changes in copepod biomass, abundance, and biogeographic affinity in recent years (Ershova et al., 2015). Therefore, survey transects of the past decade-long Russian-American Long-term Census of the Arctic (RUSALCA) program (Grebmeier et al., 2015a) and the 7-year long Chukchi Sea Ecosystem Studies Program (CSESP, Day et al., 2013) are included in the AMBON sampling grid. In addition, the AMBON observing region includes two of the DBO lines, DBO3 in the southern Chukchi Sea and DBO4 in the northern Chukchi Sea (Grebmeier et al., 2010). This overlap provides opportunities to add to the temporal (seasonal) sampling of these lines, to add biodiversity as another element to DBO sampling, and to add ecosystem elements that are not regularly sampled during the existing DBO sampling, including epibenthic invertebrates and demersal fishes.

Epibenthic invertebrate assemblages in particular are a biomass-rich ecosystem component of the Chukchi Sea shelf (e.g. Bluhm et al., 2009; Blanchard et al., 2013; Ravelo et al., 2014) fueled by high pelagic primary productivity, much of which is exported directly to the sea floor with little grazing in the water column (Grebmeier et al., 2006). Epifaunal taxa contribute to carbon remineralization (Ambrose et al., 2001), enhance habitat complexity (e.g. Wood et al., 2012), add to food web complexity (Iken et al., 2010), and act as a food source for other higher trophic level organisms, such as fishes and marine mammals (Bluhm and Gradinger, 2008; Divine et al., 2015; Gray et al., 2017). Epibenthic assemblage structure and spatial distribution is driven by a suite of environmental variables, including water mass characteristics, flow regimes, and sediment characteristics (Feder et al., 2005; Bluhm et al., 2009; Ravelo et al., 2014; Pisareva et al., 2015), in addition to trophic interactions (Iken et al., 2010). High biological and functional diversity (Rand et al., 2017), together with high longevity of most benthic invertebrates, leads to the resilience of epibenthic assemblages against short-term (seasonal to interannual) climate fluctuations (Bluhm et al., 2009; Grebmeier et al., 2015a), making them good indicators of long-term changes and useful candidates to be included in long-term observations.

Demersal fishes also are important components of the Arctic food web as they consume plankton, benthic invertebrates, and smaller fishes while serving as prey for higher trophic level organisms like birds, whales, ice seals, polar bears, and humans (Lowry and Frost, 1981; Bluhm and Gradinger, 2008). Many demersal fishes are mobile and not strictly tied to the benthos as they swim up into the water column to feed on pelagic prey (e.g. Gray et al., 2015). In addition, many demersal species have pelagic larvae and juveniles, providing important links between the pelagic and benthic environment. Current abundances of fish on the Chukchi Sea shelf are at least an order of magnitude lower than in the eastern Bering Sea (Stevenson and Lauth, 2012), but subarctic species may expand northward into the Chukchi Sea or local populations may increase in a warming climate (Hollowed et al., 2013). The implementation of the Arctic Fisheries Management Plan (NPFMC, 2009), which provides a framework for managing potential future commercial fisheries in the Arctic, has brought attention to the role Arctic fish play or could play in the ecosystem under altered climate scenarios. Similar to epifauna, demersal fish assemblage patterns are related to environmental variables, mostly water mass characteristics for larger-scale distributions (Norcross et al., 2010) or temperature and the erosional or depositional nature of sediment structure for small-scale patterns in fish assemblages (Norcross et al., 2013). The sensitivity of fish species diversity and abundance to temperature changes (Mueter and Litzow, 2008) makes them another good candidate for long-term monitoring.

In this study, we made use of the spatial overlap that the AMBON program has with stations of the DBO in the Chukchi Sea to assess how representative the subset of these stations that reflect the DBO lines in

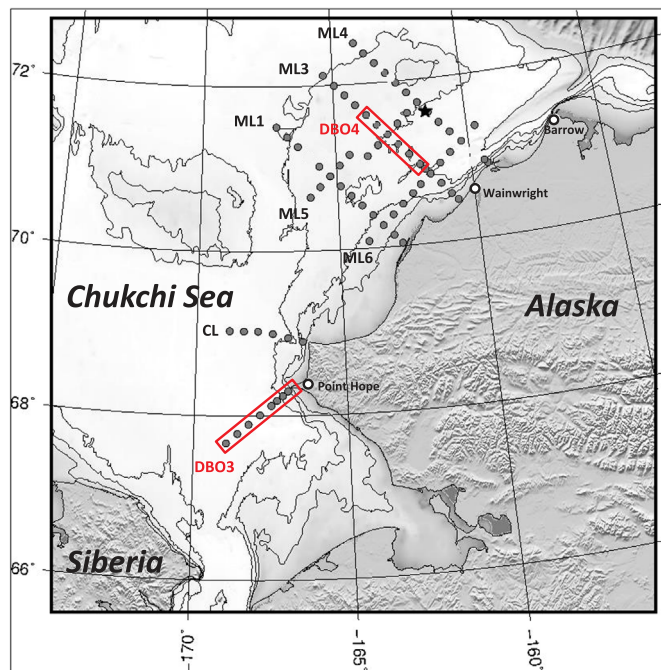


Fig. 1. Map of the AMBON study area and sampling stations; stations that represent DBO coverage are outlined in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

the Chukchi Sea are of the larger regional distribution and biodiversity of epibenthic and demersal fish assemblages covered though the AMBON project. Decisions as to which ecosystem components should be included in long-term observations are inherently driven by ecological, practical, and fiscal considerations. Hence, optimization of field efforts, particularly in remote and cost-intensive study areas in the Arctic, is prudent. Our primary research question was to assess whether the DBO stations that were selected based on biomass hotspots for macrofauna and water column productivity are also suitable to provide a sampling framework for assessing the biomass and species diversity of epibenthos and demersal fish.

2. Material and methods

Sampling was conducted at 67 stations during the AMBON cruise in the Chukchi Sea on the R/V *Norseman II* from 8 August–5 September 2015 (Fig. 1). The AMBON station coverage includes stations along the DBO3 line in the southern Chukchi Sea and along the DBO4 line in the northern Chukchi Sea (Fig. 1). Epibenthic invertebrates and demersal fishes were collected with a plumb-staff beam trawl with a 2.26 m opening and a 7-mm mesh net and a 4-mm cod end liner. Trawls were conducted during the night for 2–5 min duration at ~1.5 knots. Trawl distances ranged from 160 to 840 m, with an average of 373 m. Trawl hauls were rinsed, if necessary, and then sorted on board to the lowest taxonomic level possible. For invertebrate taxa that could not be identified on board, voucher specimens were preserved in 4% formaldehyde or 99% molecular-grade ethanol for later consultation with taxonomic experts. Most invertebrate identifications were made to species or genus level, although taxonomic resolution for several phyla was low because of lack of taxonomic expertise, especially Bryozoa, Hydrozoa and Porifera. In cases where morphologically distinct taxa within these phyla could be distinguished, we kept these as separated taxa for analysis. Fish were sorted to species or genus level. Juvenile fishes (mostly gadids) were excluded from the analysis because they are typically pelagic and were likely collected in the water column while the trawl was retrieved. All fish and invertebrate individuals, except for

colonial taxa, were enumerated; bulk wet weight was determined at the lowest taxonomic level using spring and digital hanging scales. Trawl distance was estimated by multiplying average trawling speed by the time the trawl was in contact with the bottom. Bottom contact was assessed based on depth recordings by a time-depth recorder (TDR, Star Oddi, Gardabaer, Iceland) attached to the net opening. Abundance and biomass for all taxa were then quantified for each haul as catch per unit effort (CPUE), where effort was computed as trawl distance multiplied by the width of the net opening.

Environmental conditions were assessed from water column and sediment samples. Station depth, surface and bottom temperature (°C) and salinity measurements were taken from CTD profiles (Seabird Model SBE911). Water samples from Niskin bottles attached to the CTD were used to analyze chlorophyll *a* (chl *a*) and inorganic nutrients (ammonia, phosphate, nitrite + nitrate, silicate). In addition, maximum chl *a* values at each station were used in the environmental matrix. Samples were processed as follows: Subsamples for inorganic nutrients were filtered shipboard (Whatman GFF), and frozen for post cruise analyses. Nutrient samples were analyzed at the Nutrient Analytical Services Laboratory (NASL) at the Chesapeake Biological Laboratory (see <http://nasl.cbl.umces.edu/> for standard methods used) at the University of Maryland Center for Environmental Science (UMCES). Filtered samples for chl *a* measurements were analyzed shipboard using a Turner Designs AU-20 fluorometer after 24-h dark extraction in 90% acetone at 4 °C (non-acidification or Welschmeyer method; see Cooper et al., 2012, 2013 for details). The inventory of active chl *a* in surface sediments (upper 1 cm) was measured by collecting undisturbed surface sediments from a van Veen grab with a cut-off 10 cc syringe. Sediments were incubated in the dark with 90% acetone for 12 h at 4 °C and measurements made as with water samples, using a Turner Designs AU-20 fluorometer without acidification (Welschmeyer method). Another subsample of surface sediment was collected and sediment grain size determined according to the Wentworth convention (< 0 phi – 4 phi, as well as modal size of phi; for methods see Gee and Bauder, 1986; Grebmeier et al., 1989).

Epifauna and demersal fish catch data were considered separately. While both are benthic ecosystem components, they differ considerably in their association with the bottom, especially in their ability to move. In the Chukchi Sea, demersal fishes have a strong association with water mass characteristics (Norcross et al., 2010), while epifaunal invertebrates are more closely related to substrate characteristics (Bluhm et al., 2009). In addition, the order of magnitude higher taxon number and larger biomass of epifauna over demersal fish obscures any fish-specific patterns. We confirmed that there was no correlation between epifaunal and fish biomass or taxon richness across stations (Pearson product-moment correlation coefficient $r = -0.039$ and 0.012 , respectively). While the epifauna and fish dissimilarity matrices showed some coherence (RELATE analysis in Primer-e v7, $\rho = 0.508$), we decided that the ecological differences warranted separate analyses.

Analyses of the epifaunal and fish assemblages were performed based on biomass rather than numerical abundances because these data contained all taxa, including epifauna colonial taxa, and because biomass is a more meaningful ecological indicator based on trophic and energetic considerations. All assemblage-level analyses were performed using the multivariate software package Primer-e (v7; Clarke and Gorley, 2015). A Bray-Curtis similarity matrix was created using fourth-root transformed biomass data for epifauna and fish to reduce the influence of biomass-dominant taxa on the analyses. A hierarchical cluster analysis was then used to group stations by similarity (group averaged on the similarity matrix) for both epibenthic invertebrates and fishes. All dendrograms were inspected for significantly different clusters (SIMPROF test, $\alpha = 0.05$); in the case of epibenthic invertebrates, SIMPROF resulted in an exceedingly large number of significant clusters. Here, we combined station groups at a lower level of similarity aiming to result in more interpretable station groupings. The resulting clusters were then plotted spatially according to sampling location

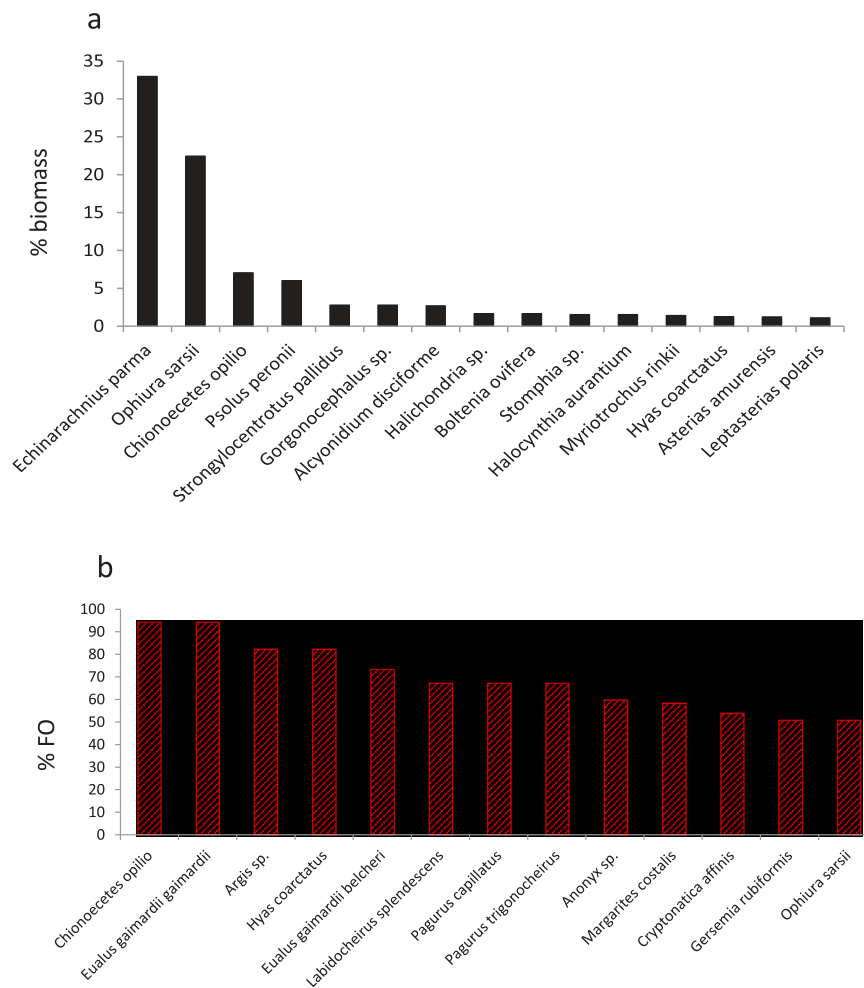


Fig. 2. Epifaunal taxa proportional biomass (a) and frequency of occurrence (FO) (b). Only taxa contributing more than 1% to total average biomass and 50% FO are shown.

(Matlab M-Map) to visualize the spatial distribution of assemblage types. A similarity percentages (SIMPER) routine was used to identify the taxa contributing most to similarities within and dissimilarities among station clusters. Epifaunal invertebrate species contributing cumulatively $\geq 30\%$ to within-cluster similarity are presented; for fishes, we present species contributing cumulatively $\geq 50\%$ to within-cluster similarity for higher resolution of species driving cluster similarity because of the generally much lower fish species richness. Coverage of assemblages by the two DBO lines versus the larger AMBON station coverage was then compared.

We tested whether biological assemblages were significantly related to observed environmental variability and, if so, identified subsets of environmental variables that were most strongly related to each assemblage. These analyses were conducted separately for the epifauna and fish assemblages; for both components, separate analyses were conducted for the full set of stations and for the DBO-stations only. Pairwise dissimilarities among stations for each biological dataset were related to pairwise Euclidean distances among environmental variables for the corresponding set of stations using the trend correlation routine called BEST in Primer-e. This is a Mantel-type test that selects the subset of environmental variables whose dissimilarities are most strongly related to the biological dissimilarities (Clarke and Ainsworth, 1993). Environmental variables were normalized to a common measurement scale in Primer and then tested for collinearity using Spearman rank correlations and pairwise scatterplots. For variables that were correlated at $> 90\%$, one of the variables was removed. This applied to the nutrients phosphate and nitrite + nitrate, of which we retained the

nitrite + nitrate measurement for the analyses.

3. Results

Across the 67 AMBON stations, we collected 317 nominal epibenthic invertebrate taxa (including morphologically distinct taxa within phyla where species identifications could not be made); of these 57 taxa were colonial. Taxon richness was dominated by the phyla Mollusca (91 taxa) and Arthropoda (83 taxa), followed by Annelida (32 taxa) and Echinodermata (29 taxa). Total wet weight biomass of epibenthic invertebrates across all stations was dominated on the class or order level by echinoids with 36% (nearly entirely driven by the sand dollar *Echinarachnius parma* abundant at some stations along line ML6), ophiuroids with 25% (mostly dominated by *Ophiura sarsii*), decapods with 11% (mostly snow crab *Chionocetes opilio*), holothurians with 8% (especially *Psolus peronii*), and ascidians (5%, mostly solitary *Boltenia ovifera*). At the species level, *Echinarachnius parma* and *Ophiura sarsii* were the two single most dominant species in terms of biomass (Fig. 2a), although they were not the species with the highest frequency of occurrence (FO, Fig. 2b). The crab *Chionocetes opilio* and the shrimp *Eualus gaimardii gaimardii* had the highest FO and occurred at 94% of all stations (Fig. 2b). Fish taxon richness was mostly represented in the Cottidae (6 taxa), followed by Agonidae (poachers), Liparidae (snail fishes), Pleuronectidae (flounders), Stichaeidae (pricklebacks) and Zoarcidae (eelpouts) (3 taxa each). In general, total fish biomass was mostly comprised (84% of total biomass) by four families: Cottidae (sculpins), Stichaeidae, Gadidae (cods), and Liparidae. Among the 24

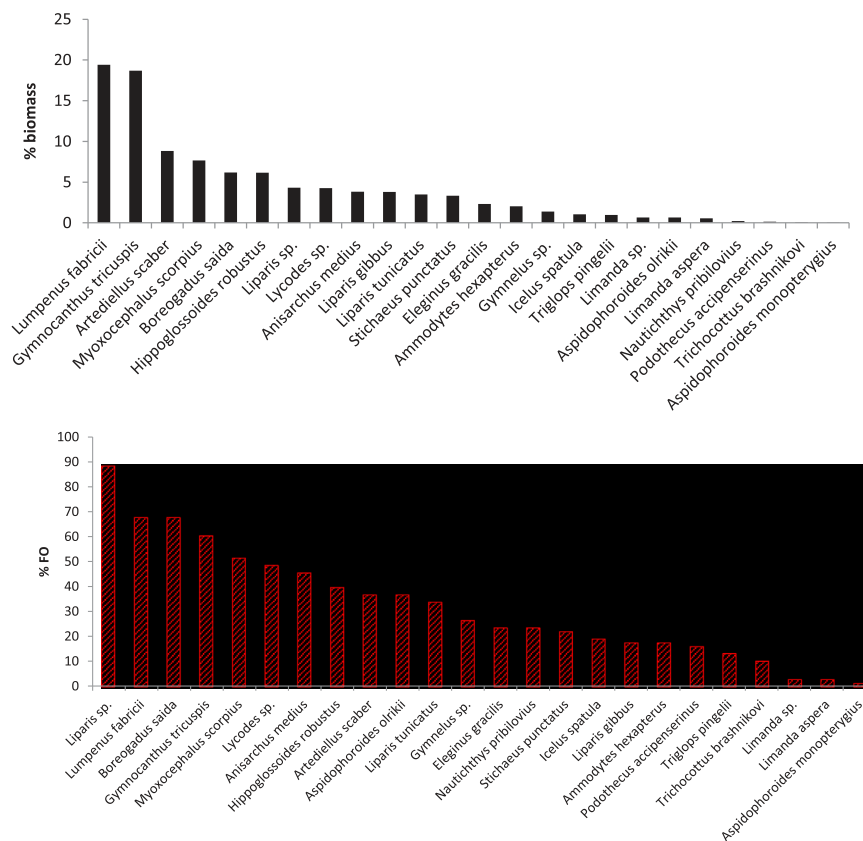


Fig. 3. Fish taxa proportional biomass (a) and frequency of occurrence (FO) (b).

collected fish taxa, total biomass was overwhelmingly dominated by just two species, the slender eelblenny *Lumpenus fabricii* (20%) and the Arctic staghorn sculpin *Gymnocanthus tricuspis* (19%). Fish taxa with high biomass contributions were not necessarily those with the highest FO; for example, *Liparis sp.* occurred in 88% of the samples but only contributed about 4% to overall fish biomass (Fig. 3). Arctic cod (*Boreogadus saida*), often the dominant species on Arctic shelves, was the fifth most abundant species by weight in our collections (~6% of total biomass) and occurred at 68% of the stations.

Taxon richness for epifaunal invertebrates ranged from 13 to 66 per station (at ML1–2 and ML5–7, respectively), and between 0 and 14 for fish taxa (at ML6–3 and ML3–6, respectively) (Fig. 4a and b). Overall epifaunal species richness was higher in the northern than southern study region (Fig. 4a). For the total study region, the DBO stations harbored 180 of the 317 total epifaunal taxa (57%). Along the DBO3 stations we encountered 97 taxa, compared with 127 taxa for the entire southern study region (DBO3 and CL lines; 76% along DBO3). A total of 133 epifaunal taxa (45%) were encountered along the DBO4 line of the 294 taxa that were found in the entire northern study region. For demersal fishes, of the 24 total fish taxa across the total study region we found 21 taxa along both DBO lines (88%). The DBO3 line was represented by 18 taxa, representing 90% of the 20 taxa total found within the entire southern study region (DBO3 and CL lines combined). Along the DBO4 line, 18 fish taxa were found compared with the 24 taxa found in the overall northern study region (75% along DBO4). Among the fish species not encountered along the DBO lines were some generally rare species (e.g. alligatorfish *Aspidophoroides monopterygius*) but also some taxa that were otherwise relatively common (e.g. sturgeon poacher *Podothecus accipenserinus*).

Biomass per station for epifauna ranged from a low of 790 g wet weight 1000 m^{-2} (stn ML3–13) to a high of 153274 g wet weight 1000 m^{-2} (stn ML6–1) (Fig. 5a). Epifaunal biomass along DBO3 was within the lower range of overall biomass while biomass along the

DBO4 line was in the intermediate range (Fig. 5a). Fish biomass ranged from 0 to 2362 g wet weight 1000 m^{-2} (ML6–3 and ML1–2), respectively; fish biomass at the DBO3 stations was in the higher range while biomass at DBO4 stations was low (Fig. 5b).

Epibenthic invertebrate assemblages separated into eleven clusters and two single stations (ML3–2 and ML5–1) (Fig. 6). Station clusters were distributed along the south-north axis as well as the inshore-offshore axis of the study area (Fig. 7). The DBO3 stations separated evenly in an inshore (A) and offshore (B) cluster. The inshore cluster was characterized mostly the ascidian *Halocynthia aurantium*, while the main character species for the offshore cluster was the snow crab *Chionoecetes opilio* (Table 1). Two of the DBO4 stations were part of a more coastal cluster (H), mostly characterized by the sea cucumber *Psolus peronii*, and the remaining four DBO4 stations were part of a mid-shelf cluster (I), mostly characterized by the brittle star *Ophiura sarsii* (Fig. 7). Between 1 and 5 species accounted for within-cluster similarity of $\geq 30\%$ (Table 1).

The demersal fish assemblage only grouped into two clusters and one single station (ML6–3), where no fish were caught (Fig. 8). One cluster (a) mostly encompassed coastal stations, including all DBO3 stations, and the other cluster (b) comprised offshore stations, including all DBO4 stations (Fig. 9). The coastal cluster was characterized by the Arctic staghorn sculpin *Gymnocanthus tricuspis*, the slender eelblenny *Lumpenus fabricii*, and snail fishes (*Liparis sp.*) (57% cumulative similarity) while the offshore cluster was characterized by snail fish (*Liparis sp.*), eelpouts (*Lycodes sp.*), and Arctic cod *Boreogadus saida* (51% cumulative similarity).

The suite of environmental variables that best explained epifaunal assemblage structure across the entire sampling region included depth, bottom and surface temperatures, and the proportion of sediment grain size $\phi \geq 5$, with a correlation coefficient of $\rho = 0.618$. Of these, sediment grain size $\phi \geq 5$ was the single variable with the highest correlation coefficient ($\rho = 0.481$) with epifaunal assemblage

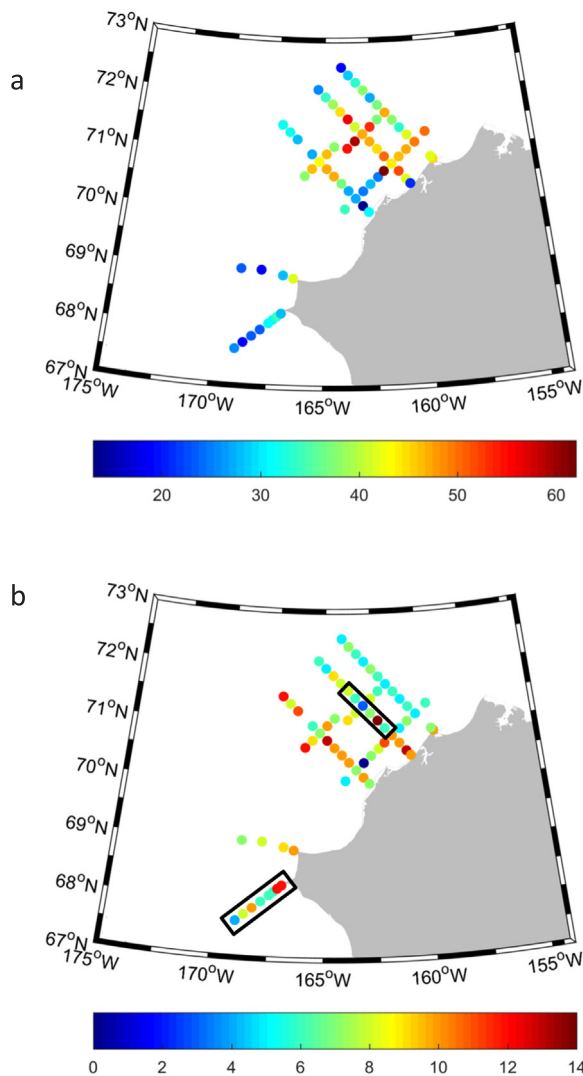


Fig. 4. Epifaunal species richness (a) and fish species richness (b). Boxes indicate stations that represent DBO coverage (see Fig. 1).

structure. When only DBO stations were considered, correlation of epibenthic assemblage structure with environmental variables was stronger at $\rho = 0.859$, with bottom temperature, surface temperature and salinity, grain size phi 2, modal grain size, and sediment chlorophyll *a* content contributing most to the correlation. Modal grain size was the single variable with the highest explanatory power ($\rho = 0.702$). For the fish assemblage, the environmental variables bottom temperature, bottom and surface salinity, and grain size phi ≥ 5 explained most of the fish assemblage structure ($\rho = 0.422$) in the whole data set, with bottom temperature being the most influential variable ($\rho = 0.330$). When only the DBO stations were considered, the combination of surface temperature and salinity had the strongest correlation to the fish assemblage ($\rho = 0.525$), with again bottom temperature as the most influential single variable ($\rho = 0.422$).

4. Discussion

We analyzed the concurrent results that two existing observing programs in the Arctic Chukchi Sea yielded for epibenthic invertebrate and demersal fish assemblages in terms of biomass and biodiversity. The two observing programs differ in their purpose and their spatial extent. The DBO's incentive is to focus on seasonal and interannual variability in macrobenthic hotspots, regions of persistent and high

benthic biomass due to high water column productivity and tight pelagic-benthic coupling (Grebmeier et al., 2010, 2015b; Moore and Grebmeier, 2018). AMBON's objective is to describe and observe the regional biodiversity of various marine ecosystem components. Given these differences in the two programs, careful consideration is needed to assess how much these two initiatives can contribute to each other's objectives to optimize sampling efforts and maximize scientific gain.

In terms of benthic biomass hotspots characterizing the two DBO lines, epibenthic invertebrates and fishes displayed opposite trends. While epibenthic biomass along the DBO3 lines was at the lower range of the epibenthic biomass distribution across the total (AMBON-wide) study region, fish biomass was comparatively high. Conversely, epibenthic biomass was relatively high but fish biomass was relatively low along the DBO4 line. This confirms that neither epibenthic invertebrates nor fishes are as tightly linked to areas of high vertical fluxes associated with high local primary production regimes as is the macrofauna, on which the hotspot definition for the DBO program is based (Link et al., 2013; Grebmeier et al., 2015b). This decoupling is likely related to the much higher mobility of many epibenthic invertebrates and especially fishes, as well as the high diversity of feeding types (particle feeders and also predators/scavengers) among these ecosystem components (e.g. Bluhm et al., 2009; Iken et al., 2010; Norcross et al., 2010; Divine et al., 2015). This decoupling is even more pronounced for the mostly predatory fishes (Whitehouse et al., 2017). Of course, predatory epifauna and fishes are linked to particle flux through their macrofaunal prey, but we show that direct relationships from primary production to fish and epifauna are often comparatively weak. This conclusion was supported by the fact that water column chl *a* was not an environmental variable driving these assemblages. Interestingly, epibenthos and fish biomass patterns were not similar, neither along the DBO lines nor the overall AMBON study region. This is likely related to the closer link of the highly mobile fishes to water mass characteristics (this study; Norcross et al., 2010) than epifauna, which is typically more closely related to sediment characteristics (this study; Bluhm et al., 2009; Pisareva et al., 2015).

Species richness captured within the AMBON spatial coverage for demersal fishes and epibenthic invertebrates was largely representative of known patterns in the region, while acknowledging that direct comparisons to other studies are challenging because of variable sampling and – in case of epifauna - identification effort. Other studies across the Chukchi Sea shelf reported very similar fish species identities and species richness as the 24 taxa we found during the AMBON sampling (33 species, Mecklenburg et al., 2007; 30 species, Norcross et al., 2010; 29 species, Norcross et al., 2013). Also, our epifaunal invertebrate species number of 127 found for the southern study region was relatively similar to the 165 species reported from a slightly larger and denser station grid reported by Bluhm et al. (2009) and 165 taxa reported from the southern US Chukchi Sea including the Chukchi Bight (Feder et al., 2005). In the northern study region, the 294 epibenthic taxa we identified are comparable to Blanchard et al.'s (2013) report of 239 taxa in a slightly smaller study region. However, both these numbers are much higher than the 44 epifaunal taxa reported from the larger Hana Shoal region (Ravelo et al., 2014), likely because of the much coarser level of identification than in the present study and the exclusion of some species-rich groups like amphipods in that study.

From the biodiversity perspective that is at the core of the AMBON project, about half of the epibenthic species that occurred in the entire AMBON study area were also observed on the DBO transects, with a much higher percentage along the DBO3 transect in the south versus the DBO4 transect in the north. The DBO3 transect represented epibenthic species richness and assemblage patterns of the southern study area quite well. Invertebrate taxa characteristic for the epifaunal assemblages in the southern study region also were similar to some of those reported previously (Bluhm et al., 2009; cluster CN in that study), namely the snow crab *Chionoecetes opilio*, the sea star *Leptasterias polaris*, and the shrimp *Argis* sp. These assemblage patterns, albeit not

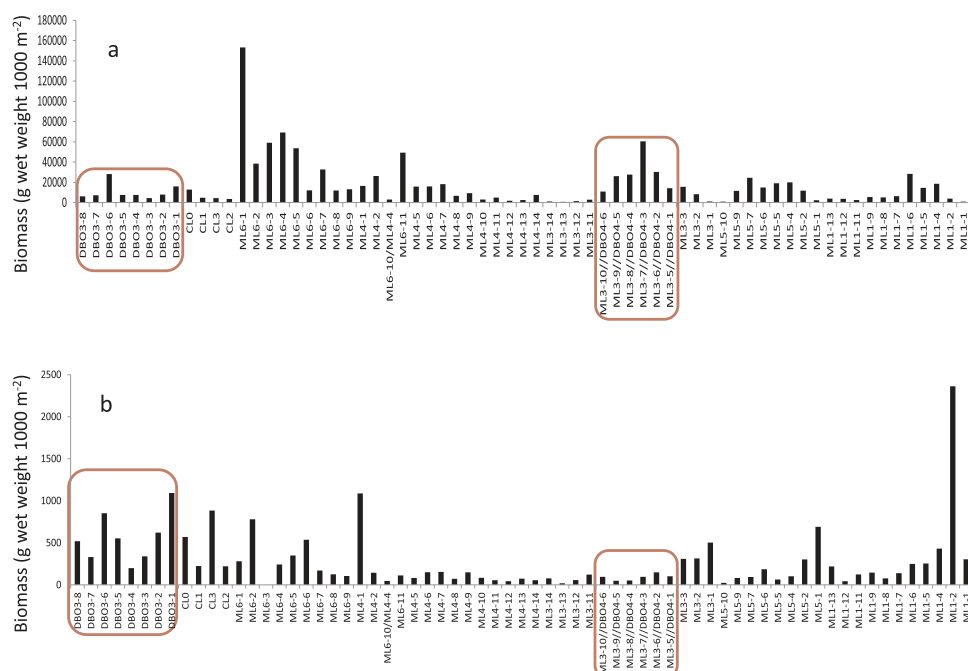


Fig. 5. Epifauna (a) and fish (b) biomass per station. Stations that represent DBO coverage are circled in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

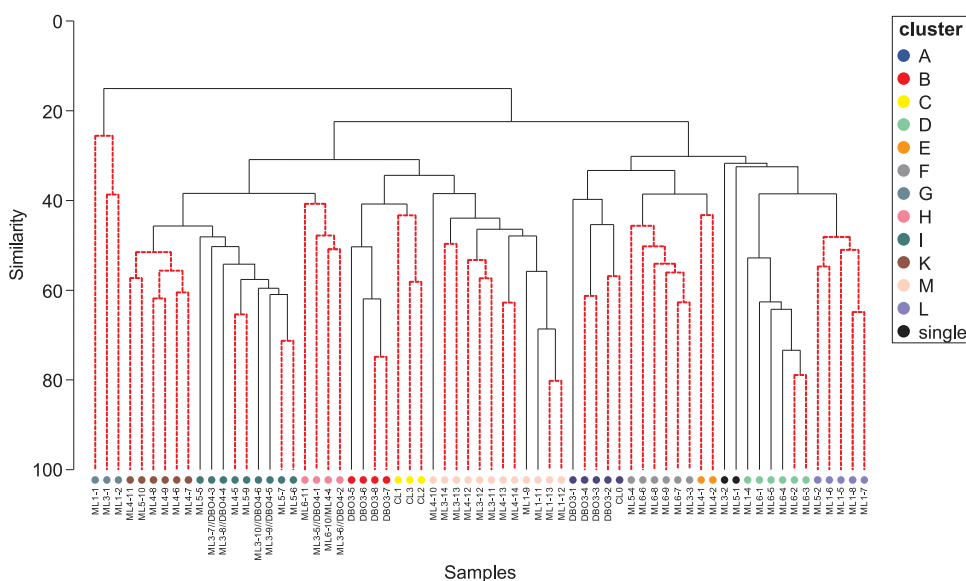


Fig. 6. Hierarchical clustering of epifaunal assemblages based on fourth-root transformed biomass data and a Bray-Curtis similarity matrix. Red lines indicate non-significant differences among stations; cluster assignment is guided by SIMPROF results but occasionally grouped at lower similarity level to obtain manageable cluster groupings. Clusters are denominated with upper-case letters A–M, “single” refers to stations that did not group with any cluster. Colors and letters are the same as in Fig. 7 but have no relationship to the fish assemblage clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

absolute biomass, have been fairly stable over at least decadal time scales (Grebmeier et al., 2015a). This suggests that despite the generally relatively low station coverage in the southern region, epibenthic communities are representatively sampled by both the AMBON and the DBO3 grid strategies. The groupings into coastal and offshore assemblage clusters align with the major water masses in that region, corresponding to inshore Alaska Coastal Current and the offshore Bering Anadyr Water (Danielson et al., 2017a), as well as sediment characteristics that drive assemblage structure (Bluhm et al., 2009). The correspondence between our results and the study by Bluhm et al. (2009), which was based on a much denser sample coverage than either AMBON or DBO station coverage, supports our results likely being a reasonable representation of the general epifaunal community patterns of the southern Chukchi region, despite limited spatial coverage. This may be in part due to the less complex hydrographic and bathymetric features in the southern compared with the northern study region,

driving more simply structured biological communities in the south (Danielson et al., 2017a; Stabeno et al., 2018).

In contrast to the southern study region, regional assemblage patterns apparent from the AMBON sampling grid were not well captured by sampling the DBO4 transect alone. The northern Chukchi Sea is hydrographically and topographically complex (Weingartner et al., 2005), so it may not be surprising that epibenthic assemblages are spatially heterogeneous, too (e.g. Blanchard et al., 2013; Ravelo et al., 2014; Tu et al., 2015). While the DBO4 line captured the northern central shelf assemblage clusters H and I very well, several of the other major northern clusters were not represented. If the DBO4 transect were extended farther in- and offshore as along AMBON's ML3 line, a much greater representation of the northern Chukchi Sea epibenthic assemblage clusters and diversity would be achieved. This would especially include the coastal cluster F and the offshore cluster M. Yet, the other abundant clusters (e.g. clusters K and L) would still not be sampled.

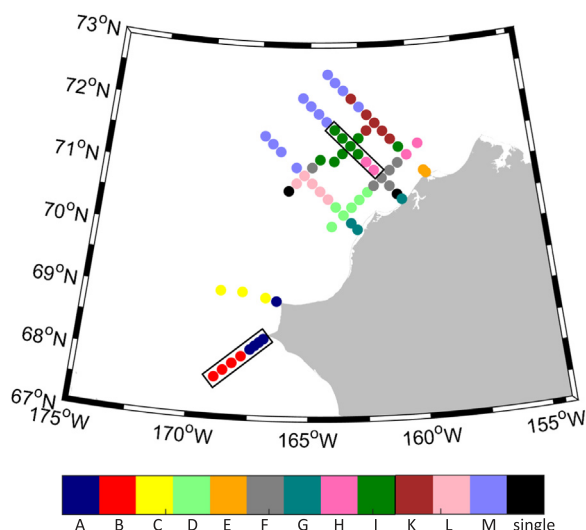


Fig. 7. Spatial distribution of epifaunal assemblage clusters (A–M). “Single” refers to stations that did not group with any cluster. Stations that represent DBO coverage are encircled. Colors and letters are as in Fig. 6 but have no relationship to the fish assemblage clusters (Figs. 8 and 9). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

At least some of these epifaunal invertebrate assemblage clusters have been stable over time, as is reflective of a generally proposed feature of Arctic benthos (Piepenburg, 2005; Renaud et al., 2007). An example for the persistent assemblages in this study is the northern coastal assemblage (cluster F) dominated by the sand dollar, *Echinarachnius parma* (also described by Grebmeier et al., 2006 and Ravelo et al., 2014). Also, the distribution of *O. sarsii* in the center of the northern study region (cluster I, which includes most of the DBO4 stations, and is also typical for the adjacent cluster K to the north) is a persistent feature, as is the high abundance of *C. opilio* in the surrounding regions to the south and offshore (clusters L and M, respectively), as previously documented (Ravelo et al., 2014; Groß et al., 2017). This stability in epibenthic community composition is likely a result of the typically high longevity of many arctic invertebrates (e.g. Bluhm et al., 1998; Ravelo et al., 2017) and the strong association with stationary environmental variables such as sediment characteristics (this study; Bluhm et al., 2009). This suggests that sampling of these epifaunal communities could occur on less than annual scales and changes could still be detected over longer time frames.

Spatial distribution of fish diversity showed a trend of higher diversity in the south and decreasing diversity to the north (lowest along line ML4). This reflects the stronger influence of the Pacific waters entering from the Bering Sea in the south and of the northern waters that were modified during their transport across the shelf, including

local cold winter water formation in the northeastern Chukchi Sea (Weingartner et al., 2013). Higher fish species richness in the south is consistent with the higher number of boreal-arctic or boreal fishes that have access to the southern Chukchi Sea versus the number of species that could be expected to occur in the more northern study region (Mecklenburg et al., 2011; Norcross et al., 2013). Fish biodiversity identified by sampling solely on the DBO transects was nearly 90% of that observed over the whole AMBON grid. This much higher diversity compared with epifaunal diversity represented along DBO transects was likely related to the much lower total species number of fishes in general and the wide distribution of most fish species across the entire shelf (also see Mecklenburg et al., 2011).

The wide distribution of fish species across the study region is the likely reason that we found little spatial fish assemblage structure. The species most characteristic for the more coastal fish assemblage (cluster a), *Gymnancistrus tricuspidis* and *Lumpenus fabricii*, are known to utilize the more physically structured coastal waters (Norcross et al., 2013; Logerwell et al., 2015). The eelpouts (*Lycodes* sp.) and snail fishes (*Liparis* sp.) characteristic of the more offshore, northern cluster (b) are among the most abundant demersal fish families in the Chukchi Sea (Logerwell et al., 2015). This assemblage cluster was also characterized by Arctic cod, a key link in Arctic food webs (Hop and Gjøsaeter, 2013) and of more arctic biogeographic affinity (Mecklenburg et al., 2011). A similar fish assemblage was also observed in 2009/2010 in a slightly smaller study area in the northern study region (Norcross et al., 2013). From an observing perspective of fish diversity, extension of the DBO4 line towards off- and inshore regions as suggested above for epifauna would be useful to include the coastal fish assemblage in the northern Chukchi Sea in the overall sampling scheme.

5. Conclusions

The results presented here indicate that the purpose and the scale of existing observing systems have to be carefully evaluated when considering which ecosystem metrics shall be monitored. For example, the DBO program was initially focused on well-defined regions where persistent benthic biomass hotspots occurred while the AMBON program has a larger scale, regional biodiversity focus. DBO locations where benthic macrofaunal hotspots occur are not as consistently high in epibenthic or fish biomass. We further documented that while the DBO3 line represents epibenthic and fish diversity and assemblage patterns well for the larger AMBON study area, sampling along the DBO4 transect alone did not represent the larger regional patterns well, at least for the epibenthic invertebrate assemblage. In assemblages with relatively high taxon mobility such as for many epibenthic invertebrates and fishes, sampling on a larger spatial scale is likely necessary to reliably capture regional community patterns (Armonies, 2000). Depending on the specific community and region, the biologically relevant area (neighborhood) for benthic invertebrates and demersal fish that is needed for monitoring and/or the development of

Table 1
Epifaunal assemblage clusters and species contributing to $\geq 30\%$ of cumulative within-cluster similarity.

Cluster	Taxa contributing to cluster similarity	Cum. Sim. %
A	<i>Halocynthia aurantium</i> , <i>Gorgonocephalus</i> sp., <i>Argis</i> sp., <i>Eualus gaimardii gaimardii</i>	34.10
B	<i>Chionoecetes opilio</i> , <i>Leptasterias polaris</i> , <i>Stomphia</i> sp.	37.24
C	<i>Chionoecetes opilio</i> , <i>Neptunea heros</i>	39.68
D	<i>Echinarachnius parma</i> , <i>Chionoecetes opilio</i>	35.39
E	<i>Strongylocentrotus pallidus</i> , <i>Eualus gaimardii gaimardii</i> , <i>Gersemia rubiformis</i>	35.23
F	<i>Psolus peronii</i> , <i>Hyas coarctatus</i> , <i>Strongylocentrotus pallidus</i> , <i>Argis</i> sp., <i>Chionoecetes opilio</i>	33.85
G	<i>Argis</i> sp.	30.37
H	<i>Psolus peronii</i> , <i>Ophiura sarsii</i> , <i>Chionoecetes opilio</i> , <i>Hyas coarctatus</i>	34.22
I	<i>Ophiura sarsii</i> , <i>Chionoecetes opilio</i> , <i>Buccinum polare</i> , <i>Nemertea</i> , <i>Lesptasterias groenlandica</i>	31.42
K	<i>Ophiura sarsii</i> , <i>Chionoecetes opilio</i> , <i>Pagurus capillatus</i> , <i>Myriotrochus rinkii</i>	30.01
L	<i>Chionoecetes opilio</i> , <i>Hyas coarctatus</i> , <i>Stomphia</i> sp., <i>Labidochirus splendescens</i>	31.30
M	<i>Chionoecetes opilio</i> , <i>Pagurus capillatus</i> , <i>Pagurus trigonocheirus</i>	31.49

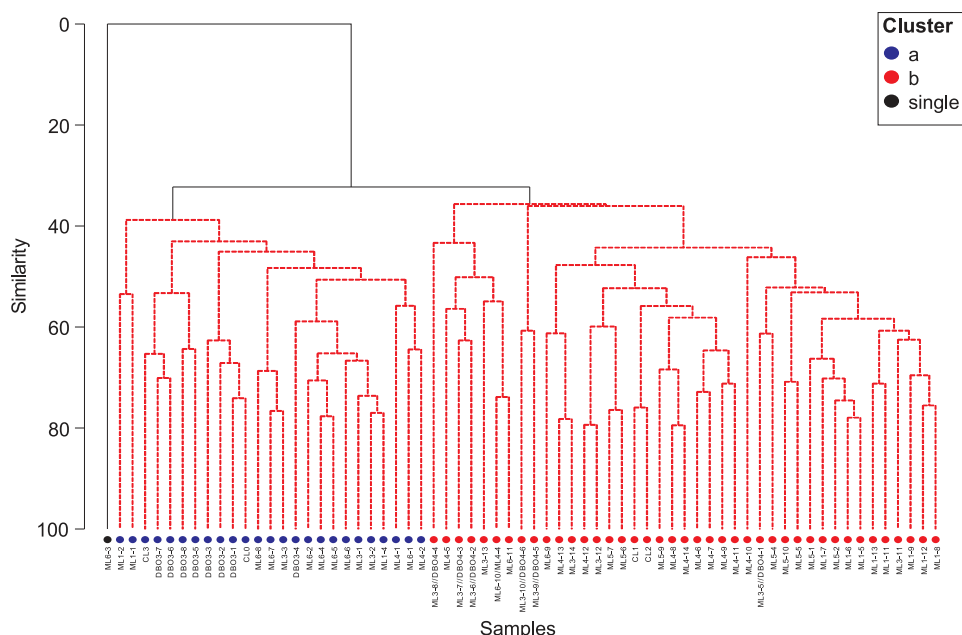


Fig. 8. Hierarchical clustering of fish assemblages based on fourth-root transformed biomass data and a Bray-Curtis similarity matrix. Clusters are assigned based SIMPROF results, with red connectors indicating non-significant differences among stations. Clusters are denominated with lower-case letters a and b; “single” refers to stations that did not group with any cluster. Colors and letters are the same as in Fig. 9 but have no relationship to the epifauna assemblage clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

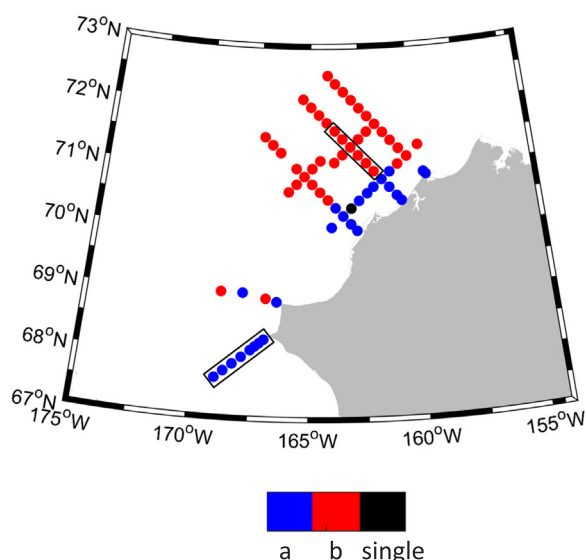


Fig. 9. Spatial distribution of fish assemblage clusters (a-b). Stations that represent DBO coverage are encircled. Colors and letters are as in Fig. 8 but have no relationship to the epifaunal assemblage clusters (Figs. 6 and 7). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Marine Protected Areas is projected to be several hundred kilometers (Palumbi, 2004). This is consistent with guiding principles in marine spatial planning approaches to take into account *context*, i.e. the larger-scale assemblage patterns, and *variability*, i.e. the level of spatial fluctuation of these assemblages (Foley et al., 2010). More recently, the development of Ecologically and Biologically Significant Areas (EBSAs) has become an important tool for monitoring arctic areas that have particularly high ecological or biological importance for the overall ecosystem (Cobb et al., 2014). EBSA development is based on seven criteria that include, among others, uniqueness of the system, importance of habitats, and biological diversity (Dunn et al., 2014). Sufficient temporal and spatial resolution data are needed to assess these criteria for arctic systems (Cobb et al., 2014). For temporal resolution, we suggest that the relative stability of arctic benthic shelf systems over time warrants that epibenthic and fish communities might not have to

be sampled on a seasonal or annual schedule but that sampling every few (2–3) years could be sufficient to observe and detect long-term changes. This is similar to what has been proposed for coastal, rocky shore arctic systems (e.g. Kortsch et al., 2012) although comparability between shelf and nearshore systems may be constrained. To reduce the discrepancy between the slower response time of epibenthic invertebrates and fishes versus the rates of changes of environmental variables, we also recommend, if possible, linking these biological surveys every few years with continuous environmental measurements from moored instrumentation that can provide important contextual data for environmental changes (Danielson et al., 2017b). In terms of spatial sampling scales, we suggest that sampling of the smaller scale such as represented by the DBO transect lines may need to be extended to better capture more of the regional characteristics of the epibenthic invertebrate and demersal fish assemblages. Larger-scale regional sampling such as through AMBON, however, is needed and useful at the beginning of observation planning as well as on longer time scales (e.g. every 5–10 years) to provide larger context for the more regionally focused sampling (Foley et al., 2010; Magurran et al., 2010). All these considerations support that the assemblage information gained from the larger-scale AMBON project are essential to determine useful long-term observing scales for these ecosystem components.

Acknowledgements

This work was funded through a National Ocean Partnership Program (NOPP Grant NA14NOS0120158) by the National Oceanographic and Atmospheric Administration (NOAA), the Bureau of Ocean Management and Shell Exploration & Production, under management of the Integrated Ocean Observing System (IOOS). We specifically appreciate the support of Gabrielle Canonico (NOAA-IOOS) and Cathy Coon (Bureau of Ocean Energy Management Alaska). We thank the captain and crew of the RV Norseman II, Norseman Maritime, for excellent field support. We also appreciate the help of students and technicians with field and lab work. We thank two anonymous reviewers for their valuable comments.

References

- Ambrose, W., Clough, L., Tilney, P., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. *Mar. Biol.* 139 (5), 937–949.
- Armonies, W., 2000. On the spatial scale needed for benthos community monitoring in

- the coastal North Sea. *J. Sea Res.* 43 (2), 121–133.
- Blanchard, A.L., Parris, C.L., Knowlton, A.L., Wade, N.R., 2013. Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009–2010. *Cont. Shelf Res.* 67, 67–76.
- Bluhm, B.A., Piepenburg, D., von Juterzenka, K., 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: echinoidea) in the northern Barents Sea. *Polar Biol.* 20 (5), 325–334.
- Bluhm, B.A., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. *Ecol. Appl.* 18 (sp2).
- Bluhm, B.A., Iken, K., Mincks, S.L., Sirenko, B.I., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. *Aquat. Biol.* 7, 269–293.
- Christiansen, J.S., Mecklenburg, C.W., Karamushko, O.V., 2014. Arctic marine fishes and their fisheries in light of global change. *Glob. Change Biol.* 20 (2), 352–359.
- Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.* 92, 205–219.
- Clarke, K.R., Gorley, R.N., 2015. *PRIMERv7: User Manual/Tutorial*. PRIMER-E, Plymouth, pp. 296.
- Cobb, D.G., Roy, V., Link, H., Archambault, P., 2014. Information to support the re-assessment of ecologically and biologically significant areas (EBSAs) in the Beaufort Sea large Ocean management area. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2014/097, 37 (iv +).
- Cooper, L.W., Janout, M.A., Frey, K.E., Pirtle-Levy, R., Guarinello, M.L., Grebmeier, J.M., Lovvorn, J.R., 2012. The relationship between sea ice break-up, water mass variation, chlorophyll biomass, and sedimentation in the northern Bering Sea. *Deep Sea Res. II* 65, 141–162.
- Cooper, L.W., Sexson, M.G., Grebmeier, J.M., Gradinger, R., Mordy, C.W., Lovvorn, J.R., 2013. Linkages between sea ice coverage, pelagic-benthic coupling and the distribution of spectacled eiders: observations in March 2008, 2009 and 2010 from the Northern Bering Sea. *Deep Sea Res.* II 94, 31–43.
- Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017a. A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. *Deep Sea Res.* II 135, 7–26.
- Danielson, S.L., Iken, K., Hauri, C., Hopcroft, R.R., McDonnell, A.M., Winsor, P., Lalonde, C., Grebmeier, J.M., Cooper, L.W., Horne, J.K., Stafford, K.M., 2017b. Collaborative approaches to multi-disciplinary monitoring of the Chukchi shelf marine ecosystem: networks of networks for maintaining long-term Arctic observations. *OCEANS–Anchorage 2017*, 1–7 (IEEE).
- Day, R.H., Weingartner, T.J., Hopcroft, R.R., Aerts, L.A., Blanchard, A.L., Gall, A.E., Galloway, B.J., Hannay, D.E., Holladay, B.A., Mathis, J.T., Norcross, B.L., 2013. The offshore northeastern Chukchi Sea, Alaska: a complex high-latitude ecosystem. *Cont. Shelf Res.* 67, 147–165.
- Divine, L.M., Bluhm, B.A., Mueter, F.J., Iken, K., 2015. Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes. *Deep Sea Res. II* 135, 124–136.
- Duffy, J.E., Amaral-Zettler, L.A., Fautin, D.G., Paulay, G., Rynearson, T.A., Sosik, H.M., Stachowicz, J.J., 2013. Envisioning a marine biodiversity observation network. *Bioscience* 63 (5), 350–361.
- Duffy, J.E., Godwin, C.M., Cardinale, B.J., 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* 549 (7671), 261–264.
- Dunn, D.C., Ardron, J., Bax, N., Bernal, P., Cleary, J., Cresswell, I., Donnelly, B., Dunstan, P., Gjerde, K., Johnson, D., Kaschner, K., 2014. The convention on biological diversity's ecologically or biologically significant areas: origins, development, and current status. *Mar. Pol.* 49, 137–145.
- Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., Matsuno, K., Nelson, R.J., Yamaguchi, A., Eisner, L.B., 2015. Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945–2012. *Oceanography* 28 (3), 100–115.
- Feder, H.M., Jewett, S.C., Blanchard, A., 2005. Southeastern Chukchi Sea (Alaska) epibenthos. *Polar Biol.* 28 (5), 402–421.
- Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.M., Prahler, E., Rohr, N., Sivas, D., Beck, M.W., Carr, M.H., 2010. Guiding ecological principles for marine spatial planning. *Mar. Pol.* 34 (5), 955–966.
- Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), *Methods of Soil Analysis*. Part 1, 2nd ed. ASA and SSSA, Madison, WI, pp. 383–411 (Agron. Monogr. 9).
- Gray, B.P., Norcross, B.L., Blanchard, A.L., Beaudreau, A.H., Seitz, A.C., 2015. Variability in the summer diets of juvenile polar cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas. *Polar Biol.* 39, 1069–1080.
- Gray, B.P., Norcross, B.L., Beaudreau, A.H., Blanchard, A.L., Seitz, A.C., 2017. Food habits of Arctic staghorn sculpin (*Gymnancistrus tricuspidis*) and shorthorn sculpin (*Myoxocephalus scorpius*) in the northeastern Chukchi and western Beaufort Seas. *Deep Sea Res. II* 135, 111–123.
- Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. *Mar. Ecol. Prog. Ser.* 51, 253–268.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog. Oceanogr.* 71 (2), 331–361.
- 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 Trans. Am. Geophys. Union* 91 (18), 161–162.
- Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Denisenko, S.G., Iken, K., Kędra, M., Serratos, C., 2015a. Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program. *Oceanography* 28 (3), 116–133.
- Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., Arrigo, K.R., Blanchard, A.L., Clarke, J.T., Day, R.H., Frey, K.E., Gradinger, R.R., Kędra, M., 2015b. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Prog. Oceanogr.* 136, 92–114.
- Groß, J., Konar, B., Brey, T., Grebmeier, J.M., 2017. Size-frequency distribution, growth, and mortality of snow crab (*Chionoecetes opilio*) and arctic lyre crab (*Hyas coarctatus*) in the Chukchi Sea from 2009 to 2013. *Deep Sea Res. II* 144, 142–155.
- Hall, C.M., Saarinen, J., 2010. *Tourism and Change in Polar Regions: Climate, Environments and Experiences*. Routledge, New York, pp. 317.
- Hollowed, A.B., Planque, B., Loeng, H., 2013. Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. *Fish. Oceanogr.* 22, 355–370.
- Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and Barents Sea. *Mar. Biol. Res.* 9, 878–894.
- Iken, K., Bluhm, B., Dunton, K., 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Res. II* 57 (1), 71–85.
- Jørgensen, L.L., Ljubić, P., Skjoldal, H.R., Ingvaldsen, R.B., Anisimova, N., Manushin, I., 2014. Distribution of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management. *ICES J. Mar. Sci.* 72 (2), 595–613.
- Jørgensen, L.L., Planque, B., Thangstad, T.H., Certain, G., 2015. Vulnerability of megabenthic species to trawling in the Barents Sea. *ICES J. Mar. Sci.* 73 (suppl.1) (i84–97).
- Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lønne, O.J., Gulliksen, B., 2012. Climate-driven regime shifts in Arctic marine benthos. *Proc. Nat. Acad. Sci. USA* 109 (35), 14052–14057.
- Link, H., Piepenburg, D., Archambault, P., 2013. Are hotspots always hotspots? The relationship between diversity, resource and ecosystem functions in the Arctic. *PLoS One* 8 (9), e74077.
- Logerwell, E., Busby, M., Carothers, C., Cotton, S., Duffy-Anderson, J., Farley, E., Goddard, P., Heintz, R., Holladay, B., Horne, J., Johnson, S., 2015. Fish communities across a spectrum of habitats in the western Beaufort Sea and Chukchi Sea. *Prog. Oceanogr.* 136, 115–132.
- Lowry, L.F., Frost, K.J., 1981. Distribution, growth, and foods of Arctic Cod (*Boreogadus saida*) in the Bering, Chukchi, and Beaufort seas. *Can. Field-Nat.* 95, 186–191.
- Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J., Watt, A.D., 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol. Evol.* 25 (10), 574–582.
- Mecklenburg, C.W., Stein, D.L., Sheiko, B.A., Chernova, N.V., Mecklenburg, T.A., Holladay, B.A., 2007. Russian-American long-term census of the Arctic: benthic fishes trawled in the Chukchi Sea and Bering Strait, August 2004. *Northwest. Nat.* 88 (3), 168–187.
- Mecklenburg, C.W., Möller, P.R., Steinke, D., 2011. Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Mar. Biodiv.* 41 (1), 109–140.
- Michalsen, K., Dalpadado, P., Eriksen, E., Gjøsæter, H., Ingvaldsen, R.B., Johannesen, E., Jørgensen, L.L., Knutsen, T., Prozorkevich, D., Skern-Mauritzen, M., 2013. Marine living resources of the Barents Sea – ecosystem understanding and monitoring in a climate change perspective. *Mar. Biol. Res.* 9 (9), 932–947.
- Miller, A.W., Ruiz, G.M., 2014. Arctic shipping and marine invaders. *Nat. Clim. Change* 4 (6), 413–416.
- Moore, S.E., Grebmeier, J.M., 2018. The distributed biological observatory: linking physics to biology in the Pacific. *Arct. Res. Arch.* 71, 1–7.
- Mueter, F.J., Litzow, M.A., 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* 18, 309–320.
- Norcross, B.L., Holladay, B.A., Busby, M.S., Mier, K.L., 2010. Demersal and larval fish assemblages in the Chukchi Sea. *Deep Sea Res.* 57 (1), 57–70.
- Norcross, B.L., Raborn, S.W., Holladay, B.A., Galloway, B.J., Crawford, S.T., Priest, J.T., Edenfield, L.E., Meyer, R., 2013. Northeastern Chukchi Sea demersal fishes and associated environmental characteristics, 2009–2010. *Cont. Shelf Res.* 67, 77–95.
- North Pacific Fisheries Management Council (NPFMC), 2009. Fishery management plan for fish resources of the Arctic management area. Anchorage, AK. 146.
- Overland, J.E., Wang, M., 2010. Large-scale atmospheric circulation changes are associated with the recent loss of Arctic sea ice. *Tellus A* 62 (1), 1–9.
- Palumbi, S.R., 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annu. Rev. Environ. Resour.* 29, 31–68.
- Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J., Halpern, B.S., Ince, L.S., Leong, J.A., Norse, E., Stachowicz, J.J., 2009. Managing for ocean biodiversity to sustain marine ecosystem services. *Front. Ecol. Environ.* 7 (4), 204–211.
- Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. *Polar Biol.* 28 (10), 733–755.
- Pisareva, M.N., Pickart, R.S., Iken, K., Ershova, E.A., Grebmeier, J.M., Cooper, L.W., Bluhm, B.A., Nobre, C., Hopcroft, R.R., Hu, H., Wang, J., 2015. The relationship between patterns of benthic fauna and zooplankton in the Chukchi Sea and physical forcing. *Oceanography* 28 (3), 68–83.
- Rand, K., Logerwell, E., Bluhm, B., Chenelot, H., Danielson, S., Iken, K., de Sousa, L., 2017. Using biological traits and environmental variables to characterize two Arctic epibenthic invertebrate communities in and adjacent to Barrow Canyon. *Deep-Sea Res. II*. <https://doi.org/10.1016/j.dsr2.2017.07.015>.
- Ravelo, A.M., Konar, B., Trefry, J.H., Grebmeier, J.M., 2014. Epibenthic community variability in the northeastern Chukchi Sea. *Deep Sea Res. II* 102, 119–131.
- Ravelo, A.M., Konar, B., Bluhm, B., Iken, K., 2017. Growth and production of the brittle stars *Ophiura sarsi* and *Ophiocten sericeum* (Echinodermata: ophiuroidea). *Cont. Shelf Res.* 139, 9–20.
- Renaud, P.E., Włodarska-Kowalczyk, M., Trannum, H., Holte, B., Węśławski, J.M., Cochran, S., Dahle, S., Gulliksen, B., 2007. Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). *Polar Biol.* 30 (3), 295–305.

- Sala, E., Knowlton, N., 2006. Global marine biodiversity trends. *Annu. Rev. Environ. Resour.* 31, 93–122.
- Soltwedel, T., Bauerfeind, E., Bergmann, M., Budaeva, N.A., Hoste, E.V., Jaeckisch, N., von Juterzenka, K.A., Matthießen, J., Mokievsky, V.A., Nöthig, E.M., Quéric, N.V., 2005. HAUSGARTEN: multidisciplinary investigations at a deep-sea, long-term observatory in the Arctic Ocean. *Oceanography* 18 (3), 46–61.
- Soltwedel, T., Schauer, U., Boebel, O., Nöthig, E.M., Bracher, A., Metfies, K., Schewe, I., Boetius, A., Klages, M., 2013. FRAM-Frontiers in Arctic marine monitoring: visions for permanent observations in a gateway to the Arctic Ocean. *OCEANS-Bergen 2013*, 1–7 (IEEE).
- Soltwedel, T., Bauerfeind, E., Bergmann, M., Bracher, A., Budaeva, N., Busch, K., Cherkasheva, A., Fahl, K., Grzelak, K., Hasemann, C., Jacob, M., Kraft, A., Lalande, C., Metfies, K., Nöthig, E.M., Quéric, N.-V., Schewe, I., Włodarska-Kowalczyk, M., Klages, M., 2016. Natural variability or anthropogenically-induced variation? Insights from 15 years of multidisciplinary observations at the arctic marine LTER site HAUSGARTEN. *Ecol. Indic.* 65, 89–102.
- Stabeno, P., Kachel, N., Ladd, C., Woodgate, R., 2018. Flow patterns in the eastern Chukchi Sea: 2010–2015. *J. Geophys. Res. Oceans* 123 (2), 1177–1195.
- Stevenson, D.E., Lauth, R.R., 2012. Latitudinal trends and temporal shifts in the catch composition of bottom trawls conducted on the eastern Bering Sea shelf. *Deep Sea Res. II* 65–70, 251–259.
- Tu, K.L., Blanchard, A.L., Iken, K., Horstmann-Dehn, L., 2015. Small-scale spatial variability in benthic food webs in the northeastern Chukchi Sea. *Mar. Ecol. Prog. Ser.* 528, 19–37.
- Wassmann, P., Duarte, C.M., Agusti, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. *Glob. Change Biol.* 17 (2), 1235–1249.
- Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D., 2005. Circulation on the north central Chukchi Sea shelf. *Deep Sea Res. II* 52 (24), 3150–3174.
- Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H., 2013. Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. *Cont. Shelf Res.* 67, 5–22.
- Whitehouse, G.A., Buckley, T.W., Danielson, S.L., 2017. Diet compositions and trophic guild structure of the eastern Chukchi Sea demersal fish community. *Deep Sea Res. II* 135, 95–110.
- Wood, A.C., Probert, P.K., Rowden, A.A., Smith, A.M., 2012. Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. *Aquat. Cons. Mar. Freshw. Ecosyst.* 22 (4), 547–563.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314 (5800), 787–790.