1 Late summer zoogeography of the northern Bering and Chukchi seas

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ABSTRACT

Ocean currents, water masses, and seasonal sea ice formation contribute to determining relationships among the biota of the Bering and Chukchi seas. The Bering Sea communicates with the Chukchi Sea via northward advection of water, nutrients, organic matter, and plankton through Bering Strait. We used data from concurrent surveys of zooplankton, pelagic fishes and jellyfish, epibenthic fishes and invertebrates, and seabirds to identify faunal distribution patterns and environmental factors that are related to these faunal distributions within the US portions of the Chukchi Sea shelf and Bering Sea shelf north of Nunivak Island. Regional differences in late summer (August-September) distributions of biota largely reflected the underlying hydrography. Depth, temperature, salinity, stratification, and chlorophyll *a*, but less so sediment-related or nutrient-related factors, were related to the distributions of the assemblages (zooplankton: depth, salinity, stratification; pelagic fishes and jellyfish: depth, stratification, chlorophyll *a*; epibenthic fishes and invertebrates: depth, temperature, salinity; seabirds: temperature, salinity, stratification). The assemblages were principally structured from nearshore to offshore and from south to north. The nearshore to offshore contrast usually was stronger in the south, where the enormous discharge of the Yukon River is more apparent and extends farther offshore, influencing zooplankton, pelagic fish/jellyfish, and seabird assemblages. Some assemblages overlapped spatially (e.g., seabird and zooplankton), indicating shared influential environmental factors or trophic linkages among assemblages. The gradients in assemblage composition were gradual for epibenthic taxa, abrupt for zooplankton taxa, and intermediate for pelagic fish/jellyfish and seabird taxa, implying that zooplankton assemblage structure is most strongly tied to water mass, epibenthic least, with the other two taxa intermediate. Three communities (i.e., cross-assemblage groupings) emerged based on maps of ordination axes and core use areas by taxa; one associated with Alaska Coastal Water (warmer, fresher, nutrient depauperate), a second associated with Chirikov Basin and the southern Chukchi Sea (colder, saltier, nutrient rich), and a third associated with the northern Chukchi shelf. Gradients in species composition occurred both within and between these communities. The Chirikov Basin / southern Chukchi Sea community was characterized by distinct zooplankton and seabird taxa, but was not strongly associated with distinct pelagic or epibenthic fish and invertebrate taxa. Although comprehensive data were only available for a single year and annual variation may affect the generality of our

results, our comprehensive ecosystem survey approach yielded new insights into the ecological relationships (specifically, gradients in assemblage composition and identification of communities) of this Arctic region.

Key words: Bering Sea, Chukchi Sea, zoogeography, zooplankton, fishes, invertebrates, seabirds

1. Introduction

This paper describes the integrated zoogeography of zooplankton, fishes, epifaunal invertebrates, and seabirds in the northern Bering and Chukchi seas during late summer and identifies the environmental factors structuring these assemblages. The zoogeography of the northern Bering and Chukchi seas has previously been characterized for zooplankton (Hopcroft et al., 2010; Eisner et al., 2013; Ershova et al., 2015), pelagic fishes (Eisner et al., 2013), epibenthic fishes and invertebrates (Bluhm et al., 2009; Norcross et al., 2010, 2013; Ravelo et al., 2014; Logerwell et al., 2015) and seabirds (Piatt and Springer, 2003; Kuletz et al., 2015), as well as for macrofaunal benthos, which we did not include here (Feder et al., 2007; Blanchard et al. 2013a,b; Petryashov et al., 2013; Grebmeier et al., 2015a). Our study is novel in that we characterize all four assemblages simultaneously. Another study (Sigler et al., 2011) also characterized these four assemblages simultaneously but used data collected from different, widely scattered years, whereas our study uses data collected in a single year (2012), except for epibenthic fishes and invertebrate data for the northern Bering Sea, which were collected in 2010. This approach allows us to infer whether these four assemblages are linked to the same environmental factors or whether and how the influential factors differ among assemblages.

Understanding the environmental factors that influence the structure of these assemblages on a large, regional scale will provide insight into current assemblage structure and information for others to forecast community responses to climate change. Changes in climatic conditions as well as biological production and faunal distribution patterns in the region have already been recorded for recent decades (Grebmeier et al., 2006; Mueter and Litzow 2008; Arrigo and van Dijken 2015), and are expected to continue (e.g., Hollowed et al., 2013). The simultaneous surveys of the four assemblages provide a benchmark for assessing climate effects as more surveys are conducted in the future. In the meantime, the simultaneous surveys also provide a space-for-time substitution as a temporary alternative to long-term studies (Pickett, 1989).

Space-for-time substitution is one of the most common techniques in ecology and in general, is the extrapolation of a temporal trend from a series of different-aged samples (Pickett, 1989). In our application, latitude substitutes for time, with the current state of southerly locations serving as a proxy for the future state of northerly locations (i.e., as influenced by climate change (Blois et al., 2013)).

The faunal assemblages considered here are directly or indirectly influenced by several features. First, ice seasonally covers the northern Bering and Chukchi seas (Fig. 1), with the extent of the seasonal sea ice advance and retreat being the largest of any of the Arctic or subarctic regions, averaging ~1,700 km, while interannual variability has been as great as ~400 km, or ~25% of the seasonal range (Niebauer et al., 1999; Frey et al., 2014). Sea ice covers the northern Bering and Chukchi seas each winter, and by late summer, open water recurs over most or even all of these shelf regions. Second, the northern Bering (Grebmeier et al., 2006; Sigler et al., 2011, Stabeno et al., 2012) and Chukchi shelves are strongly connected by Pacific origin waters flowing northward through Bering Strait, including nutrient-rich Anadyr Water near the Siberian coast, Bering Shelf Water, and nutrient-poor Alaska Coastal Water flowing northward along the Alaskan coast (Coachman et al., 1975; Woodgate et al., 2005a, b). Currents generally flow northward through Bering Strait due to differing sea-level heights between the North Pacific and Arctic oceans (Stigebrandt, 1984; Aagaard et al., 2006) and are thence topographically steered across the Chukchi Sea along three primary pathways: Herald Canyon in the west, Barrow Canyon in the east, and the Central Channel in between (e.g., Weingartner et al., 2005). This flow pattern redistributes nutrients and algal production, organic carbon, organisms and hydrographic properties originating along the Bering slope and the central Bering shelf into the northern Bering and Chukchi seas (e.g., Walsh et al., 1989; Grebmeier et al., 2015b). Third, while Bering Shelf Waters and Anadyr Waters mix within and downstream of Bering and Anadyr straits, a strong density front typically separates the Alaska Coastal Water from the offshore waters both in the Bering Sea and farther north (Hunt and Harrison, 1990; Gawarkiewicz et al., 1994; Weingartner et al., 2005). In the northern Chukchi Sea, these two main water bodies encounter and interact with Arctic-origin waters with typically lower temperatures and somewhat different community dominants (e.g., Spall, 2007; Petryashev et al., 2013). Fourth, the seasonal ice retreat and subsequent effects on stratification in combination with the nutrient-rich waters promote early blooms with relatively little pelagic grazing, so that a

large amount of *in situ* and advected pelagic production settles onto the seafloor, above-average benthic biomass is established (e.g., Grebmeier et al., 2006, 2015a), and characteristic feeding aggregations of marine mammal benthivores occur (e.g., Jay et al., 2012). Fifth, fish populations and individual fish body sizes in the northern Bering and Chukchi Seas are very small compared to the southeastern Bering and Barents seas, which support huge commercial fisheries (Stevenson and Lauth, 2012; Hunt et al., 2013; Norcross et al., 2013). These patterns form the backdrop for biological community structure and their distribution across the study area on the large, regional scale, in addition to biological - such as trophic - interactions, which we focus less on here.

We chose environmental factors for analysis that previously have been shown to influence assemblages in the study region. The selected factors include temperature (Bluhm et al., 2009; Hopcroft et al., 2010; Norcross et al., 2010; Eisner et al., 2013; Ravelo et al., 2014; Ershova et al., 2015), salinity (Hopcroft et al., 2010; Norcross et al., 2010; Eisner et al., 2013), dissolved inorganic nitrogen (DIN) (Piatt and Springer, 2003; Eisner et al., 2013), mean water column stratification (Piatt and Springer, 2003), integrated chlorophyll *a* (Chl*a*, Piatt and Springer, 2003), total organic carbon (TOC) in sediments (Bluhm et al., 2009; Ravelo et al., 2014), and percent of silt and clay (% silt/clay) in sediments (Bluhm et al., 2009; Norcross et al., 2010). The physical environmental factors that we use in our analysis (temperature, salinity, and stratification) are known to be structured by regional circulation and wind stress (Danielson et al., 2014; Woodgate et al., 2012, 2005b), air-sea-ice heat fluxes (Drucker et al., 2003), ice retreat (Paquette and Bourke, 1981), water mass mixing (Woodgate et al., 2005a), coastal discharges (Aagaard et al., 2006), and topographic controls (Kinder et al., 1986; Weingartner et al., 2005; Woodgate et al., 2005a; Spall, 2007). The biochemical and geochemical environmental factors (DIN, Chl*a*, TOC, and % silt/clay) depend on the physical environment but also on the phytoplankton bloom dynamics, nutrient cycling, and grazing pressures (Walsh et al., 1989). Collectively, these factors also characterize fundamental aspects of the study area environment including the water column (temperature and salinity), sediment (TOC and % silt/clay), and productivity (DIN, stratification, and Chl*a* (a measure of phytoplankton biomass)).

In our analyses, we first identify spatial gradients in assemblages and then determine the environmental factors most closely linked to these gradients and therefore presumably most

influential in structuring these assemblages. This approach, known as indirect gradient analysis, first analyzes patterns in biological assemblages separately from patterns in the environment before examining the influence of environmental factors and has been applied in previous zoogeography analyses of the Chukchi and Bering seas (Bluhm et al., 2009; Ravelo et al., 2014). An alternative approach is to identify spatial gradients or spatial structure in the environment and then determine the associated assemblages. This alternative approach also has been applied in previous zoogeography analyses of the Chukchi and Bering seas, which first identify discrete water masses and then determine the assemblages associated with each water mass (Hopcroft et al., 2010; Norcross et al., 2010; Eisner et al., 2013; Ershova et al., 2015). We chose our approach for two reasons. First, we chose an approach that focuses on spatial patterns in assemblages because these patterns are our primary interest. Second, the alternative approach typically begins with categorizing environmental data into discrete water masses. However, water mass boundaries are typically indistinct (e.g., as noted earlier, Bering Shelf Waters and Anadyr Waters mix within and downstream of Bering and Anadyr straits (Pisareva et al., 2015)), whereas treating the environmental data as continuous variables, as in our approach, avoids this issue. Thus, we first identify patterns in assemblages independent of water mass structure before quantifying links between these patterns and observed environmental gradients.

Our study objectives were to 1) identify environmental factors that most influence assemblage distributions within the US portions of the Chukchi Sea shelf and northern Bering Sea shelf north of Nunivak Island (~60 °N [Stabeno et al., 2012]); 2) identify spatial gradients in assemblage composition; and 3) identify relationships among assemblages. We focus on four biological assemblages: zooplankton, pelagic fishes and jellyfish, epibenthic fishes and invertebrates, and seabirds. We, thereby, expect to capture relevant environmental conditions both in the water column and at the seafloor.

2. Methods

The data were collected primarily in August-September 2012 with one vessel focused on conducting a bottom trawl survey of the Chukchi Sea and a second vessel focused on conducting zooplankton, surface trawl, and acoustic-midwater trawl surveys of the northern Bering and Chukchi seas. The latter vessel also collected most of the environmental data used herein (physical, chemical and biological oceanographic) and included a seabird biologist to record

seabird densities. A bottom trawl survey of the northern Bering Sea was conducted in August-September 2010 and the 2012 pelagic and environmental surveys of the northern Bering and Chukchi seas were repeated in August-September 2013. Because no bottom trawl survey was conducted in 2013, we focus on the comprehensive 2010/2012 survey data and conduct only a limited comparison with the 2013 data.

The sampling design for the Chukchi Sea was based on a 56 km (30 nautical mile (nmi)) square grid pattern, resulting in a total of 73 sampling locations, which were occupied during both the bottom trawl survey and the pelagic and environmental surveys. In the northern Bering Sea, the sampling design differed between the two surveys, which followed historical survey patterns established for the southeastern Bering Sea. For the pelagic and environmental surveys, the sampling design was based on a 56 km square grid pattern, resulting in a total of 39 stations. For the bottom trawl survey, the sampling design was based on a 37 km square grid pattern, resulting in a total of 142 stations (Lauth 2011). More stations were sampled during the bottom trawl survey because station density was higher and also because a larger area of the northern Bering Sea was sampled (i.e., sampling extended further offshore). When analyzed alone, the full bottom trawl survey data set was included, but when compared to other data sets, only data within the area sampled by both surveys was included.

2.1. Environmental data

Our analyses included ten environmental variables: sea surface temperature, bottom (near-bottom water) temperature, sea surface salinity, bottom salinity, surface DIN, bottom DIN, stratification, water column integrated Chl a concentration, sediment % silt/clay, and sediment TOC (Fig. 2). Data for the first eight variables were collected during 2010, 2012, and 2013 (Table 1). In contrast, data for the two sediment-related variables were collected during 1970-2012 (Grebmeier and Cooper, 2014). We selected more recent data, starting with 2006, when the annual sample rate increased. The 2006-2012 sediment data were pooled in order to increase sample size, which varied annually (from 34 in 2011 to 154 in 2009). Pooling was justified because there was no significant trend in either % silt/clay or TOC during this time period.

Conductivity-temperature-depth (CTD) measurements were collected with an RD Instruments Citadel CTD-NV during the 2010 bottom trawl survey and Sea-Bird (SBE) 911 or

SBE 25 CTD to determine surface and bottom temperature and salinity in 2012 and 2013. The Sea-Bird CTD was equipped with a Wetlabs Wet-Star fluorometer to estimate *in vivo* Chl*a* fluorescence. Water samples for nitrogenous nutrients (nitrate, nitrite, and ammonium) and Chl*a* were collected every 10 m during the upcast with Niskin bottles attached to the CTD. Nutrient samples were filtered through 0.45 μm cellulose acetate filters, frozen at -80 °C and analyzed at a shore-based facility using colorimetric methods (JGOFS, 1994). DIN was estimated by summing nitrate, nitrite, and ammonium. Chl*a* samples were filtered through Whatman GF/F filters (nominal pore size 0.7 μm). Filters were stored frozen (-80 °C) and analyzed within 6 months with a Turner Designs (TD-700) bench-top fluorometer following standard methods (Parsons et al., 1984). *In vivo* fluorescence data, calibrated with discrete Chl*a* samples, were used to calculate water column integrated Chl*a*. Stratification (mean water column Brunt-Vaisala frequency) was calculated from the temperature and salinity measurements (Gill, 1982).

Several environmental variables were highly skewed and included a few large outliers. These characteristics could have a strong impact on subsequent correlation and regression analyses. Hence, we examined and, as necessary, transformed environmental variables to approximate normality by determining the best Box-Cox transformation (Box and Cox, 1964) and choosing the closest ‘natural’ transformation (log, fourth-root, square-root). This improved the models substantially and revealed more fine-scale spatial structure, which was otherwise dominated by a few extreme values. The transformed variables were DIN ($\log_e$), stratification (fourth-root), Chl*a* ($\log_e$), and % silt/clay (square-root).

To visually examine environmental variability, we first mapped all environmental measures used in the analyses by predicting values over a regular grid that encompassed the sampling area. Interpolated values were estimated by fitting spatial Gaussian models to the data using ordinary or universal kriging. One very low salinity value at a nearshore station in Norton Sound was eliminated from this analysis to highlight patterns over the main sampling region, which mostly comprised offshore waters (> 20 m depth). Spatial autocorrelation was modeled using a spherical or exponential model with or without a nugget effect. The best fitting model for each variable was determined based on visually examining empirical and theoretical variograms and comparing fitted variograms based on the Akaike information criterion (AIC), following Diggle and Ribeiro (2007). All models were fit using the geoR package (Ribeiro and Diggle,

2001), version 1.7, in the statistical programming language R, version 3.1.2 (R Development Core Team, 2014).

Most of these environmental data were collected concurrently at each station with two exceptions. The exceptions resulted in missing data and values were simulated to fill these gaps. Missing data were filled based on transformed values, when necessary. The first exception occurred when individual samples occasionally were missing due to some problem with these samples (e.g., equipment failure) (Table 1). Values for these missing data were estimated as follows: a general additive model (GAM) with Gaussian errors was fit to the available data (predicted mean = $f(\text{latitude, longitude}) + g(\text{depth})$, where f and g are smoothing splines with the degree of smoothing determined by cross-validation); missing values at a given location were then simulated by adding a random residual to the predicted mean for that location. Random residuals were drawn from a normal distribution with mean zero and variance equal to the estimated residual variance from the GAM. We used this algorithm to generate realistic values for missing observations rather than using predicted means in order to appropriately reflect uncertainty in further analyses (see, e.g., Little and Rubin, 2002). The second exception occurred for sediment samples, which were not collected concurrently with the 2010, 2012, or 2013 cruises. The % silt/clay and TOC were matched with the other types of environmental data. Each location of concurrently collected environmental data was associated with the nearest sediment sample. If the nearest sample was more than 20 km distant, then the sediment-related values were estimated by the same method as used for missing data estimation. The sediment data had less spatial coverage than the other environmental data (Fig. 2); some extrapolated values may be biased because of the patchy distribution of sediments. Values were estimated for all missing data except for some bottom DIN values for 2010 (Table 1). No bottom DIN samples were collected for the outer shelf of the northern Bering Sea. Although samples were collected for the adjacent middle shelf, no values were estimated to substitute for the missing data for the outer shelf because the oceanographic characteristics of these two regions differ (Coachman, 1986).

2.2. *Biological assemblages*

Zooplankton were sampled with a 60 cm MARMAP-style bongo frame with a 505 μm mesh net. Oblique tows from the surface to within 5 – 10 m of the bottom were conducted primarily during daylight hours. Volume filtered was measured with calibrated General Oceanics

flowmeters mounted inside the nets. All samples were preserved in 5% formalin, buffered with seawater for later processing. In the lab, the mesozooplankton samples were processed as follows: each sample was poured into a sorting tray and large organisms, primarily shrimp and jellyfish, were removed and enumerated. The samples were then sequentially split using a Folsom splitter until the smallest subsample contained about 200 specimens of the most abundant taxa. All taxa in the smallest subsamples were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. Blotted wet weights of all specimens of each taxa and stage in each sample were taken as outlined in earlier papers (Coyle et al., 2008, 2011) and the coefficient of variation in average wet weight was computed. If the coefficient of variation for any given taxon and stage changed by less than 5% when additional weights were taken from subsequent samples, wet weights were no longer measured for that taxon for that cruise, and the wet weight biomass was estimated by multiplying the specimen count by the mean wet weight. In practice, only calanoid copepods had consistent wet weights after weighing each taxon and stage in about 10-15 samples. Therefore, wet weights of chaetognaths, shrimp and other larger and soft-bodied taxa were measured and recorded for each sample. Wet weight measurements were made with a Cahn Electrobalance or Mettler top loading balance, depending on the size of the animal. All animals in the samples were identified to the lowest taxonomic category possible. Juveniles of various epibenthic gammarids were not identified to the species level and were grouped in one category Gammaridea. Sibling species *Calanus marshallae* and *C. glacialis* co-occurring in the Bering and Chukchi seas (e.g., Nelson et al., 2009) were not discriminated and are named as *C. marshallae* hereafter. Copepodid stages were identified and recorded. Catch per unit effort (CPUE) values by station were computed for each species in grams m⁻³ of filtered volume. Many adult euphausiids on the shelves of the Bering and Chukchi seas remain within 1 – 2 m of the bottom during the day (Coyle and Pinchuk, 2002) and those in the water column are difficult to quantitatively capture due to net avoidance (e.g. Sameoto et al., 1993; Wiebe et al., 2004); therefore, adult euphausiids were not included in the analyses.

Pelagic fishes and jellyfish were sampled with a midwater rope trawl with a mean horizontal spread of 55 m, configured to sample the top 15-20 m of the water column (Farley et al., 2007). The net had hexagonal mesh wings and a 1.2-cm mesh codend liner. Trawls were towed at 3.5 – 5 knots (6.5-9.3 km h⁻¹) for 30 min. The catch was sorted to species (Mecklenburg

et al., 2002) and counted. For large catches, a random subsample was sorted and counted, and results were extrapolated to estimate the total catch by taxon. Individual species were weighed in aggregate and counted, and then these numbers were expanded to the total catch weight. CPUE values by station were computed for each taxon (fish and invertebrate) in kilograms per hectare (1 ha = 10,000 m²) and number of fish per hectare; area swept (ha) was computed as the distance towed multiplied by the mean net width.

Epibenthic fishes and invertebrates were sampled with an 83-112 Eastern bottom trawl, which has a 25.3-m (83 ft) headrope and a 34.1-m (112 ft) footrope. Mesh sizes were 10.2 cm (4 in) in the wings and body and 8.9 cm (3.5 in) in the intermediate and codend. The codend also had a liner of 3.2 cm (1.25 in) mesh. Tow durations were 30 min during the northern Bering Sea survey and 15 min during the Chukchi Sea survey. Tow durations were shorter for the Chukchi Sea because this region has a greater biomass of epibenthic invertebrates and small fishes compared to the Northern Bering Sea (Stevenson and Lauth, 2012); a longer tow would result in larger catches and would require subsampling, which would introduce more uncertainty into the abundance estimates. For both surveys, the tow was conducted near the center of the grid cell of the selected station when possible, and the vessel maintained a single heading during the tow. A bottom contact sensor (inclinometer/accelerometer) was used to assess the bottom tending performance of the net and to determine when the footrope was in contact with the seafloor. Net mensuration sensors were used to assess net performance and to provide net width data used to calculate the area swept by the bottom trawl. Total catch samples weighing less than 1,150 kg (2,500 lb) were placed directly onto a sorting table and the catch was sorted and enumerated in its entirety. Larger catch samples were weighed in aggregate and subsampled before sorting. After subsampled catches were sorted, individual species were weighed in aggregate and counted, and then these numbers were expanded to the total catch weight. Catches were sorted to the lowest taxonomic level practicable (Mecklenburg et al., 2002; Stevenson and Hoff, 2009). Mean CPUE values by station were computed for each taxon (fish and invertebrate) in kilograms per hectare as described for pelagic fishes and jellyfish.

Seabird surveys were conducted by US Fish and Wildlife Service (USFWS) biologists onboard the vessel conducting zooplankton and pelagic fishes and invertebrates surveys in 2012 and 2013. To obtain estimates of seabird densities, visual surveys were conducted from the

inside bridge using the USFWS pelagic survey protocol (Kuletz et al., 2008). Surveys were conducted when the ship was underway and conditions were favorable (sufficient daylight to identify species and seas ranging from Beaufort Sea State 0 to 5). Transect width was occasionally truncated to 200 m or 100 m in a given transect if observation conditions (i.e., fog or swells) restricted visibility. The single observer used strip transect methodology, with 10x binoculars for identification, and recorded all birds on one side of the bridge within a 300-m arc, extending 90° from the bow to the beam. Birds were identified to species when possible or to genus, along with number of birds in each observation. Birds on the water were counted continuously, while flying birds were counted in instantaneous scans of the survey window at ~1 min intervals (depending on speed of the vessel) to avoid overestimating the density of flying birds (Tasker et al., 1984; Gould and Forsell, 1989). Observations were entered directly into a laptop computer using DLOG3 (Ford Ecological Consulting, Portland, OR) with a GPS interface. Along with each observation, location (latitude and longitude) was automatically recorded at 20-sec intervals to track survey effort. The surveyed transects were later divided into ~ 3-km segments to calculate bird density (birds km⁻²), thereby correcting for effort but not for detectability of each species. The centroid of each 3-km segment was used to georeference estimated seabird densities for each segment. Approximately 12,000 km were surveyed over both years.

The data were compiled into tables for use in the analyses described in the next section. There was one table for each survey, totaling four tables (zooplankton, pelagic fishes and jellyfish, epibenthic fishes and invertebrates, and seabirds). Each data table was a station-by-taxon matrix of CPUE data in terms of weight (zooplankton (g m⁻³), pelagic fishes and jellyfish (kg ha⁻¹), epibenthic fishes and invertebrates (kg ha⁻¹)) or number (seabirds observed (number km⁻²)). Rare species that occurred at less than 5% of the total stations were excluded (McGarigal et al., 2000) as they can have a strong impact on the analysis (Poos and Jackson, 2012). Our goal was to focus on broad spatial patterns rather than possible noise or local features that may be associated with rare species. This reduced the number of taxa for each assemblage from 53 to 35 zooplankton taxa, 77 to 29 pelagic fishes and jellyfish taxa, 446 to 163 epibenthic fishes and invertebrates taxa, and 48 to 23 seabird taxa. In addition, all CPUE data were fourth-root transformed to reduce the influence of a few high abundances.

2.3 Statistical analyses

We used multivariate analysis, regression, and correlation to 1) visualize spatial gradients in species composition; 2) determine which physical habitat characteristics structure the species assemblages; and 3) test if the species composition in a given assemblage was related to that in other assemblages.

2.3.1 Visualize spatial gradients in species composition

We first conducted a nonmetric multidimensional scaling (NMDS) ordination separately for each of the four assemblages to reduce variability in the abundance of multiple taxa (23 to 163 taxa per assemblage) to two major modes, reflecting the dominant gradients in species composition across stations. Similarities in species composition between each pair of stations were quantified using the Bray-Curtis distance measure computed on the fourth-root transformed CPUEs (Bray and Curtis, 1957). The resulting matrix of Bray-Curtis dissimilarities was used as input for an NMDS ordination and goodness of fit was evaluated using Kruskal's stress criterion (Kruskal, 1964). Stress values greater than 0.3 indicate that the configuration is no better than arbitrary and configurations should only be interpreted if stress values are less than 0.2, and ideally less than 0.1 (Clarke, 1993). Regardless of stress, all ordinations were conducted in two dimensions to allow for easy visual examination of the resulting ordination diagram. The computed NMDS scores (NMDS₁ along x-axis and NMDS₂ along y-axis) were used as indices of species composition in the subsequent analyses. We visualized the spatial patterns of the major gradients in the species composition of each assemblage by mapping the NMDS scores for each ordination axis. A total of 8 maps (4 assemblages x 2 NMDS axes) were constructed by fitting a smooth surface (thin-plate regression spline) to each set of NMDS scores as a function of latitude and longitude. Regression splines were fit using a general additive modeling (GAM) approach to determine the optimum amount of smoothing (Wood, 2006). These NMDS scores reflect the turnover of species along a continuous gradient.

In order to interpret these gradients, we fit linear and Gaussian (dome-shaped) regressions between the CPUEs of individual taxa and each ordination axis to identify the taxa that were most strongly associated with each axis, which we termed "indicator species". The best-fitting model was selected based on the AIC, goodness of fit was quantified using the

coefficient of determination (R^2), and the model was compared to the null model (no relationship) using an F -test. Species were selected as “indicator species” if the best-fitting model was significant ($p < 0.05$) and explained at least 20% of the variability in CPUE ($R^2 > 0.2$). The “core use area” of the indicator species was defined by the NMDS scores that encompassed the middle 50% of the area under the fitted curve (i.e., the highest CPUE values); the “core use area” is a measure of niche space for these indicator species.

We applied a second ordination method, correspondence analysis (CA), which provides a measure of the proportion of variability in the underlying CPUE data that is captured by each ordination axis (Greenacre, 1984). NMDS based on Bray-Curtis dissimilarities is an appropriate ordination method to summarize the species composition of assemblages consisting of many species, most of which may be absent from the majority of stations (Clarke, 1993), but cannot provide a meaningful measure of the proportion of this variability in the underlying CPUE data that is captured by each ordination axis. CA was performed on each of the station-by-species matrices and the first two CA axes were qualitatively compared to the NMDS results (visual comparison of ordination diagrams and spatial patterns) and were generally found to be very similar. Therefore, we used CA to quantify the proportion of overall variability in the CPUE data that can be captured by two dominant modes of species composition. We note that even if this proportion is low, much of the interpretable information in the station-by-taxon matrices may be contained in the first two axes because CPUE data typically have a low signal to noise ratio.

2.3.2 Environmental factors structuring biological assemblages

We examined relationships between the species composition of each assemblage and relevant environmental variables using several approaches to determine the drivers structuring each biological assemblage. In the analyses, depth, surface water characteristics (temperature, salinity, DIN) and integrated Chl a were used to examine relationships with zooplankton, pelagic fishes and jellyfish, and seabird assemblages, while depth, bottom water characteristics (temperature, salinity, DIN), and sediment characteristics (TOC, % silt/clay) were included in analyses involving the epibenthic assemblage.

First, we examined relationships visually by constructing biplots depicting the relationship between each environmental variable and the ordination axes. In these biplots,

environmental variables are displayed as vectors originating from the center of the ordination diagram and the projection of a given environmental vector on a given ordination axis reflects the correlation between the environmental variable and the NMDS scores. Therefore, the length of a given vector provides a relative measure of the importance of the corresponding variable in structuring the assemblage.

Second, we used a canonical correlation analysis to test the overall significance of the relationship between each biological assemblage and the full set of relevant environmental variables. This test finds the linear combination of environmental variables that maximizes the correlation with a linear combination of the NMDS₁ and NMDS₂ scores and uses a permutation test to assess its significance (Legendre, 2005). The analysis also provides a measure of the proportion of variability in species composition, as summarized by NMDS, that is accounted for by the full set of explanatory variables, known as the canonical coefficient of determination or canonical R^2 . We used the bias-adjusted version of the canonical R^2 recommended by Peres-Neto et al. (2006).

Third, if we found an overall significant relationship between environmental variables and NMDS scores, we determined which variables were most strongly related to the observed differences in species composition among stations using the BIO-ENV procedure (Clarke and Ainsworth, 1993). For this procedure, we computed rank-based correlations between all pairwise station dissimilarities based on environmental variables (Euclidean distances) and all pairwise station dissimilarities based on species abundances (Bray-Curtis distances), also known as Mantel correlations. We then identified the subset of variables that maximized these Mantel correlations using the BIO-ENV procedure as implemented in the ‘vegan’ package for R (Oksanen et al., 2015). For each biological assemblage, we present the subsets of the “best” 1, 2, 3, etc., environmental variables that resulted in the highest correlation with the pairwise biological dissimilarities. This procedure was considered exploratory (no significance test is available) and was used to identify potentially useful explanatory variables to consider in more detailed analyses.

Finally, we examined and quantified relationships between the two NMDS scores and selected environmental variables using a multiple regression approach. We modeled the NMDS₁ and NMDS₂ scores as a function of the explanatory variables identified in the BIO-ENV

procedure. We used GAM regressions with a cubic spline smoother to allow for potential nonlinearities in the relationships, but constrained the smooth functions to biologically realistic forms (maximum of three degrees of freedom allowing for linear, dome-shaped, asymptotic and sigmoidal relationships). We fit models using all and selected subsets of the explanatory variables and determined the best model using a generalized cross-validation criterion (Wood, 2006) to determine the degree of smoothing and using the AIC to determine the subset of variables to include.

2.3.3 Relationships among biological assemblages

To identify relationships among the four biological assemblages, we used canonical correlation analyses as described above. Canonical correlations were computed between the NMDS scores of a given assemblage and those of each of the other three assemblages. We estimated the proportion of variability in one assemblage (the “response” assemblage) that can be explained by variability in another assemblage (the “explanatory” assemblage) using the adjusted canonical R^2 as described above and assessed the significance of the relationship between their respective species compositions using a permutation test (Legendre, 2005). We only considered relationships that reflect “bottom-up” processes (e.g., seabirds responding to zooplankton variability), with the exception of the relationship between the assemblage of pelagic fishes and jellyfish and the assemblage of epibenthic fishes and invertebrates, which was quantified in two ways with either assemblage explaining variability in the other.

3. Results

We focus on the results of the 2012 surveys combined with the 2010 survey of epibenthic taxa for the northern Bering Sea. For brevity, we refer to these samples as the “2012 surveys”. The results of the 2013 surveys are compared with the 2012 surveys in the last section of the results, section 3.5, and are not presented elsewhere in this paper.

3.1. Environmental data

Water mass analysis (Danielson et al., this volume) identified five distinct temperature-salinity modes that encompassed all observed water types in the survey, which Danielson et al. (this volume) described as 1) cool and low-salinity surface waters influenced by ice melt, 2)

warm and low-salinity waters influenced by coastal discharges and heating in shallow water depths, 3) cold waters remnant from the previous winter, 4) salty waters influenced by Atlantic water in the Arctic basin, and 5) waters with intermediate temperatures and salinities that encompass Anadyr, Bering, and Chukchi shelf summer waters. Temperatures were higher and salinities were lower in the shallow, nearshore zone (Fig. 2), reflecting the influence of coastal discharge and other freshwater in the Alaska Coastal Current and the ability of solar radiation to induce greater warming in shallow waters. Bottom DIN also was lower nearshore, reflecting the presence of the nutrient-depleted Alaska Coastal Waters. Over the northeastern Chukchi shelf, this pattern changed and bottom and surface temperatures were colder and bottom salinity and DIN were higher everywhere except immediately adjacent to the Alaska coast, reflecting the presence of Chukchi Winter Water (Weingartner 1997). In this region, cool temperatures and low surface salinities indicate the influence of ice melt. Stratification generally was highest where surface salinities were low, likely due to runoff in the coastal waters of Norton Sound and eastern Bering Strait and due to ice melt water on the northern Chukchi shelf. Surface DIN and integrated *Chla* concentration were highest north of St. Lawrence Island and within Bering Strait, particularly on the less stratified western side. These elevated values likely were due to vertical mixing of nutrient-rich Anadyr water created by water funneling between land masses (e.g., Bering and Anadyr straits separating Russia and Alaska).

3.2. Spatial gradients in species composition

The two major NMDS axes captured much of the variability in the underlying CPUE data for the four assemblages. These two axes accounted for 23-38% of the variability (Table 2) based on correspondence analysis (CA), which was used as a proxy for the proportion of variability captured by the two NMDS axes. Based on this result, we conclude that the NMDS ordination is a suitable tool for examining the structure of these four assemblages.

For the zooplankton assemblage, higher NMDS₁ scores were associated with Alaska Coastal Water and scores were lower in the Chirikov Basin and Chukchi Sea (Fig. 3). NMDS₁ showed strong relationships with the densities of 17 species (termed indicator species, as defined in the methods), with two distinct groupings of species (Fig. 4a). Twelve indicator species were related to negative NMDS₁ scores and were associated with the Chirikov Basin and Chukchi Sea. This first grouping was clearly separated from five indicator species, which were related to the

highest positive values and were associated with the Alaska Coastal Water (see Appendix for species distribution maps of indicator species). NMDS₂ scores showed strong relationships with seven species, again with two distinct groupings of species. Five indicator species were related to negative NMDS₂ scores and were associated with the Chirikov Basin and southern Chukchi Sea. This first grouping was clearly separated from two taxa, which were related to positive values (Fig. 4a) and were associated with the northern Chukchi Sea. Together these results (Fig. 3 and 4a, Appendix) imply an assemblage affiliated with the Alaska Coastal Water, a Chirikov Basin / southern Chukchi Sea assemblage, and a northern Chukchi Sea assemblage (parsed from the Chirikov Basin and Chukchi Sea grouping for NMDS₁).

For the pelagic fishes and jellyfish assemblage, NMDS₁ values increased northward and NMDS₂ values were highest offshore and lowest at the southernmost as well as some of the northernmost stations (Fig. 3). NMDS₁ showed strong relationships with nine species (Fig. 4a). The NMDS₁ scores reached the lowest negative values for three indicator species, intermediate negative values for four indicator species and positive values for two indicator species. The first group of indicator species is associated with Alaska Coastal Water as is the second group, which occurs somewhat farther from shore. The species in the third group are associated with more offshore waters, but *Chrysaora melanaster* is much more widespread from the northern Bering Sea through the northern Chukchi Sea (Appendix). We did not assign a geographic label to this group in Figure 3 because of this distributional difference among group members. NMDS₂ also showed strong relationships with seven species. The NMDS₂ scores were negative for six indicator species, which were associated with the eastern Bering Sea, and positive for one indicator species (the jellyfish *Cyanea capillata*), which occurred throughout much of the study region. Arctic cod (*Boreogadus saida*) commonly was caught but was not selected as one of the indicator species because the best-fitting model explained less than 20% of the variability in CPUE ($R^2 < 0.2$). Together these results imply an assemblage associated with the Alaska Coastal Water, and an eastern Bering Sea assemblage (Fig. 3 and 4a, Appendix). The jellyfish species, except for *Aurelia* sp., which is associated with the Alaska Coastal Water, had the widest distribution (core use areas) of all the indicator species for pelagic fishes/jellyfish (Fig. 4a).

For the epibenthic fishes and invertebrates assemblage, NMDS₁ values were higher offshore and NMDS₂ values were higher southward (Fig. 3). NMDS₁ showed strong

relationships with 54 species, but unlike the previous assemblage types (zooplankton, pelagic fishes/jellyfish), which showed comparatively clear grouping of species, the epibenthic taxa were characterized by a gradual turnover along a gradient of NMDS₁ values (Fig. 4b), implying a lack of distinct assemblages or at least strong species overlap between them. The only grouping of numerous species sharing a common core use area was at the highest positive values with about 19 indicator species falling into this group. NMDS₂ showed strong relationships with 45 species, with a gradual turnover along the NMDS₂ gradient like for NMDS₁, but with some grouping of species for the highest positive values (a group of about 20 species) and for the lowest negative values (a group of about 10 species). For the epibenthic taxa, the species distribution maps revealed some striking patterns (Appendix). Negative NMDS₁ values were associated with Alaska Coastal Water. The positive NMDS₁ values were associated with an offshore assemblage in both the northern Bering and Chukchi seas (e.g., the crab species *Chionoecetes opilio*) or exclusive to the northern Bering Sea (e.g., Greenland halibut (*Reinhardtius hippoglossoides*)) for the highest positive values. These Greenland halibut were juveniles and adults whereas the Greenland halibut found nearshore during pelagic sampling were larvae. The negative NMDS₂ values were associated with a typically Chukchi Sea assemblage (e.g., the anemone *Urticina crassicornis*) but this assemblage was also found in the northern Bering Sea (e.g., the sea star *Crossaster papposus*). The positive NMDS₂ values were associated with a northern Bering Sea assemblage, which most often is exclusive to the northern Bering Sea south of St. Lawrence Island (e.g., arrowtooth flounder), but not always (e.g., the sea star *Ctenodiscus crispatus*). As for the pelagic fishes/jellyfish assemblage, Arctic cod commonly was caught but was not selected as one of the indicator species because the best-fitting model explained less than 20% of the variability in CPUE ($R^2 < 0.2$). Together these results imply a nearshore assemblage affiliated with the Alaska Coastal Water, a northern Bering Sea assemblage, and a Chukchi Sea assemblage (Fig. 3 and 4b, Appendix).

For the seabird assemblage, NMDS₁ values were higher near the Chukchi shelf break as well as nearshore in Norton Sound and southward, whereas these values were lower in Chirikov Basin and the southern and central Chukchi Sea; NMDS₂ values generally were lower associated with Alaska Coastal Water (Fig. 3). NMDS₁ showed strong relationships with eight species, all of which were associated with negative NMDS₁ values (Fig. 4c) and define a Chirikov Basin / southern Chukchi Sea assemblage. The core use areas of these eight indicator species on NMDS₁

mostly overlapped except that short-tailed shearwater (*Puffinus tenuirostris*) was shifted towards less negative values indicating limited overlap with the other indicator species. NMDS₂ values showed strong relationships with only two species, with black-legged kittiwake (*Rissa tridactyla*) abundant at the most negative values of the NMDS₂ gradient and crested auklet (*Aethia cristatella*) most abundant at positive NMDS₂ values. The black-legged kittiwake were associated with the nearshore. Together these results imply an assemblage affiliated with the Alaska Coastal Water and a Chirikov Basin / southern Chukchi Sea assemblage (Fig. 3 and 4c, Appendix).

3.3. Environmental factors structuring biological assemblages

The NMDS axes for each of the four assemblages were significantly related to the full set of environmental variables, based on canonical correlation analysis ($p < 0.0001$, Table 3), indicating that these environmental variables substantially influence the structure of the four assemblages. The environmental variables explained from 41% to 59% (adjusted canonical R^2) of the variability in species composition of the four assemblages, as captured by the NMDS ordination.

For the zooplankton assemblage, depth, sea surface temperature, sea surface salinity, and stratification were strongly correlated with the NMDS axes (Fig. 5). However, because depth and temperature are correlated with each other (Pearson's correlation = -0.728, $p < 0.001$), the combination of environmental variables that resulted in the highest rank-based Mantel correlation with the zooplankton assemblage were depth, surface water salinity, and stratification (Mantel's $r = 0.536$, Table 4). Substituting temperature for depth resulted in a similar correlation (Mantel's $r = 0.504$), but the zooplankton assemblage varied more strongly along the depth gradient (Mantel's $r = 0.414$ when only depth is included) than along the surface water temperature gradient (Mantel's $r = 0.213$ when only temperature is included). The best GAMs of NMDS scores confirmed that the zooplankton assemblage varied strongly and in nonlinear ways along gradients of depth, sea surface salinity, and stratification, which accounted for 71% and 15% of the variability in NMDS axes 1 and 2, respectively (Fig. 6 and 7). As a reminder, the Mantel's r -values were produced with an exploratory analysis that identified potentially useful explanatory variables; this analysis was followed by the GAMs that examined and quantified relationships between the NMDS scores and environmental variables (see methods for details).

For the pelagic fishes/jellyfish assemblage depth, sea surface temperature, DIN, and stratification were strongly correlated with one or both NMDS axes (Fig. 5), while depth, stratification, and Chl a resulted in the highest Mantel correlation (Table 4). The best GAMs of NMDS scores confirmed that the pelagic assemblage varied strongly and in nonlinear ways along gradients of depth, stratification, and Chl a , which accounted for 66% and 15% of the variability in NMDS axes 1 and 2, respectively (Fig. 6 and 7).

For the epibenthic assemblage depth, bottom temperature and salinity, and % silt/clay were most strongly correlated with the NMDS axes (Fig. 5). Similarly, the same variables had the highest Mantel correlations with the assemblage metrics (Mantel's $r = 0.573$, Table 4). Depth, bottom water temperature and salinity, but not % silt/clay, were retained in the best GAMs and accounted for 66% and 16% of the variability in NMDS 1 and 2, respectively (Fig. 6 and 7).

For the seabird assemblage depth, sea surface temperature, sea surface salinity, and integrated Chl a , were most strongly correlated with the NMDS axes (Fig. 5), while depth, sea surface temperature, sea surface salinity, and stratification had the highest Mantel correlation (Mantel's $r = 0.337$, Table 4). Of these, the best GAMs of NMDS scores confirmed that the seabird assemblage varied strongly and in nonlinear ways along gradients of sea surface temperature, sea surface salinity, and mean stratification, but not depth or integrated Chl a , which accounted for 17% and 49% of the variability in NMDS axes 1 and 2, respectively (Fig. 6 and 7).

Overall, six environmental variables were significantly related to the structure of the four assemblages (NMDS scores), based on the best GAM models (Fig. 6 and 7). These six were bottom depth, sea surface temperature, bottom temperature, sea surface salinity (but not bottom salinity), stratification, and integrated Chl a (Fig. 8). The relationships are correlative; possible mechanisms are described in the discussion. The sediment-related environmental variables (TOC, % silt/clay) and surface and bottom DIN were excluded from the best GAM models. In addition, environmental variables accounted for less of the variability in the seabird assemblage metrics than in the other assemblages (smaller Mantel's r , smaller R^2 of GAMs).

3.4. Relationships among biological assemblages

There was significant and substantial shared variability among the zooplankton assemblage, the pelagic fishes/jellyfish assemblage, and the epibenthic fishes/invertebrates assemblage (adjusted canonical $R^2 > 0.46$, Table 5). In contrast, the seabird assemblage was significantly but weakly linked to the other three assemblages (adjusted canonical $R^2 < 0.26$, Table 5). This analysis suggests that the zooplankton assemblage substantially influences both the pelagic fishes/jellyfish assemblage and the epibenthic fishes/invertebrates assemblage, and that the pelagic fishes/jellyfish assemblage substantially influences the epibenthic assemblage, and vice versa (Fig. 8). Because these relationships are correlative (i.e., not necessarily mechanistic), the two-way relationship between the pelagic and epibenthic assemblages may be due to shared effects of environmental factors and/or zooplankton prey on these assemblages, rather than direct interactions of these two biological assemblages.

3.5. Comparison with 2013

We tested whether the same environmental factors influenced distributions of biota and whether the same relationships among assemblages occurred in 2013 (excluding the epibenthic assemblage that was not sampled in 2013). In 2013, as in 2012, the NMDS scores for each of the three assemblages had a statistically significant relationship with the full set of environmental variables, based on canonical correlation analysis ($p < 0.0001$). In 2013, the environmental variables explained from 29% to 57% of the variability in NMDS scores, depending on the assemblage, based on the adjusted canonical R^2 (Table 3). More of the variability in NMDS scores was explained in 2012 than 2013 for pelagic fishes/jellyfish (41% vs. 30%) and seabird (49% vs. 34%) taxa whereas explained variability for zooplankton taxa was the same in 2012 and 2013 (57%).

More variability was explained in 2012 than 2013 by the combination of environmental variables that resulted in the highest rank-based Mantel correlation (Mantel's $r = 0.536$ in 2012 and 0.406 in 2013 for zooplankton taxa, 0.434 vs 0.307 for pelagic fish/jellyfish taxa, and 0.335 vs. 0.222 for seabird taxa, Table 4). The best set of explanatory variables, while not identical in 2012 and 2013, shared one to three variables. Zooplankton taxa shared three of the best set variables in 2012 and 2013 (depth, mean stratification, and surface salinity), as did seabird taxa (surface temperature, surface salinity, and mean stratification). While the pelagic fishes/jellyfish assemblage shared only one variable in 2012 and 2013 (Chl a), the Mantel's r value for the best

set of explanatory variables identified for 2012 (0.254) was only slightly less than the Mantel's r value for the best set of explanatory variables identified for 2013 (0.307). In 2013, as in 2012, there was significant shared variability among the zooplankton, pelagic fishes/jellyfish, and seabird assemblages, based on the adjusted canonical R^2 ($p < 0.0001$, Table 5). Explained variability ranged from 11% to 51% in 2012, and 26% to 34% in 2013, for the relationships among these three assemblages (Table 5). We conclude that these environmental and trophic relationships held in 2013 as in 2012, but often less variability was explained in 2013.

4. Discussion

4.1. Influential environmental factors

Six of the measured environmental factors (bottom depth, sea surface and bottom water temperature, sea surface salinity, stratification, and Chl a) were related to the compositions of one or more of the zooplankton, pelagic fishes/jellyfish, epibenthic, and seabird assemblages (Fig. 8). Three factors influenced each assemblage. Connections among these factors were inferred based on the best GAM models (Fig. 6, 7). Bottom depth influenced the zooplankton, pelagic fishes/jellyfish, and epibenthic assemblages, but not the seabird assemblage. Temperature and salinity together characterize water mass and one or both influenced three of four assemblages (except pelagic fishes/jellyfish) in the Mantel correlations and the GAM models. Instead depth influenced the pelagic fishes/jellyfish assemblage; because depth and bottom temperature are correlated, by implication bottom temperature also influenced the pelagic fishes/jellyfish assemblage. The strength of stratification or Chl a influenced three of four assemblages (all except epibenthic).

Temperature, salinity, and/or water mass have been cited commonly as structuring factors for zooplankton (Hopcroft et al., 2010; Eisner et al., 2013; Ershova et al., 2015), epibenthic fishes/invertebrate (Bluhm et al., 2009; Norcross et al., 2010; Blanchard et al., 2013a, b), and seabird (Piatt and Springer, 2003; Gall et al., 2013) assemblages. Some water mass-zooplankton associations reflect populations transported from elsewhere, such as the transport of Bering Slope-Anadyr Water through Bering Strait (Piatt and Springer, 2003; Hopcroft et al., 2010; Eisner et al., 2013). When large zooplankton are transported, seabirds also may concentrate and forage at these locations (Piatt and Springer, 2003; Gall et al., 2013; Kuletz et al., 2015).

Zooplankton species composition and population size also may reflect annual effects of temperature variation on primary and secondary productivity (Ershova et al., 2015). Temperature or salinity were not classified as most influential for the pelagic fishes/jellyfish assemblage; similarly Eisner et al. (2013) found that the best correlation between pelagic fishes assemblage structure and several environmental variables excluded temperature and salinity. Instead we found that Chla and stratification were more influential and Eisner et al. (2013) found that latitude was more influential. Assemblages of small epibenthic fishes in the Chukchi Sea, however, are influenced by bottom salinity and bottom temperature as well as by sediment type (Norcross et al., 2010), which may arise from the effects of topography on northward-flowing water, that create regions of slower currents, and consequently, higher organic deposition (Blanchard et al., 2013a, b).

Salinity appeared as a major structuring force for the zooplankton assemblage. The relationship between zooplankton species composition and salinity (Fig. 6, 7) reflected a strong contrast between nearshore, neritic species and typical shelf or oceanic species (Fig 4a). NMDS₂ values reflected the contrast between an assemblage associated with low-salinity meltwater in the northern Chukchi Sea (characterized by *Clione limacina* and Gammaridea) and more saline Pacific waters associated with *Neocalanus* spp., Euphausiacea and *Eucalanus bungii* (Fig. 3 and 4a). Salinity (bottom salinity, in particular) also was a strong structuring variable for zooplankton assemblage composition in September 2007 in the Chirikov Basin and eastern Chukchi Sea (Eisner et al., 2013) and across the Chukchi Sea between 2004-2012 (Ershova et al., 2015). The influence of salinity on the zooplankton assemblage structure is based on the tight linkage between salinity, macronutrients, and phytoplankton biomass in the productive Anadyr Waters (and the associated Anadyr flow field), in comparison to the less productive Alaska Coastal Water (Springer and McRoy, 1993).

The strength of stratification or Chla concentration (a measure of phytoplankton standing stock) influenced three of four assemblages (all except epibenthic). Stratification often influences primary production; early in the year some initial level of stratification is necessary to increase production in the surface layer and trigger the spring phytoplankton bloom (e.g., Wassmann and Reigstad, 2011). When (or where) nutrients are depleted from the upper water column, strong stratification can reduce production by limiting the vertical fluxes of nutrients into the euphotic

zone. *Chla* reflects production mediated by stratification; the standing stock influences zooplankton distribution, likely through a trophic connection. Stratification also may influence higher trophic levels, such as the seabird assemblage, by concentrating prey near the surface or near the pycnocline, as well as through the physical forcing and accumulation of plankton (and fishes that prey on them) at layer boundaries or fronts (Hunt et al., 1990; Decker and Hunt, 1996; Mehlum et al., 1998; Gall et al., 2013). Nutrients (DIN) also influence primary production but no statistically significant effect was found for any assemblage in either the GAMs or the Mantel correlations. This likely occurred because the influence of DIN is indirect and delayed and thus masked by the more direct influence of *Chla*.

The depth range across the Bering-Chukchi shelf is small in absolute terms, yet highly influential on both the assemblage structure and the flow field. A change in seafloor depth of only 10 m represents 20% to 50% of the total water depth over most of the survey area. Vorticity and continuity constraints associated with such large relative changes in water column depth are sufficient to exert dominant control over the low frequency circulation field (Spall, 2007) and influence the distribution of water masses, sediment grain size, and organic carbon content in the region, thereby playing a leading role in at least epibenthic assemblage structure in the northeastern Chukchi Sea (Blanchard et al., 2013 a, b).

Bottom substrate type as characterized by % silt/clay and TOC was not retained in the best GAM models (Fig. 6, 7), but was an influential environmental variable for the epibenthic assemblage in the maximum rank-based Mantel correlations (Table 4). This relationship was weak; the Mantel's *r* values were similar with and without % silt/clay (Table 4). This weak relationship is inconsistent with previous studies in the northern Bering and Chukchi seas which found substrate type to be moderately influential (Bluhm et al., 2009; Cui et al., 2010; Norcross et al., 2010; Blanchard et al., 2013a, b; Ravelo et al., 2014). Either depth or other variables are a sufficient proxy for sediment characteristics, the relationship is weak at the broad scale examined here, or our interpolated sediment measures did not adequately reflect sediment characteristics at the sampling stations (in the previous studies, the sediment and biological sampling co-occurred). In addition, the large grain size fraction of the substrate was not included in the environmental variables considered in our study; large-grained sediment such as gravel and boulders provide substrate for taxa that need attachment, in particular filter-feeders such as

sponges and ascidians. Such hard bottom habitat tends to be available in areas of high current flow such as Bering Strait, in Barrow Canyon, and under sections of the Alaska Coastal Current, and increases epibenthic species richness in areas where hard substrate is available (Mayer et al., 1996; Bluhm et al., 2009, Pisavera et al., 2015). Finally, distributions of sediment-related factors did not directly match the distribution of water masses as characterized by the temperature and salinity distribution; rather the distributions of sediment-related factors are more closely linked to the current velocity field (Grebmeier et al., 2015), which was not considered in this study. TOC and % silt/clay were higher southwest of St. Lawrence Island and on the south-central and northeastern Chukchi shelf than in the Chirikov Basin and southeast of St. Lawrence Island (Fig. 2). Sediment grain size was also generally coarse nearshore (Grebmeier et al., 2006; see also region-wide trend in source data: Grebmeier and Cooper, 2014). This characterizes the south-central and (part of the) northeastern Chukchi shelf as depositional areas.

Thus, the six environmental factors that most influenced distributions of zooplankton, pelagic fishes/jellyfish, epibenthic fishes and invertebrate, and seabird assemblages likely can be simplified to three factors reflecting bottom depth, water mass, and their stratification and productivity (which are tightly linked in the study region). Combined, these factors influence prey availability to the ecosystem components analyzed here. Their influence can be explained by mechanistic connections. Water masses transport nutrients, particulate organic matter, and organisms from the Bering Sea northward (e.g., transport of Bering Slope-Anadyr Water into Chirikov Basin) and result in ecosystem connectivity between the northern Bering and southern Chukchi seas as reflected in the cross-assemblage zoogeographic patterns. At the same time, water masses reflect *in situ* modifications as they transit the shelves resulting, for example, in temperature-related regional differences in metabolic rates and species specific temperature preferences (e.g., Laurel et al., 2015). The influence of Alaska Coastal Water, which is warmer, fresher, and nutrient-poor (Springer and McRoy, 1993), is typically spatially coincident with slightly shallower depths, although sufficient winds can spread these waters offshore to deeper regions (e.g., Danielson et al., this volume). Stratification triggers the spring bloom and later limits vertical nutrient fluxes, and thus food availability for zooplankton and in turn for planktivorous fishes and seabirds. As previous programs have pointed out, the implication for future studies is that the three environmental factors depth, water mass, and productivity regimes

should be a focal point for system-level evaluations (for example, this is key to the design of the Distributed Biological Observatory; Grebmeier et al., 2010).

4.2. Spatial gradients in species composition

The ordination of assemblages was principally structured from nearshore to offshore and from south to north (Fig. 3). This pattern is most obvious for the epibenthic assemblage, but an obvious north-south gradient was also found for the zooplankton and pelagic fishes/jellyfish assemblages. The nearshore to offshore contrast usually is stronger in the south, where the enormous discharge of the Yukon River is more apparent and extends farther offshore (e.g., Danielson et al., this volume). For the seabird assemblage, ‘hotspots’ were identified near the Chukchi shelf break for some seabird species, particularly shearwaters, black-legged kittiwakes and other surface feeding birds (Kuletz et al., 2015). Surface feeding seabirds are known to aggregate near shelf breaks, where upwelling concentrates prey (Yen et al., 2006; Hunt et al., 2014).

Zooplankton assemblage structure was strongly tied to water masses, whereas epibenthic assemblage structure was much less so; seabird and pelagic fishes/jellyfish assemblages were intermediate. This conclusion is based on the gradients in assemblage composition, which were gradual for epibenthic taxa, abrupt for zooplankton taxa, and intermediate for pelagic fishes/jellyfish and seabird taxa (Fig. 4). These patterns are logical consequences of differences in lifestyle, motility and degree of water mass-association of the four assemblages. The turnover of epibenthic indicator species (as evident in core use area) was very gradual (Fig. 4b), which implies epibenthic assemblages with broad distribution ranges and transitions, facilitated by the advective character of the study area that transports meroplanktonic stages across the northern Bering and Chukchi seas (e.g. Grebmeier et al., 2015b). Adult epibenthic invertebrate assemblages are relatively stable in their spatial distribution and are not carried with water masses. Thus, compared with zooplankton and other pelagic assemblages, these assemblages are unable to adjust to short-term (e.g., seasonal) or medium-term (interannual) variations in water mass characteristics and instead reflect the long-term integration of water mass spatial distributions (Blanchard et al., 2013; Ravelo et al., 2014, 2015). Arctic epibenthic invertebrates are also typically quite long lived and as such integrate over multiple years of environmental variation (Carroll et al., 2011). While benthic (especially infaunal) biomass strongly reflects

water mass properties and processes (e.g., Grebmeier et al., 2006, 2015a, b), the connection between water mass and epibenthic assemblage structure is looser (Bluhm et al., 2009).

In contrast to the other assemblages, zooplankton indicator species were distinctly grouped along both axes (Fig. 4a). This implies that zooplankton taxa form assemblages, at least within core use areas, that are more distinct than those of epibenthic taxa. We identified three distinct assemblages: a nearshore assemblage affiliated with the Alaska Coastal Water, a southern Chukchi assemblage corresponding to Bering Sea Shelf and Anadyr waters, and a northern Chukchi shelf assemblage associated with the near-bottom Winter Water and surface ice melt water separated by a pycnocline. In addition, our analysis discriminated an assemblage of species (e.g., *Calanus marshallae*, *Themisto libellula*) abundant in the two latter assemblages, but generally scarce in the neritic assemblage. *Calanus marshallae* and *Themisto libellula* typically occur in the Arctic Ocean and on the continental shelves of sub-Arctic seas and appear to be tied to the specific environment (the presence of cold water layers throughout the summer) rather than to a specific water mass. One of the indicator species for the northern Chukchi Sea, the pteropod *Clione limacina*, while limited to the northern Chukchi Sea in our surveys, is widely distributed in boreal waters, including the North Pacific and Arctic oceans. In terms of zoogeography, the neritic and southern Chukchi assemblages comprise Bering Sea expatriates advected into the Chukchi Sea, while the northern Chukchi assemblage is reflective of the resident Chukchi Sea fauna.

The distinct zooplankton assemblages in the Chukchi Sea and their linkages to certain water masses have been reported by multiple studies as early as the 1930s (e.g. Stepanova, 1937; Wirketis, 1952; Pavshits, 1984) and these earlier findings have been corroborated by later studies (Hopcroft et al., 2010; Eisner et al., 2013; Questel et al., 2013; Ershova et al., 2015). The studies agreed that Bering Sea Shelf (including Anadyr) waters, while also populated with widespread shelf species (e.g., *Calanus marshallae*), are best characterized by large oceanic copepods *Neocalanus* spp. and *Eucalanus bungii*. These copepods originate from the Bering Sea outer shelf and are excellent tracers of Pacific intrusion even in the high Arctic. *Neocalanus* spp. can be especially abundant in the vicinity of the Bering Strait (Pinchuk, 1993) in early and mid-summer. In Bering Strait, turbulent upwelling of nutrient-rich Anadyr water at Anadyr and Bering straits further enhances high levels of primary production (Eisner et al., 2013; Lee et al.,

2013) and helps sustain the zooplankton entrained in the Anadyr Current, and concomitantly an abundant and diverse seabird assemblage (Piatt and Springer, 2003). The neritic assemblage associated with Alaska Coastal Water typically comprises small (<1.5 mm) copepods *Acartia hudsonica*, *Eurytemora* spp. and the cladocerans *Evadne* spp. and *Podon* spp., which can be abundant in the nearshore areas (e.g., Ershova et al., 2015). Zooplankton for our study were collected with coarser mesh nets, which allowed quantification of only larger neritic copepods *Epilabidocera amphitrites* and *Centropages abdominalis* in addition to hydrozoan jellyfish *Proboscya* *flavicerrata* and *Eutonina indicans*, and crangonid zoea as indicator species.

The seabird assemblage identified for the Bering Strait and southern Chukchi Sea matches a region with a well-defined zooplankton assemblage. This region has previously been noted for high seabird densities, particularly the planktivorous *Aethia* auklets and larger, piscivorous common and thick-billed murre (although the latter also consumes euphausiids and *Themisto libuella*) (Piatt and Springer, 2003; Gall et al., 2013; Wong et al., 2014; Kuletz et al., 2015). Hence, an overlap of seabird and zooplankton assemblages would be expected. Throughout the study area, the most abundant species is the least auklet (Gall et al., 2013; Kuletz et al., 2015), which consumes small to medium-sized copepods (*C. marshallae* and *N. plumchrus*), whereas the larger-bodied crested auklet consumes large copepods (*N. cristatus*) and *Thysanoessa* euphausiids (Gall et al., 2006; Sheffield-Guy et al., 2009).

The summer distribution of seabirds at sea is strongly influenced by location of their breeding colonies, and large seabird colonies exist in summer on St. Lawrence Island, King Island, the Diomed Islands in Bering Strait, and immediately north and south of Point Hope (Stephensen and Irons, 2003; Piatt and Springer, 2003; Kuletz et al., 2015). However, few auklets (small numbers of parakeet auklets) nest north of Bering Strait. Since auklets are estimated to forage approximately 50 km from their colonies (Obst et al., 1995), the high numbers of crested auklets found in the central and northern Chukchi Sea must be non- or post-breeding birds (Kuletz et al., 2015); this may be one reason this seabird indicator species shows a different relationship with NMDS₂, compared to most seabirds. Similarly, the short-tailed shearwater is a summer visitor that breeds in the southern hemisphere, and the limited overlap between shearwaters and other seabird indicator species may be partly due to its non-restricted foraging range, as well as its more omnivorous diet (Armstrong, 1995).

Arctic cod were an abundant epibenthic fish in previous Chukchi Sea surveys (Barber et al., 1997; Norcross et al., 2010, 2013) and the most abundant epibenthic fish during the Chukchi Sea portion of the 2012 bottom trawl survey (Goddard et al., 2014). Age-0 Arctic cod were highly abundant in the surface trawl surveys and in midwater habitats of the northern Chukchi shelf in acoustic-trawl measurements conducted as part of the 2012 and 2013 surveys (De Robertis et al., this issue). However, despite their abundance, Arctic cod in our analyses were not identified as an indicator species because they fell below the threshold for inclusion (association with an NMDS axis, $R^2 < 20\%$) as a result of their wide distributed throughout the study area and their highly variable CPUE (e.g., bottom trawl survey, mean = 1.6, SD = 5.3). It is well known that Arctic cod use multiple habitats (e.g. Logerwell et al, 2015), and the strongest gradient in Arctic cod distribution was north-south, similar to epibenthic assemblages.

4.3. Relationships among assemblages

The advective character of the study area results in the generally high faunistic and biogeographic connectivity of the northern Bering and Chukchi seas, in particular the southern Chukchi Sea. Three main cross-assemblage geographical groupings (i.e., communities) emerged, with one community associated with the Alaska Coastal Water, a second community associated with the Chirikov Basin and southern Chukchi Sea, and a third community associated with the northern Chukchi shelf (Fig. 9). Both of the first two communities connect the northern Bering and southern Chukchi seas. The Alaska Coastal Water community is characterized by a mixture of zooplankton, fish, invertebrate, and seabird taxa; the Chirikov Basin / southern Chukchi community is characterized by large crustacean zooplankton and seabird taxa; and the northern Chukchi shelf community is characterized by several epibenthic and pelagic invertebrate species. The Alaska Coastal Water is warmer, fresher, and nutrient depauperate; the Chirikov Basin and southern Chukchi Sea are colder, saltier, and nutrient rich; and the northern Chukchi shelf is colder and saltier but not as nutrient rich (Coachman et al., 1975). The narrow range of NMDS₁ values across much of the Chukchi shelf for the zooplankton, pelagic fishes/jellyfish, and epibenthic assemblages implies that these assemblages are fairly homogeneous across this region. Likewise, either NMDS₁ values or NMDS₂ values, depending on the taxa, are consistent nearshore and south, implying fairly homogeneous assemblages associated with the Alaska Coastal Water, which extends further offshore in the south than in the north. In addition to these

three communities, a northern Bering, offshore (fourth) community includes species characteristic of the southeastern Bering Sea such as walleye pollock and is associated with Bering Shelf Water. The definition of the fourth community was based only on epibenthic fishes and invertebrates because only the bottom trawl survey extended this far offshore.

The Chirikov Basin / southern Chukchi Sea community was different in that it was characterized by distinct zooplankton and seabird taxa, but was not strongly associated with distinct pelagic or epibenthic fish and invertebrate taxa. This region is considered an extension of the Bering Sea greenbelt and Anadyr Current (Piatt and Springer, 2003), which are rich with nutrients and zooplankton, including a number of oceanic and outer shelf/slope species advected onto the northern Bering Sea shelf and through Bering Strait (Piatt and Springer, 2003; Gibson et al., 2013). This richness is enhanced by turbulent upwelling of this nutrient-rich water at Anadyr and Bering straits (Piatt and Springer, 2003). The location of these nutrient-rich waters flowing past the Bering Sea islands accounts for the exceptionally large seabird colonies in the region (Piatt and Springer, 2003; Stephensen and Irons, 2003). In contrast to zooplankton, which are advected onto the shelf, the fish community throughout the northern Bering Sea and the southern Chukchi Sea is an extension of a subset of the Bering shelf community, although biomass, species diversity, and mean size of fishes decline rapidly from south to north (Stevenson and Lauth, 2012; Mueter et al., 2013).

The zooplankton assemblage was related to the distributions of both the pelagic fishes/jellyfish and epibenthic assemblages (Fig. 8). These relationships may reflect both direct connections through trophic relationships and indirect connections through shared environmental influences. In contrast, the relationship between the zooplankton assemblage and the distribution of the seabird assemblage was weak, although statistically significant. The weak relationship was surprising given the obvious spatial overlap of the zooplankton and seabird assemblages in Bering Strait and southern Chukchi Sea and the prominence of planktivorous birds in the region (Piatt et al., 1991; Gall et al., 2013; Kuletz et al., 2015). Two of the most abundant seabirds found in the area, least auklets and short-tailed shearwaters, can be highly variable in abundance and distribution, apparently in response to changes in stratification and salinity (Hunt and Harrison, 1990; Gall et al., 2013), which might contribute to the weak associations between seabirds and other biota or factors. The relationship also may be diluted by a ‘colony effect’ for

seabirds that is not reflected in the zooplankton assemblage (Fig. 3). Seabirds often were abundant near Point Hope (e.g., common murre, thick billed murre, horned puffin [Kuletz et al., 2015]), whereas zooplankton generally were not (Appendix). Additionally, within the seabird assemblage, prey selection is variable and changes interannually. For example, the least auklet will feed its chicks the smaller copepod *C. marshallae*, but its breeding success increases when the larger *N. flemingeri* is predominate in its diet. The larger-bodied crested auklet will also feed its chicks *N. flemingeri*, but has higher reproductive success when even larger zooplankton (*N. cristatus* and euphausiids) are available (Gall et al., 2006; Sheffield-Guy et al., 2009). The largest diving birds, thick-billed murres and short-tailed shearwaters, also consume euphausiids, but often eat a variety of pelagic fishes (Piatt et al., 1991). In addition, euphausiids were poorly sampled by our zooplankton net. Thus, the variety and flexibility of seabird diets, as well as the lack of euphausiid data, might further dilute the overall relationship between seabirds and zooplankton.

Commonly zoogeography is examined for one (e.g., epibenthic fishes and invertebrates; Bluhm et al., 2009) or two assemblages (e.g., zooplankton and pelagic fishes/jellyfish; Eisner et al., 2013), whereas our study is novel in examining the zoogeography of several assemblages (zooplankton, pelagic fishes and jellyfish, epibenthic fishes and invertebrates, and seabirds) simultaneously. This approach yielded new insights into how gradients in assemblage composition differed among assemblages (e.g., more abrupt for zooplankton taxa) and allowed us to identify the communities of this Arctic region (Alaska Coastal Water, Chirikov Basin / southern Chukchi Sea, and northern Chukchi Sea) and the environmental factors influencing them. We also can speculate on how climate change will affect these communities based on space-for-time substitution (Pickett, 1989). The most likely (and obvious) effect will be for the northern Chukchi Sea community to retreat northward as the Alaska Coastal Water and Chirikov Basin / southern Chukchi Sea communities advance. A similar advance of temperate bottom fish on the southeastern Bering Sea shelf during warm years has already been documented (Mueter and Litzow, 2008). The magnitude of advance will be affected by conditions for water sources upstream of these areas (i.e., frequency of ice-free winters in the southeastern Bering Sea) and will be tempered by the continued persistence of ice-cover during winter in the northern Bering and Chukchi seas in the future (Stabeno et al., 2012; Hermann et al., 2013).

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The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1

Sample sizes for environmental data, including the number of observations (obs.), missing values (miss.) and, for the missing values, the number that were estimated (est.). For example for surface temperature in 2012, there were 106 observations and 3 missing values and values were estimated for all 3 missing values. The year indicates collection year except for sediment samples, which were collected during 2006-2012. Only bottom-related data were included for 2010 because the only recent bottom trawl survey of the northern Bering Sea occurred in 2010. DIN abbreviates dissolved inorganic nitrogen.

Environmental variable	Year								
	2010			2012			2013		
<u>Surface-related</u>	obs.	miss.	est.	obs.	miss.	est.	obs.	miss.	est.
Surface temperature				106	3	3	94	6	6
Surface salinity				106	3	3	94	6	6
Surface DIN				99	10	10	99	1	1
Stratification				106	3	3	94	6	6
Integrated chlorophyll <i>a</i>				109	0	0	100	0	0
<u>Bottom-related</u>									
Bottom temperature	202	0	0	106	3	3	94	6	6
Bottom salinity	145	57	57	106	3	3	94	6	6
Bottom DIN	111	91	30	199	10	10	99	1	1
% silt/clay	68	134	134	50	59	59	42	58	58
Total organic carbon	74	128	128	54	55	55	47	53	53

1281

1282 **Table 2.**

1283 Cumulative proportion of the overall variability in 4th root transformed abundances (station-by-
 1284 species matrix, after eliminating rare species) that can be explained by the first two axes from a
 1285 correspondence analysis (CA). Based on 2012 samples for all taxa and areas except 2010
 1286 samples for epibenthic taxa in the northern Bering Sea.

Response variables (assemblage)	CA1	CA2
zooplankton	0.255	0.379
pelagic	0.192	0.328
benthic	0.133	0.228
seabirds	0.135	0.233

1287

1288

1289 **Table 3.**

1290 Relationships between indices of species composition (NMDS scores) and six explanatory
 1291 variables (see text) measured at 79 stations based on canonical correlation analysis. In addition to
 1292 canonical correlations for the first and second canonical axes, adjusted canonical coefficient of
 1293 determination (R^2) value and permutation-based significance level (p -value) for each analysis are
 1294 shown. One station with several unusual values for environmental variables was removed prior
 1295 to analysis ($n=79$). Results in columns 1-4 are based on 2012 samples for all taxa and areas
 1296 except 2010 samples for epibenthic taxa in the northern Bering Sea; results in column 5 are
 1297 based on 2013 samples.

Response variables (assemblage)	Canonical correlations	adjusted canonical R^2	p -value	2013 adj R^2
zooplankton	0.869, 0.533	0.571	< 0.0001	0.571
pelagic	0.774, 0.458	0.408	< 0.0001	0.296
benthic	0.891, 0.299	0.588	< 0.0001	
seabirds	0.768, 0.679	0.489	< 0.0001	0.343

1298

1299

1300 **Table 4.**

1301 Best sets of 1, 2, 3, etc., explanatory variables and maximum rank-based Mantel correlations (in
 1302 parentheses) between each set of variables and indices of species composition (NMDS scores)
 1303 for four biological assemblages. Highest overall Mantel correlations for each assemblage are
 1304 highlighted in bold. Abbreviations are bottom depth (Depth), surface and bottom temperature
 1305 (SST, BT), surface and bottom salinity (SSS, BS), mean stratification (Strat), integrated
 1306 chlorophyll (Chla), and percent of silt and clay in the sediment (%SC). Results in rows 1-6 are
 1307 based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the
 1308 northern Bering Sea; results in rows 7-8 are based on 2013 samples. The alternate set for 2013
 1309 (row 8) shows Mantel correlations for variables that were best for the 2012 data.

1310

# of variables	zooplankton	pelagic	benthic	seabird
1	Strat (0.427)	Strat (0.346)	Depth (0.545)	Strat (0.240)
2	Depth + Strat (0.527)	Strat + Chla (0.400)	Depth + BS (0.563)	Strat + SST (0.316)
3	Depth + Strat + SSS (0.536)	Depth + Strat + Chla (0.434)	Depth + BT + %SC (0.563)	Strat + SST + SSS (0.335)
4	Depth + Strat + SSS + SST (0.516)	Strat + Chla + Depth + DIN (0.433)	Depth + BT + %SC + BS (0.573)	Strat + SST + SSS + Depth (0.337)
5	Depth + Strat + SSS + SST + DIN (0.477)	Strat + Chla + Depth + DIN + SSS (0.427)	Depth + BT + %SC + BS + DIN (0.576)	Strat + SST + SSS + Depth + Chla (0.305)
6	All (0.409)	All (0.393)	All (0.551)	All (0.257)
Best set 2013	Depth + SSS + DIN + Strat (0.406)	SST + SSS + Chla (0.307)		SST + SSS + Strat (0.222)
Alternate set 2013	Depth + Strat + SSS (0.394)	Depth + Strat + Chla (0.254)		Strat + SST + SSS + Depth (0.209)

1311

1312

1313

1314 **Table 5.**

1315 Relationship among indices of species composition (NMDS scores) for four biological
 1316 assemblages measured at 80 stations based on canonical correlation analysis. Each row
 1317 summarizes the relationship between a “response” assemblage and an “explanatory” assemblage
 1318 based on the canonical correlations for the first and second canonical axes, the adjusted
 1319 canonical coefficient of determination (R^2) and a permutation-based significance level ($p <$
 1320 0.0001 for all relationships). Results in columns 1-5 are based on 2012 samples for all taxa and
 1321 areas except 2010 samples for epibenthic taxa in the northern Bering Sea; results in column 6 are
 1322 based on 2013 samples.

explanatory	response	Canonical correlations	adj. canonical R^2	2013 adj. canonical R^2
zooplankton	pelagic	0.850, 0.391	0.511	0.275
zooplankton	benthic	0.855, 0.052	0.589	
zooplankton	seabirds	0.738, 0.144	0.258	0.344
pelagic	benthic	0.874, 0.166	0.609	
pelagic	seabirds	0.587, 0.038	0.105	0.258
benthic	pelagic	0.874, 0.166	0.465	

1323

1324

1325 **Figure legends**

1326 **Fig. 1.** The Bering, Chukchi, and Beaufort Seas form a continuum between the North Pacific
1327 Ocean and the Arctic Ocean. This idealized schematic denotes some of the important water
1328 masses and currents that impact regional differences in physical habitat characteristics. Figure
1329 courtesy of S. Danielson and T. Weingartner, University of Alaska Fairbanks.

1330

1331 **Fig. 2.** Environmental conditions in surface waters (top) and bottom waters (bottom), including
1332 surface and bottom temperature (SST, BT), surface and bottom salinity (SSS, BS), dissolved
1333 inorganic nitrogen (DIN) (surface upper row, bottom lower row), mean stratification (Strat),
1334 integrated chlorophyll (Chl a), total organic carbon in sediments (TOC), and percent of silt and
1335 clay in the sediment (%SC). All surface values are based on 2012 samples. Bottom temperatures,
1336 salinity and DIN are based on 2012 samples in the Chukchi Sea and 2010 samples in the
1337 northern Bering Sea, resulting in a discontinuity in Bering Strait (horizontal black bars). Values
1338 for TOC and %SC are based on samples obtained between 1970 and 2012. Color scale in each
1339 panel ranges from minimum (dark blue) to maximum (dark red) of predicted values from
1340 geospatial models (on transformed scale where applicable, see text). Single contour in each panel
1341 corresponds to mean isoline (on transformed scale where applicable).

1342

1343 **Fig. 3.** NMDS plots by taxa. Spatial patterns of first mode of species composition (NMDS axis
1344 1) plotted in upper row and second mode (NMDS axis 2) plotted in lower row. Red values are
1345 positive and blue values are negative. Based on 2012 samples for all taxa and areas except 2010
1346 samples for epibenthic taxa in the northern Bering Sea. The text labels (e.g., Chirikov Basin,
1347 Chukchi) lie near areas of similar NMDS values and match the labels in Figure 4.

1348

1349 **Fig. 4a.** Zooplankton (left column) and pelagic (right column) taxa for indicator species (defined
1350 in methods). Bar graphs of core use area (defined in methods). The related geographic plots of
1351 NMDS axis values are shown in Figure 3. Axis 1 values in upper row and axis 2 values in lower
1352 row. Names of identified assemblages are shown beside the bars, as described in the results.
1353 Dashed lines indicate groups of similar NMDS values and match the labels in Figure 3. Based on
1354 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern
1355 Bering Sea.

1356 **Fig. 4b.** Epibenthic indicator species (defined in methods). At left, bar graphs of core use area
1357 (defined in methods). The related geographic plots of NMDS axis values are shown in Figure 3.
1358 Axis 1 values in left column and axis 2 values in right column. Names of identified assemblages
1359 are shown beside the bars, as described in the results. Dashed lines indicate groups of similar
1360 NMDS values and match the labels in Figure 3. Based on 2012 samples for all taxa and areas
1361 except 2010 samples for epibenthic taxa in the northern Bering Sea.

Fig. 4c. Seabird indicator species (defined in methods). Bar graphs of core use area (defined in methods). The related geographic plots of NMDS axis values are shown in Figure 3. Axis 1 values in upper row and axis 2 values in lower row. Names of identified assemblages are shown beside the bars, as described in the results. Dashed lines indicate groups of similar NMDS values and match the labels in Figure 3. Indicator species were identified from 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

Fig. 5. Bi-plots by taxa and environmental variables including bottom depth (Depth), sea surface and bottom temperature (SST, BT), sea surface and bottom salinity (SSS, BS), dissolved inorganic nitrogen (DIN) (surface values for zooplankton, pelagic, and seabirds; bottom values for epibenthic), mean stratification (Strat), integrated chlorophyll (Chla), total organic carbon in sediments (TOC), and percent of silt and clay in the sediment (%SC). Results are based on 2012 samples for all taxa and areas, except 2010 samples were used for epibenthic taxa in the northern Bering Sea.

Fig. 6. Relationships (best model: plots and R^2) between indices of species composition (NMDS1) and environmental variables. The R^2 values are 0.732 (zooplankton), 0.707 (pelagic), 0.656 (benthic), and 0.168 (seabird). The sediment-related environmental variables did not enter the best model. Temperature and salinity are surface values for all taxa except epibenthic, which are bottom values. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea. Percentages listed in panels denote partial R^2 values, defined as the proportional reduction in residual sum of squares achieved by adding a given term to a reduced model without that term. There is no percentage listed in panels for taxa with only a single explanatory variable, which simply is the overall R^2 (i.e., 0.656 for benthic).

Fig. 7. Relationships (best model: plots and R^2) between indices of species composition (NMDS2) and environmental variables. The R^2 values are 0.199 (zooplankton), 0.150 (pelagic), 0.157 (benthic), and 0.490 (seabird). The sediment-related environmental variables were not statistically significant. Temperature and salinity are surface values for all assemblages except epibenthic, which are bottom values. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea. Percentages denote partial R^2 values, defined as the proportional reduction in residual sum of squares achieved by adding a given term to a reduced model without that term. There is no percentage listed in panels for taxa with only a single explanatory variable, which simply is the overall R^2 (e.g., 0.199 for zooplankton).

Fig. 8. Diagram linking assemblages, based on indices of species composition (NMDS scores) and environmental variables, with connections based on best GAM models (Figures 6 and 7). The diagram also links among taxa, with connections based on adjusted canonical $R^2 > 0.4$ (Table 5). Connectivity between pelagic and epibenthic assemblages was quantified and tested for significance because they may influence each other. Other connections are assumed to be one-way. Total organic carbon (TOC), % silt/clay (%SC), and dissolved inorganic nitrogen

(DIN) were included in the analyses but are not significantly related. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

Fig. 9. Map showing polygons outlining regions of three cross-taxa assemblages (i.e., communities) with selected indicator species listed. The three regions are Chukchi shelf (green), Chirikov Basin / southern Chukchi (red), and Alaska Coastal Current (blue). The regions are approximate and based on NMDS axes maps (Figure 3) and core use areas (Figure 4), as explained in the results section “Ordination of assemblages”. A northern Bering shelf community located offshore (e.g., walleye pollock) is not shown because it is based only on epibenthic data. The dots represent station locations in 2012. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

Appendix. Species distribution maps for indicator species. The species are ordered the same as in Figure 4 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea. In the plot for epibenthic axis 2, *Chionocetes* hybrid is between *C. bairdi* and *C. opilio*.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4a.

Fig. 4b.

Epibenthic fishes and invertebrates

Fig. 4c.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Northern Chukchi shelf community

Chirikov Basin and southern Chukchi community

Alaska Coastal Water community

Appendix.

Zooplankton axis 1

Appendix.

Zooplankton axis 1

Appendix.

Zooplankton axis 1

Appendix.

Zooplankton axis 2

Appendix.

Pelagic fishes/jellyfish axis 1

Appendix.

Pelagic fishes/jellyfish axis 2

Appendix.

Epibenthic axis 1

Appendix.

Epibenthic axis 1

Appendix.

Epibenthic axis 1

Appendix.

Epibenthic axis 1

Appendix.

Epibenthic axis 1

Appendix.

Epibenthic axis 1

Appendix.

Epibenthic axis 2

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Epibenthic axis 2

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Epibenthic axis 2

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Epibenthic axis 2

Appendix.

Epibenthic axis 2

Appendix.

Seabird axis 1

Appendix.

Seabird axis 2