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## Using biological traits and environmental variables to characterize two Arctic epibenthic invertebrate communities in and adjacent to Barrow Canyon



Kimberly Rand<sup>a,\*</sup>, Elizabeth Logerwell<sup>a</sup>, Bodil Bluhm<sup>b</sup>, H elo ise Chenelot<sup>c</sup>, Seth Danielson<sup>c</sup>, Katrin Iken<sup>c</sup>, Leandra Sousa<sup>d</sup>

<sup>a</sup> Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA

<sup>b</sup> Department of Arctic and Marine Biology, UiT – The Arctic University of Norway, Troms , Norway

<sup>c</sup> College of Fisheries and Ocean Sciences, University of Alaska, 905 N. Koyukuk Drive, Fairbanks, AK 99775, USA

<sup>d</sup> Department of Wildlife Management, North Slope Borough, PO BOX 69, Barrow, AK 99723, USA

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### ABSTRACT

The Arctic's Barrow Canyon, located in the northeastern Chukchi and western Beaufort seas, supports a rich and diverse benthic ecosystem and is often termed an ecological “hotspot” of productivity. Within and adjacent to Barrow Canyon, the epibenthic invertebrate communities vary, with biomass and taxonomic distributions related to habitat variation. Here we asked if the patterns observed are due to Barrow Canyon's variation in near-seafloor physical hydrography, and whether differences in taxonomic distribution also reflect differences in functional properties of the epibenthic invertebrate community. Data were collected using a standardized 83–112 bottom trawl during two surveys in and adjacent to Barrow Canyon: the northeast Chukchi Sea survey in 2013 and the western Beaufort Sea survey in 2008. A portion of the Beaufort Sea survey also used a liner to retain smaller organisms. A suite of nine environmental variables were examined, that included depth, bottom water temperature, bottom hardness as measured by acoustics, and circulation model hindcast current speed. They explained 18–47% of observed variance for each of the three data sets (Chukchi Sea, Beaufort Sea lined net (LN), Beaufort Sea unlined net (UN)). In the Chukchi Sea, bottom hardness and depth were significant variables. In the Beaufort Sea LN hauls, depth, bottom temperature, and the mean current speed on the day of sampling were significant variables and in the Beaufort Sea UN hauls, depth was the only significant variable. Of the 150+ collected taxa from each survey, ~20 made up 90% of the total biomass in the Beaufort and Chukchi Seas, and six of the 20 taxa were common to both study areas. We used biological traits analysis (BTA) of body morphology, trophic, and reproductive traits to further characterize the epibenthos at the head of Barrow Canyon in the Chukchi Sea and into Barrow Canyon in the Beaufort Sea. Although the Chukchi and Beaufort seas differed taxonomically in abundance and distribution, they were functionally similar based on the biological traits we examined. A traits analysis can advance knowledge of a community of organisms; however, it is most informative if used as a complement to a taxonomic composition analysis of abundance and distribution.

### 1. Introduction

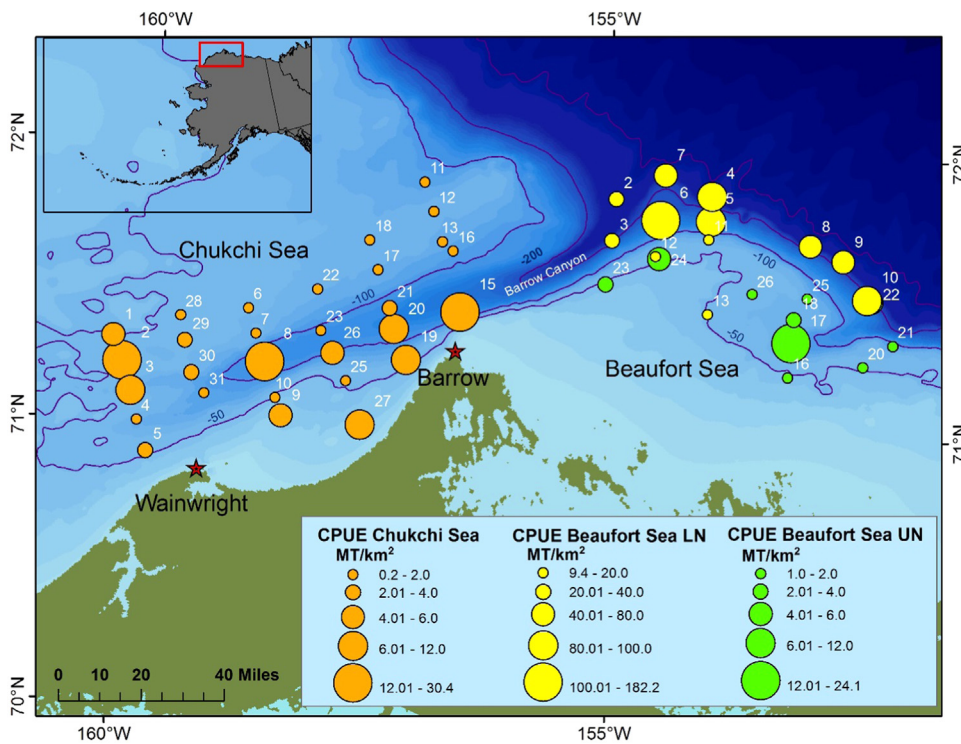
Barrow Canyon (Fig. 1) is an important marine geologic feature situated in the northeast Chukchi Sea and is frequently referred to as the gateway to the Pacific Arctic Basin. The head of Barrow Canyon starts approximately 150 km southwest of Point Barrow and extends into the Beaufort Sea with depths up to 300 m. Several water masses transiting from the Bering and Chukchi continental shelves flow northward into the Arctic Basin through Barrow Canyon (Weingartner

et al., 2005a; Gong and Pickart, 2015). Upwelling in Barrow Canyon causes locally elevated primary production (Hill and Cota, 2005) which supports large numbers of both pelagic- and benthic- feeding seabirds (Kultez et al., 2015; Lovvorn et al., 2015) and marine mammals (Moore et al., 2010) during the summer months. Arctic cod (*Boreogadus saida*) are also common, both within the vicinity of Barrow Canyon and in the canyon itself, where abundance is highest in colder and more saline near-bottom waters (Logerwell et al., 2018). In the areas adjacent to Barrow Canyon, the Chukchi and Beaufort Sea shelves, epibenthic

\* Corresponding author.

E-mail address: [kimberly.rand@noaa.gov](mailto:kimberly.rand@noaa.gov) (K. Rand).

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**Fig. 1.** The catch-per-unit-effort (CPUE metric tons (MT) wet weight/km<sup>2</sup>) by hauls in and near Barrow Canyon. The Chukchi Sea survey was in 2013 (yellow) and the Beaufort Sea LN (green), and UN (orange) surveys were in 2008; The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with no net liner. All hauls are labeled in white text for reference. The CPUE scale is different for the Beaufort Sea LN hauls; the lowest and highest CPUE estimate for the Beaufort UN and Chukchi hauls also varies. Note: Haul 22, Beaufort Sea UN survey, is masked by haul 10, Beaufort Sea LN survey due to a lower CPUE estimate. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

communities have been well described (Feder et al., 1994; Bluhm et al., 2009; Blanchard et al., 2013a, b; Ravelo et al., 2014, 2015; Grebmeier et al., 2015a, b; Ravelo et al., 2015), including a macrofaunal benthic “hotspot” that has persisted for decades, just northwest of the canyon on the Chukchi shelf (Grebmeier et al., 2015). However, despite the oceanographic and biological importance of Barrow Canyon, few studies have explicitly examined the benthic invertebrate fauna within the canyon. In this study, we examined two communities that together encompass most of Barrow Canyon; the Chukchi study area is located at the head of Barrow Canyon, extends onto the Chukchi shelf, and is relatively shallow. The Beaufort study area is located north of the Chukchi study area, in the deeper portion of Barrow Canyon and extends onto the Beaufort Shelf.

In both the northeast Chukchi and western Beaufort seas, benthic invertebrate communities are characterized by moderate species diversity, compared to other Arctic shelf seas (Piepenburg et al., 2011), and high biomass (~5000 kg/km<sup>2</sup>) when compared to the corresponding benthic fish communities (Rand and Logerwell, 2011; Logerwell et al., 2011). Within each community, patchiness of both species distribution and biomass are common (Ravelo et al., 2014, 2015). Several features of the local habitat influence the structure of Arctic benthic communities, such as currents (Grebmeier et al., 2006), nutrient fluxes and food availability (Grebmeier et al., 1989; Cusson and Bourget, 2005; Dunton et al., 2005), and geological characteristics (e.g., sediment, geological structure; Feder et al., 1994; Cusson and Bourget, 2005). The study region's currents within and adjacent to Barrow Canyon consists of swift flows associated with the Alaskan Coastal Current (ACC), the Beaufort Gyre, the Beaufort shelfbreak jet, and wind-driven events (including upwelling), that cause meanders and eddies to disrupt the background circulation field (Pickart et al., 2013). The ACC typically flows from the Chukchi Shelf along the axis of Barrow Canyon toward the continental slope where the Chukchi and Beaufort seas meet (Fig. 2). The Barrow Canyon mean flow opposes the prevailing winds that blow from the northeast but the winds are often strong enough to reverse the circulation here and that of the shelfbreak jet, as well as cause upwelling of subsurface waters within Barrow Canyon and along the Beaufort Slope (Mountain et al., 1976;

Weingartner et al., 1998; Pickart et al., 2013; Danielson et al., 2016; Danielson et al., 2017). Elevated levels of turbulent mixing within the canyon is likely biologically important (Shroyer, 2012). The waters leaving Barrow Canyon, in general, tend to follow topographic isobaths eastward and transition into the Beaufort shelfbreak jet (Nikolopoulos et al., 2009; von Appen and Pickart, 2012; Gong and Pickart, 2015). The complex bathymetry of the canyon and slope intersection routinely causes eddies to form near the canyon mouth (Pickart et al., 2005; Watanabi and Hasumi, 2009) which propagate into the deep adjoining basin or get caught in the westward-flowing Beaufort Gyre (Watanabe et al., 2011). The currents here evolve over time as a function of the wind and the various water densities, together determining the structure of the flows in and adjacent to Barrow Canyon. This energetic flow environment – and associated fronts, advection, convergence, turbulent mixing, and particulate export – sets the stage for areas of locally elevated biological activity and benthic production in and near Barrow Canyon. How the currents and thermohaline properties influence the structuring of the local benthic invertebrate community is complex (Day et al., 2013) and not well understood in detail.

While the Chukchi and Beaufort Sea shelves benthic and pelagic communities are reasonably well characterized with respect to species diversity (e.g. richness and evenness), biomass, relative abundance, and trophic structure (Feder et al., 1994; Bluhm et al., 2009; Blanchard et al., 2013a, b; McTigue and Dunton, 2014; Ravelo et al., 2014; Divine et al., 2015; Grebmeier et al., 2015a, b; Ravelo et al., 2015), other functions performed by dominant benthic organisms in this region are less well characterized. At the most basic level, functional ecology is defined as the study of ecological processes, patterns, and underlying mechanisms within an ecological community (Diaz and Cabido, 2001; Petchey and Gaston, 2006). Further, a functional or biological trait (herein the same) infers the underlying processes of that trait, such as feeding or growth. The degree of overlap between species diversity and functional diversity is different among systems. A system that may be rich in species diversity could have little functional diversity (i.e. most species feed similarly) or very high functional diversity (e.g. several different feeding strategies; Hewitt et al., 2008). Thus, functional community structure can inform us about the energy flow and resource

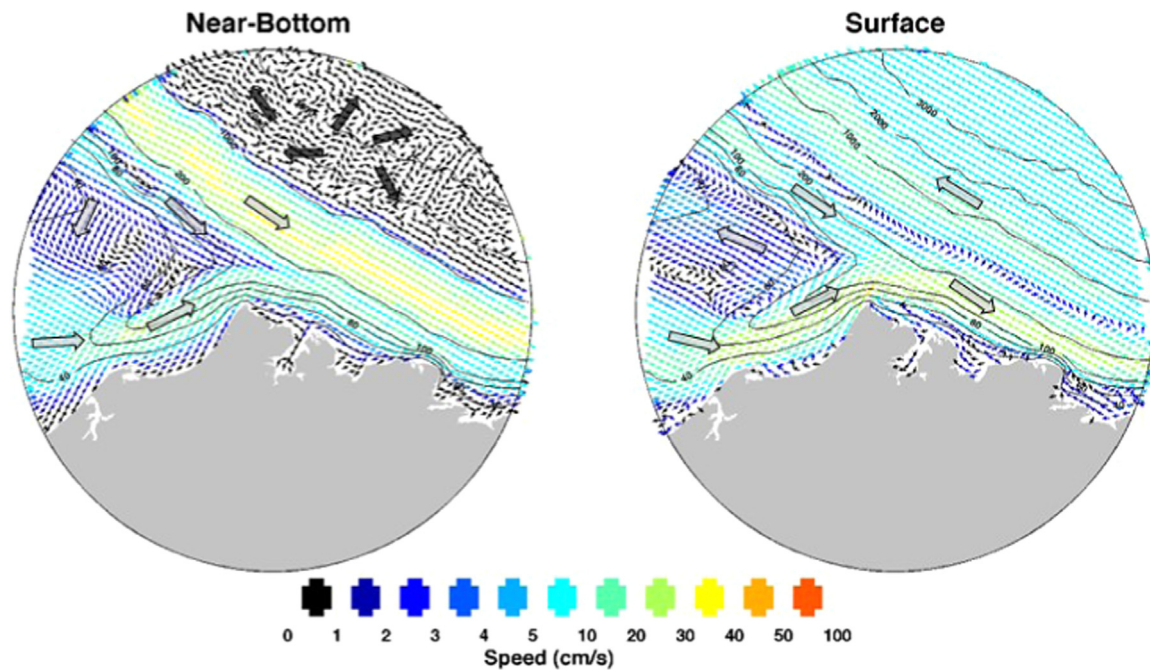


Fig. 2. Average near bottom current velocities; results were produced by a 3-dimensional ocean and ice circulation numerical hindcast model, which was integrated over 2005–2011 with the Regional Ocean Modeling System (ROMS) framework. Large arrows were overlaid to show general current trajectories.

partitioning in a system and provide insight into a system's resilience to change. Incorporating ecological function into a diversity analysis is especially important in the benthic marine system because of the strong relationship between habitat variability and taxonomic diversity and distribution (Hewitt et al., 2008).

In addition to characterizing the epibenthic community structure in these communities, we applied a biological traits analysis (BTA) to better understand the influence of bottom hardness and hydrography on the ecological functions of epibenthos in and adjacent to Barrow Canyon. This approach has been used most recently in other Arctic communities (Oug et al., 2012; Krumhansl et al., 2016), including the Barents Sea (Cochrane et al., 2012; Wlodarska-Kowalczyk et al., 2012), and the Canadian Arctic (Krumhansl et al., 2016). A BTA approach (Bremner et al., 2003, 2006) is a tool used to examine a suite of biological traits simultaneously across the dominant taxa in a study system to aid in identifying those habitat characteristics that may influence the selection of traits (Bremner et al., 2003). Our approach in this study followed the general framework of several earlier studies that used biological traits to characterize invertebrates in freshwater (Jackson, 1993; Usseglio-Polatera et al., 2000; Haybach et al., 2004; Bonada et al., 2007; Conti et al., 2014), lagoons (Sigala et al., 2012), estuaries (Alves et al., 2014), and marine ecosystems (Bremner et al., 2006; Hewitt et al., 2008; Pacheco et al., 2010; Paganelli et al., 2012; Krumhansl et al., 2016). To our knowledge, a BTA approach has not been used to examine the epibenthic community structure in both the Chukchi Sea or US Beaufort Sea.

In this study, we assessed both the taxonomy and biological traits of two adjacent epibenthic communities in a hydrographically complex region of the Pacific Arctic shelf; the Chukchi community that sits at the head of Barrow Canyon and the Beaufort community that sits in Barrow Canyon and onto the Beaufort shelf. Because the Chukchi and Beaufort portions of Barrow Canyon share similar water masses, we expected that the epibenthic invertebrate communities shared both taxonomic and biological trait similarities. Specifically, we 1) used environmental variables to explain the spatial variability in benthic invertebrate taxa that comprise the top 90% of the biomass, and further we 2) described each community using a suite of biological traits to identify patterns in their distribution and how these relate to the regional oceanographic

characteristics. Finally, we discuss how a biological traits analysis could be potentially useful in monitoring the effects of change within the Arctic epibenthic invertebrate communities.

## 2. Methods

### 2.1. Data collection in the Chukchi Sea

Chukchi Sea samples were taken during the 2013 SHELFZ (Shelf Habitat and Ecology of Fish and Zooplankton) survey in the northeast Chukchi from Wainwright (160°W) to Point Barrow (155°W) and encompassed the southern portion of Barrow Canyon from 17 August to 5 September 2013 (Fig. 1). Epibenthic invertebrates were collected from 29 bottom hauls. The standardized 83–112 eastern otter trawl net (Stauffer, 2004) was used for all sampling and has a 25.3-m headrope and a 34.1-m footrope with a 10.16 cm mesh in the wings and body, and an 8.89 cm mesh in the intermediate and codend. The net towed at constant speed (3 knots) on a relatively straight tow path for 15 min, maintaining constant bottom contact as measured by the HOBO Pendant G Acceleration Data Logger. The measured net opening was approximately 2 m from the head rope to the foot rope and 18–20 m in width, from wing to wing. The width and spread of the net were measured using wing and head rope sensors by Marport Deep Sea Technologies (Milford, NH) to insure the net maintained consistent specifications, and bottom contact measured distance fished. All hauls were conducted during daylight hours. The catch was brought onboard the vessel, sorted to the lowest taxonomic level, counted and weighed in its entirety on a motion compensated Marel scale. The invertebrate portion of the catch was quantitatively subsampled for species composition. The invertebrate subsample was identified to the lowest possible taxonomic level and within the lowest taxonomic level, counted and weighed to obtain a total for each taxonomic group in the subsample. Total invertebrate catch compositions, counts and weights were extrapolated by weight from the subsample.

In addition to processing the bottom haul catch, water column hydrographic profiles were collected. Conductivity, temperature, and depth (CTD) data were collected using a Seabird SBE-19 equipped with a fluorometer and photosynthetically available radiation sensor. Data

**Table 1**

The taxa listed comprise 90% of the total biomass of epibenthic invertebrates, used in all analyses, separated by survey and, within the Beaufort survey, by lined net (LN) or unlined net (UN). The mean is the cube-root transformed CPUE kg/km<sup>2</sup> with the standard deviation kg/km<sup>2</sup>.

Species	Common name (class)	Survey	Mean kg/km <sup>2</sup>	Std dev kg/km <sup>2</sup>
<i>Beringius beringii</i>	sea snail (gastropod)	Chukchi	2.22	1.56
<b>Bryozoa</b>	bryozoa	Chukchi	1.42	2.15
<i>Crossaster papposus</i>	sea star (asteroidea)	Chukchi	3.52	1.27
<i>Ctenodiscus crispatus</i>	mud star	Chukchi	1.60	3.25
<i>Eualus sp.</i>	shrimp	Chukchi	0.57	1.82
<i>Gersemia rubiformis</i>	coral	Chukchi	2.26	3.08
<i>Gorgonocephalus spp.</i>	basket star (ophiuroid)	Chukchi	4.79	6.96
<i>Hyas coarctatus</i>	lyre crab (crab)	Chukchi	2.34	2.40
<i>Musculus discors</i>	mussel	Chukchi	1.40	4.21
<i>Neptunea heros</i>	sea snail (gastropod)	Chukchi	3.61	2.65
<i>Neptunea ventricosa</i>	sea snail (gastropod)	Chukchi	1.84	2.05
<i>Pagurus trigonochirus</i>	hermit crab	Chukchi	2.17	2.96
<i>Psolus peronii</i>	sea cucumber	Chukchi	3.00	6.76
<i>Pyrulofusus deformis</i>	sea snail (gastropod)	Chukchi	2.22	1.85
<i>Solaster dawsoni arcticus</i>	sea star (asteroidea)	Chukchi	4.21	2.98
<i>Strongylocentrotus droebachiensis</i>	sea urchin	Chukchi	1.73	3.25
<i>Urticina crassicornis</i>	sea anenome	Chukchi	1.76	2.77
<b>Actiniaria</b>	sea anenome	Beaufort LN	5.01	7.32
<i>Buccinum polare</i>	sea snail (gastropod)	Beaufort LN	5.86	5.30
<i>Chionoecetes opilio</i>	snow crab (crab)	Beaufort LN	16.16	9.57
<i>Ctenodiscus crispatus</i>	mud star	Beaufort LN	9.32	8.93
<i>Gorgonocephalus spp.</i>	basket star (ophiuroid)	Beaufort LN	2.79	5.61
<i>Musculus sp.</i>	mussel	Beaufort LN	5.97	11.32
<i>Neptunea sp.</i>	sea snail (gastropod)	Beaufort LN	6.89	3.12
<b>*Ophiura sp.</b>	brittle star (ophiuroid)	Beaufort LN	25.55	15.69
<i>Psolus peronii</i>	sea cucumber	Beaufort LN	5.31	6.89
<i>Strongylocentrotus sp.</i>	sea urchin	Beaufort LN	3.48	6.60
<i>Voluta middendorffii</i> and <i>Habeolutopsius</i>	sea snail (gastropod)	Beaufort LN	7.05	4.42
<i>Chionoecetes opilio</i>	snow crab (crab)	Beaufort UN	2.78	1.77
<i>Ctenodiscus crispatus</i>	mud star	Beaufort UN	3.48	4.21
<i>Halocynthia aurantium</i>	sea peach	Beaufort UN	6.53	5.79
<i>Hyas coarctatus</i>	lyre crab (crab)	Beaufort UN	4.16	2.04
<i>Neptunea heros</i>	sea snail (gastropod)	Beaufort UN	1.44	3.07
<i>Pagurus trigonochirus</i>	hermit crab	Beaufort UN	4.72	2.06
<i>Polymastia sp.</i>	sponge (demosponge)	Beaufort UN	2.33	4.98
<i>Psolus peronii</i>	sea cucumber	Beaufort UN	4.25	4.65
<i>Pyrulofusus deformis</i>	sea snail (gastropod)	Beaufort UN	2.36	2.58
<i>Stomphia sp.</i>	sea anenome	Beaufort UN	4.31	1.67
<i>Strongylocentrotus sp.</i>	sea urchin	Beaufort UN	3.46	5.45
<i>Vulcanella sp.</i>	sponge (demosponge)	Beaufort UN	3.86	6.79

\*95% of the *Ophiura sp.* was comprised of *Ophiura sarsi*

were processed using a combination of the manufacturer's software (Seabird Electronics, 2012) and custom Matlab software (version 14a, 2014, Mathworks) designed for visual inspection and despiking of the profile data. Raw data were binned to 1 decibar pressure levels (approximately 1 m depth intervals). The measured environmental variables used in the analysis of taxonomic distribution in the Chukchi Sea survey were bottom temperature (°C), bottom depth (m), bottom

salinity, and bottom hardness, as measured by acoustics. Acoustic measurements for bottom hardness were collected using a Simrad ES60 echosounder operating at 38 kHz (12° beam angle between half power points). The echosounder was calibrated prior to the survey. Water column and seabed backscatter (i.e. reflected echoes) were recorded continuously along survey transects, sampling at a rate of 1 Hz. All transects were divided into 100 m horizontal bins. Bottom types were quantified using substrate hardness metrics (unitless) on a scale of 1 (least) to 10 (most) by integrating the first and second bottom reflections in Echoview software (v6.1). The entire second bottom echo was integrated for the bottom hardness metric based on the acoustic impedance mismatch between the seabed and the water column (Chivers et al., 1990). To estimate bottom hardness at the Chukchi Sea bottom trawl stations, approximately 20 bottom hardness data points, as measured with acoustics, were selected using ESRI ArcGIS version 10.3 at or within the vicinity of the bottom trawl location. These selected points were then averaged within ArcGIS to give a single estimate of bottom hardness for that station. The number of data points selected (~20) was based on the average distanced fished by the bottom trawl.

## 2.2. Data collection in the Beaufort Sea

Epibenthic invertebrates were surveyed in the western Beaufort Sea in 2008. The survey extended from Point Barrow (155°W) east to 152°W (Fig. 1). The survey also used an 83–112 Eastern otter trawl; however, in a portion of the hauls a small mesh liner was added to the codend (mesh liner was 3.8 cm). The portion of the survey using a lined net is termed Beaufort LN and the portion of the survey using an unlined net is termed Beaufort UN. Because the net and possibly the catchability of the net were altered with the mesh liner, the data were analyzed separately and the two gear types were considered two surveys; Beaufort Sea LN and Beaufort Sea UN hereafter. Full details of the survey and the effects of the different gear types can be referenced in Rand and Logerwell (2011). The invertebrate catch was quantitatively subsampled, counted and weighed using the same procedure outlined in the Chukchi Sea survey. All invertebrates were identified to the lowest possible taxonomic level and counted and weighed at that level to obtain a total for each taxon in the subsample. For both regions, field identifications were confirmed in the lab from voucher material with the assistance of the taxonomic experts listed in the acknowledgments and taxonomic names were standardized to the World Register of Marine Species.

The water column profile characteristics were measured using the Seabird 19-Plus at or near the bottom haul stations, and processed following the procedures described for the Chukchi Sea survey.

The measured environmental variables used in both the Beaufort Sea LN and Beaufort Sea UN hauls were the same as those used in the Chukchi Sea survey with the exception of bottom hardness. Although an acoustic-trawl survey took place in the Beaufort Sea in 2008, the second bottom echo data were not collected, precluding bottom hardness as an environmental variable in the Beaufort Sea analysis.

## 2.3. Epibenthic invertebrate density

The catch-per-unit effort (CPUE) in kg wet weight km<sup>-2</sup> was estimated for both the Chukchi and Beaufort Sea surveys for all taxa. To calculate CPUE, the net width and distance fished was used to estimate the area swept by the net for each haul and estimated catch weight (kg) was divided by area swept (km<sup>2</sup>). This gives an estimate of biomass density for each species or taxa in each haul. To estimate the average CPUE for each taxa in each survey, zero catches were also included at each station for taxa that were not present in the haul. All analyses were done on individual taxa, by survey, (Table 1) and all three surveys were treated independently. To reduce skewness that is common with CPUE data, CPUE estimates were cube-root transformed preceding analyses.

## 2.4. Biological traits

To focus on those invertebrates and the biological traits that dominated each of the three data sets, only the taxa in the top 90% by total biomass estimated from CPUE were used in all analyses. This reduced the number of taxa whose biological traits we examined for each system from > 100 to less than 20 (Table 1). The taxa from the top 90% by total biomass were selected for each survey, independent of the other surveys. Any invertebrates in the trawls that were generally considered infaunal (e.g. polychaetes) were further removed from the top 90%. We chose the taxa that made up the top 90% total biomass for each survey to address the basic ecological function of the epibenthic invertebrates that dominate areas in and adjacent to Barrow Canyon. Detailed life history information for even the dominant invertebrate taxa in the sub-arctic and Arctic is sparse at best. The 10% of invertebrate taxa not used in the analysis were even more difficult to collect life history information on and often times would reflect the life histories of those taxa found in the top 90%, since the family level was often used in assigning trait modalities.

Ten biological traits that summarize basic biological characteristics (size, shape) as well as fundamental trophic (feeding type and mechanisms), reproductive and life history ecology (dispersal and larval types) were selected and divided into 31 trait modalities (Table 2). The selected traits are common to several recent studies using biological traits analysis (Bremner et al., 2003; Haybach et al., 2004; Hewitt et al., 2008; Paganelli et al., 2012), and maximize some of the fundamental differences in the biology and ecology of species. The only biological trait that was quantitatively measured was Size, determined as the average weight per individual animal for each taxon calculated from the catch. An extensive literature search was used to assign each taxon to a category in each of the ten trait groups. When little or no information on a species' life history could be found, information from the genus level or species within the same family was used.

**Table 2**

The biological traits for those taxa in Table 1 used in the FCA analysis. Within each biological trait are several trait modalities; each unique combination of trait and modality is assigned a trait code.

Biological trait	Trait modalities	Trait code
Size	small (< 10 g)	S1
	medium (10–50 g)	S2
	large (> 50 g)	S3
Body Design	soft	BD1
	soft/protected	BD2
	endoskeleton	BD3
	hard exoskeleton	BD4
	hard shell	BD5
Body Form	erect	BF1
	round	BF2
	flat	BF3
General Prey Type	herbivore	PT1
	omnivore	PT2
	carnivore	PT3
Feeding Mechanism	deposit feeder	FM1
	filter/suspension	FM2
	opportunist/scavenger	FM3
	predator	FM4
Degree of attachment	none	DA1
	semi-permanent	DA2
	permanent	DA3
Mobility	sessile	M1
	motile	M2
Propagule Dispersal	pelagic	PD1
	substrate	PD2
Reproductive Mode	sexual/release eggs	RM1
	sexual/release larvae	RM2
	sexual/brood	RM3
Larval Development	direct	LD1
	planktrophic	LD2
	lecithotrophic	LD3

Three matrices were produced for the analyses: 1) a haul by taxon biomass (CPUE) matrix, 2) taxon by trait matrix, and 3) haul by trait matrix. The third matrix was a product of the haul by taxon biomass matrix and taxon by trait matrix (Bremner et al., 2003). This was constructed by multiplying trait modalities for each taxon present in a haul by its CPUE in that haul, and then summing the biomass across each trait modality over all taxa present in that haul to obtain a single value for each trait modality in each haul. Essentially, this weights the occurrence of a biological trait or trait modality across taxa at the haul level (Charvet et al., 1998).

## 2.5. Numerical model integration

In order to depict the mean regional circulation field for the purpose of providing additional environmental context to the biological analyses and interpretations, we compiled results from a 3-dimensional ocean and ice circulation numerical hindcast model (Curchitser et al., 2013; Danielson et al., 2016), which was integrated over 2005–2011 within the Regional Ocean Modeling System (ROMS) framework (Fig. 2). Quantitative comparisons of model output to year-long in situ mooring-based current velocity data show that the model reproduces (at the 95% confidence level) the observed mean velocity vector components at nearly all of the 19 Beaufort and Chukchi evaluation sites (Curchitser et al., 2013). Results from the new integration (Danielson et al., 2016) and this study are driven with the same initial conditions, boundary conditions and atmospheric forcing described in Curchitser et al. (2013). A number of improvements were implemented in the present version including extending the Pacific side southern boundary from Bering Strait to south of the Bering Sea, an improved sea-ice formulation, and more realistic coastal river discharges (Danielson et al., 2016). Model horizontal resolution is about 6 km in the Barrow Canyon region and there are 50 terrain-following layers in the vertical dimension. Several model-derived variables were included in the initial analyses for all three surveys: speed of the near-bottom current averaged over the day of sampling (Speed Day of Sample), eastward velocity component averaged over the day of sampling (East Velocity), northward velocity component averaged over the day of sampling (North Velocity), year-long mean near-bottom speed at this sampling site (Mean Year Speed), and year-long mean near-bottom speed variance at this sampling site (Mean Year Speed Var).

## 2.6. Statistical analysis

The taxa in the top 90% by biomass were analyzed in two ways: 1) a canonical correspondence analysis (CCA) using taxon biomass estimates and environmental variables (Cajo and Braak, 1986; McGarigal et al., 2000), and 2) a fuzzy correspondence analysis (FCA) to quantify the variation in biological trait distribution for each survey (Chevenet et al., 1994).

For the taxonomic distribution and environmental variables analysis, the taxon biomass matrix was ordinated using a constrained ordination (i.e. a CCA), and displays only the variation that can be explained by the constraining variables (e.g. temperature, depth) using Chi-square distances. Further, the haul scores are constrained to be linear combinations of the constraining variables. Because of the small sample size in the Beaufort Sea LN and Beaufort Sea UN surveys, the environmental variables examined were limited to those that were not tightly correlated. For example, density and salinity are tightly correlated, therefore we chose a single variable, salinity, for the analysis. Even though intercorrelated variables do not affect the CCA, a reduced number of variables can aid in interpretability, especially when the number of variables approaches the number of samples, as in the case of the Beaufort LN and UN hauls (McGarigal et al., 2000). Also, if the ordination contains as many variables as samples, the ordination is no longer “constrained” by the environmental variables, also termed overfitting. The initial CCA analysis was completed for each survey and

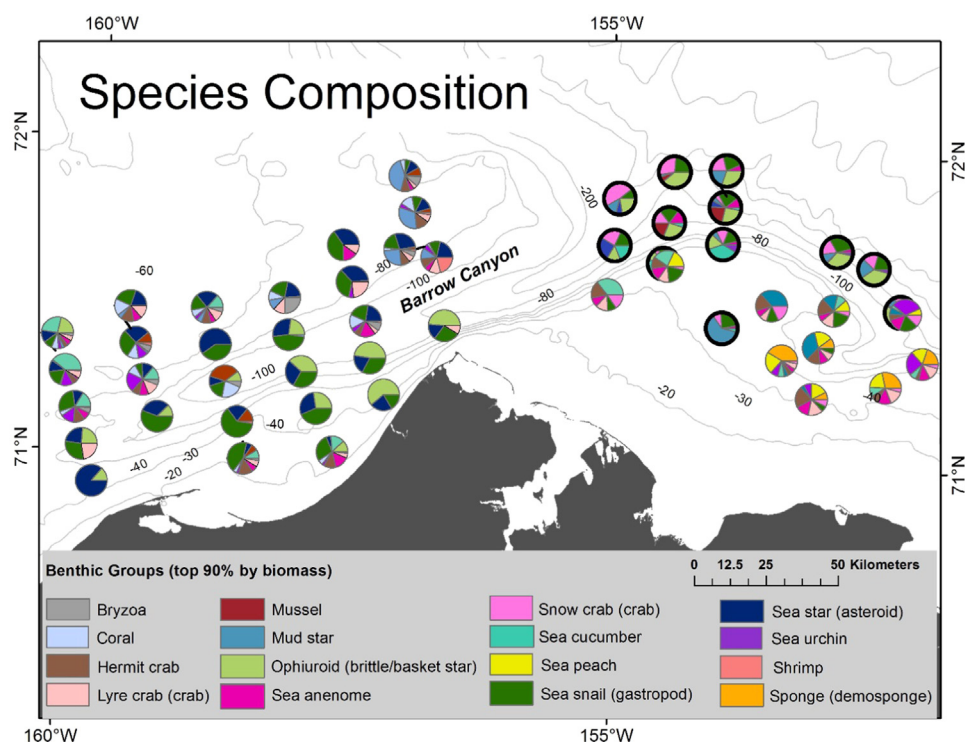


Fig. 3. Benthic invertebrate species composition for the top 90% by biomass (CPUE kg/km<sup>2</sup>) for the Chukchi Sea, Beaufort Sea LN (pie charts are shown with thicker outline), and Beaufort Sea UN hauls. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with no net liner. Each pie chart represents one haul. Several taxa were lumped together under a common name for better map interpretation (e.g., sea stars).

included all variables (9 for the Chukchi and 8 for the Beaufort LN and UN surveys). Initially, we performed a variance inflation factor (VIF) test, which measures the extent of multicollinearity between variables. This aided in informing which variables would be used in the final CCA analysis and which variables could be eliminated (i.e. high VIF). Additionally, variables whose arrows were in close proximity (same length and direction), a single variable was selected for further analysis. In all three surveys, salinity and bottom depth were tightly correlated along with year-long mean near-bottom speed at the sampling site (Mean Year Speed) and year-long mean near-bottom speed variance at the sampling site (Mean Year Speed Var); the variables used in the model were bottom depth and Mean Year Speed. In the Chukchi survey, bottom hardness and Mean Year Speed were tightly correlated, bottom hardness was the variable used in the model for further analysis. After the variables were selected, the final CCA was performed on the taxon biomass and the selected variables (termed the “full model”). The first two axes from the final CCA were permuted ( $x = 999$ ) and an ANOVA-like test (“pseudo-F statistic”) was used to determine those variables that were most significant at  $p < 0.05$  (Dray and Dufour, 2007a, b). This analysis tested the reduced model's results after removing a variable against the full model's results.

For the biological traits analysis, the haul by traits matrix was ordinated using fuzzy coding correspondence analysis (FCA) (Chevenet et al., 1994). It is used to assign multiple modalities to a single taxon using percentages. This process accounts for differences in trait modalities within and among life history stages. For example, a gastropod species may be both predator (70% of the time) and scavenger (30% of the time) during the adult phase. In the absence of this detailed information for many of the Arctic species in this analysis, we instead chose a binary coding procedure where each taxon is assigned to one category within each biological trait based on what the taxon exhibits a majority of the time. For example, the species *Neptunea heros* was classified as a predator under the trait modality “feeding mechanism”; however, this species may also be an “opportunist/scavenger” at times. FCA is an extension of correspondence analysis (CA) that incorporates discrete variables such as biological traits that are either coded as binary (i.e., 0,1) or fuzzy (i.e., 0.3, 0.7). FCA is able to correct for the fact that each biological trait (e.g. Body Design) has multiple trait

modalities (e.g. “soft”, “hard shell”) and the sum of all trait modalities within a biological trait can be no more than one. Even though biological traits data in this analysis were binary and not coded as fuzzy, this sets up the framework for incorporating additional trait information should it become available. The results of an FCA explain the amount of variation in trait distribution on each axis. To interpret the results, the relationship of hauls (rows) can only be compared to other hauls (rows) and columns (traits) to other columns (traits). Hauls that have similar FCA coordinates and are close to one another on the ordination plot are similar relative to the frequency of traits. Since the haul by traits matrix table contained the same trait modalities for all three surveys, a Kruskal-Wallis test was used to determine if the first axis scores from the FCA ordination for all three surveys differed from one another. The first axis scores account for the greatest amount of variation. No statistical difference would suggest that the variation in biological trait distributions within in each of three surveys were the same. To quantify how much of the variance was accounted for by each biological trait and trait modalities (Table 2) on each axis, correlation ratios and eigenvalues were calculated for each biological trait. Correlation ratios represent percentage of variance accounted for by a given axis. The eigenvalues can be considered the amount of variance as part of the total variance (i.e. total inertia) accounted for by each axis.

Statistical analysis and graphical results were carried out in the statistical program R (R Development Core Team, 2014), version 3.1.2, with R packages ade4 (Chessel and Dufour, 2004; Dray and Dufour, 2007a, b) and Vegan (Oksanen et al., 2015). All maps were created in ESRI ArcGIS version 10.3.

### 3. Results

#### 3.1. Diversity and dominant taxa

The number of taxa in the Chukchi Sea survey ranged from 26 to 57 per haul with a total of 215 taxa identified, of those 151 were identified to species. The number of taxa ranged from 27 to 58 per haul in the Beaufort Sea LN survey with a total of 132 taxa. The number of taxa ranged from 35 to 50 per haul in the Beaufort Sea UN survey with a total of 109 taxa. In total, 17 taxa made up 90% of the total biomass in

the Chukchi Sea survey, 10 taxa in the Beaufort Sea LN survey, and 11 taxa in the Beaufort Sea UN survey (Table 1). Within the species contributing the top 90% wet weight biomass, the northeastern Chukchi Sea survey and the western Beaufort Sea surveys (LN and UN combined) shared at least six benthic invertebrate species.

The CPUE estimates in the Chukchi Sea hauls were highest at the western-most portion of the study area (Fig. 1). The dominant invertebrates in the Chukchi Sea hauls from nearshore to the canyon were *Gorgonocephalus* spp. (basket star), and other ophiuroids, and four species of large gastropods (Fig. 3) (Table 1). Of the other biomass-dominant taxa, the sea star, *Solaster dawsoni arcticus*, occurred in all the Chukchi Sea hauls (Fig. 3) while the mud star *Ctenodiscus crispatus*, only occurred on the outer shelf in the north part of the Chukchi study area (Fig. 3). The sea cucumber, *Psolus peronii*, was only present in the western portion of the Chukchi study area (Fig. 3).

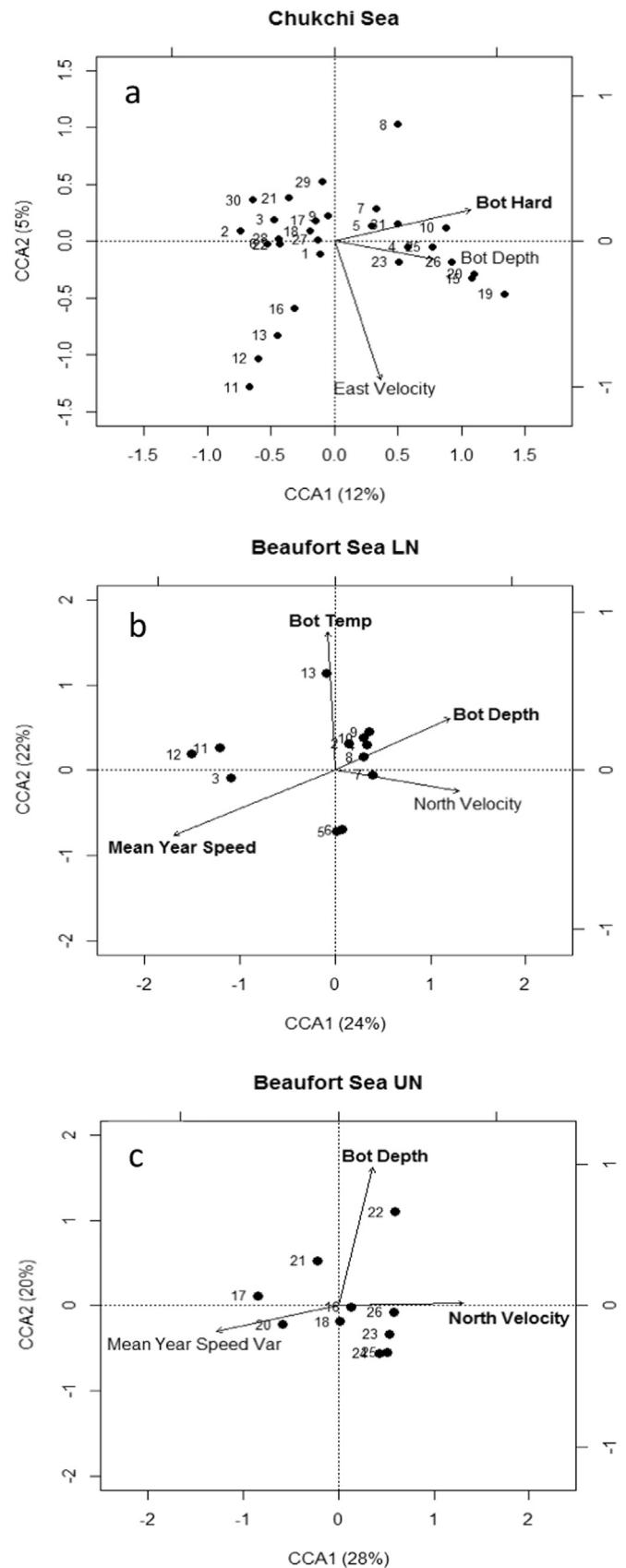
In order to spatially note the taxonomic composition for all three surveys, several taxa were lumped into a single group and were mapped using pie charts (Fig. 3). The Beaufort Sea LN hauls occurred predominantly on the Beaufort slope and in Barrow Canyon (> 200 m) and were dominated by brittle stars (mostly *Ophiura sarsii*), snow crab (*Chionoecetes opilio*) and gastropods (Fig. 3). Total CPUE estimates were consistently high in the mouth of Barrow Canyon and along the western Beaufort Sea shelf break in water deeper than 300 m (Figs. 2 and 3). Overall, the CPUE estimates for the Beaufort Sea LN hauls were two to three times greater than the estimates for both the Beaufort Sea UN and Chukchi Sea hauls. This discrepancy is in part related to the smaller mesh size (Fig. 1) used for the Beaufort Sea LN hauls; of 12 hauls, only two (12 and 13) had CPUE estimates considerably lower than all other hauls.

The Beaufort Sea UN hauls occurred mostly on the shelf and were dominated by a sea cucumber (*Psolus peronii*) and hermit crab (*Pagurus trigonocheirus*) in the two western hauls, next to Barrow Canyon (Fig. 3) (Table 1). The catch composition transitioned to hauls dominated by the mud star (*Ctenodiscus crispatus*) and the same hermit crab (*Pagurus trigonocheirus*) in the central part of the study area to hauls dominated by the sea peach (*Halocynthia aurantium*) and two genera of demosponges, *Polymastia* and *Vulcanella*, in the east part of the study area (Fig. 3) (Table 1). The CPUE estimates varied across all hauls, but was, with the exception of haul 17, lower than the western- and southern-most Chukchi Sea hauls, and there was no quantitative pattern relating to depth or location (Fig. 1).

### 3.2. Environmental variables and epifaunal biomass

The bottom temperature ranges observed in the Chukchi Sea survey during the sampling period ranged from -1.72 to 2.68 °C, the bottom salinity ranged from 30.93 to 33.28, and bottom depths ranged from 26 to 155 m. Bottom hardness measurements at or near the bottom trawl stations ranged from 3.5 (least hard) to 5.9 (most hard) within the Chukchi Sea study area. During the Beaufort Sea LN survey, the bottom temperatures ranged from -1.70 to 1.94 °C, the bottom salinity ranged from 30.94 to 34.85, and bottom depths ranged from 47 to 445 m. During the Beaufort Sea UN survey, the bottom temperatures ranged from -1.26 to 2.19 °C, the bottom salinity ranged from 30.69 to 34.11, and bottom depths ranged from 40 to 187 m.

The three environmental variables in the CCA accounted for 17% of the variability in taxon biomass (Fig. 4a) (Table 3) on the first two axes, and the only significant term from the ANOVA was bottom hardness on the CCA1 axis ( $p < 0.05$ ) (Table 3). All the hauls with a positive CCA1 axis score (Fig. 4a) corresponded to those hauls located either in or in close proximity to Barrow Canyon; this aligned with both an increase in bottom hardness and current flow (Fig. 1). The hauls with both a negative CCA1 and CCA2 score were those hauls located on the upper Chukchi shelf in the northern most stations (Figs. 1 and 4a, hauls 11, 12, 13, and 16). These hauls were also located close to 180° degrees from the direction of bottom hardness, which indicates a decrease in



(caption on next page)

Fig. 4. Results of the canonical correspondence analysis (CCA) on species biomass (CPUE kg/km<sup>2</sup>) for the Chukchi Sea (a), Beaufort Sea LN, and Beaufort Sea UN surveys. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with no net liner. The hauls (numbered black dots) and environmental variables (arrows) are shown on each plot. Species associated with the hauls are in light gray text. Significant variables are in bold text. The label “Bot” refers to “bottom”. The percentages refer to the amount of variance explained by each axis.

**Table 3**

Results of the CCA analysis on species abundance constrained by environmental variables. The observed variance accounted for by the variables are shown in percent for both axes CCA1 and CCA2. Variables that were used in the CCA are listed under “Variables Full Model” and the corresponding significance level from the ANOVA test are listed under “Significance ( $p < 0.05$ )”; significant values are in bold.

Survey	CCA 1	CCA 2	Variables full model	Significance ( $p < 0.05$ )
Chukchi Survey	12%	5%	Bottom Hardness	<b>0.001</b>
			Bottom Depth	0.085
			East Velocity	0.140
Beaufort LN Survey	24%	22%	Bottom	<b>0.004</b>
			Temperature	
			Bottom Depth	<b>0.004</b>
			Mean Year Speed	<b>0.010</b>
Beaufort UN Survey	28%	20%	North Velocity	0.279
			Bottom Depth	<b>0.020</b>
			Mean Year Speed Var	0.168
			North Velocity	<b>0.051</b>

bottom hardness in the location of these hauls (Fig. 4a).

In the Beaufort Sea LN hauls four environmental variables were used in the CCA and accounted for 46% of the variability in taxon biomass (Fig. 4b) (Table 3) on the first two axes. The ANOVA permutations resulted in three significant terms ( $p < 0.05$ ); bottom temperature, bottom depth, and Mean Year Speed (Table 3). The arrows for bottom depth and Mean Year Speed are at a 180° angle indicating these two variables are inversely related; at deeper hauls, current flow is slower (Fig. 4b). Hauls 3, 11 and 12 (Fig. 4b) were at the shallowest stations but had the highest current flows whereas all the hauls clustered in the upper right quadrant were the deepest stations and had the lowest current flows.

In the Beaufort Sea UN hauls, 48% of the variability on taxon biomass in the CCA was accounted for by bottom depth, North Velocity, and Mean Year Speed Var (Fig. 4c). The significant variables from the ANOVA were bottom depth and North Velocity (Table 3).

### 3.3. Biological traits analysis

The FCA accounted for 58% of the variance in the distribution of traits for the Chukchi Sea hauls (Fig. 5a–b) (Table 4). Hauls with a positive axis 1 score were dominated by large, predatory carnivores that sexually reproduce and shed eggs (Fig. 5b). Flat bodied, predatory organisms with an endoskeleton also dominated these hauls and similar to the results of the taxon biomass and environmental variables, these traits occurred where there was an increase in hard bottom (Fig. 5a, black circle). Hauls 11–13 and 16 had a positive axis 2 score and grouped together; these hauls were dominated by small opportunistic scavengers with a hard exoskeleton (Fig. 5a–b). These four hauls were located on the Chukchi shelf, north of Barrow Canyon (Fig. 1).

The FCA accounted for 73% of the variance in the distribution of traits for the Beaufort Sea LN hauls (Fig. 5c–d) (Table 4). Similar to the results based on taxon abundance and environmental variables, the tight cluster of hauls with a negative axis 1 score were hauls that corresponded to the stations  $> 200$  m in the Beaufort Sea survey (Fig. 5c, black circle). These hauls were dominated by small, flat bodied deposit feeders, and predators with a hard exoskeleton, reflecting the

dominance of brittle stars and snow crab in these hauls (Fig. 5c–d). Those hauls with a positive axis 1 score were dominated by soft, medium/large bodied, filter/suspension feeders (Fig. 5d). These stations were positioned from the slope onto the Beaufort shelf and, in general, were in water  $< 200$  m (Fig. 5c–d).

The FCA accounted for 79% of the variance in the distribution of traits for the Beaufort Sea UN hauls (Fig. 5e–f) (Table 4). Unlike the clustering of hauls in the Chukchi and Beaufort LN surveys, the Beaufort Sea UN survey showed little clustering among the hauls based on traits. This likely reflects the higher degree of taxonomic diversity where many of the species do not overlap in trait similarities compared to the Chukchi and Beaufort LN surveys (Fig. 5e). Traits with a positive axis 1 and axis 2 score were dominated by soft body/protected, erect, and medium size traits and were associated with hauls 23 and 24 (axis 2) on the southern slope/shelf of Barrow Canyon, which also coincided with a predominance of sea cucumbers in these two hauls (Fig. 3c). Hauls that had a negative axis 2 score (17, 20, 21) occurred on the Beaufort Sea shelf in the east part of the Beaufort study area, and were dominated by large, filter/suspension feeders that sexually reproduce and shed larvae (Fig. 5e–f). Flat bodied deposit feeders dominated hauls 18 and 26 and were located on the Beaufort Sea shelf (Fig. 5e–f).

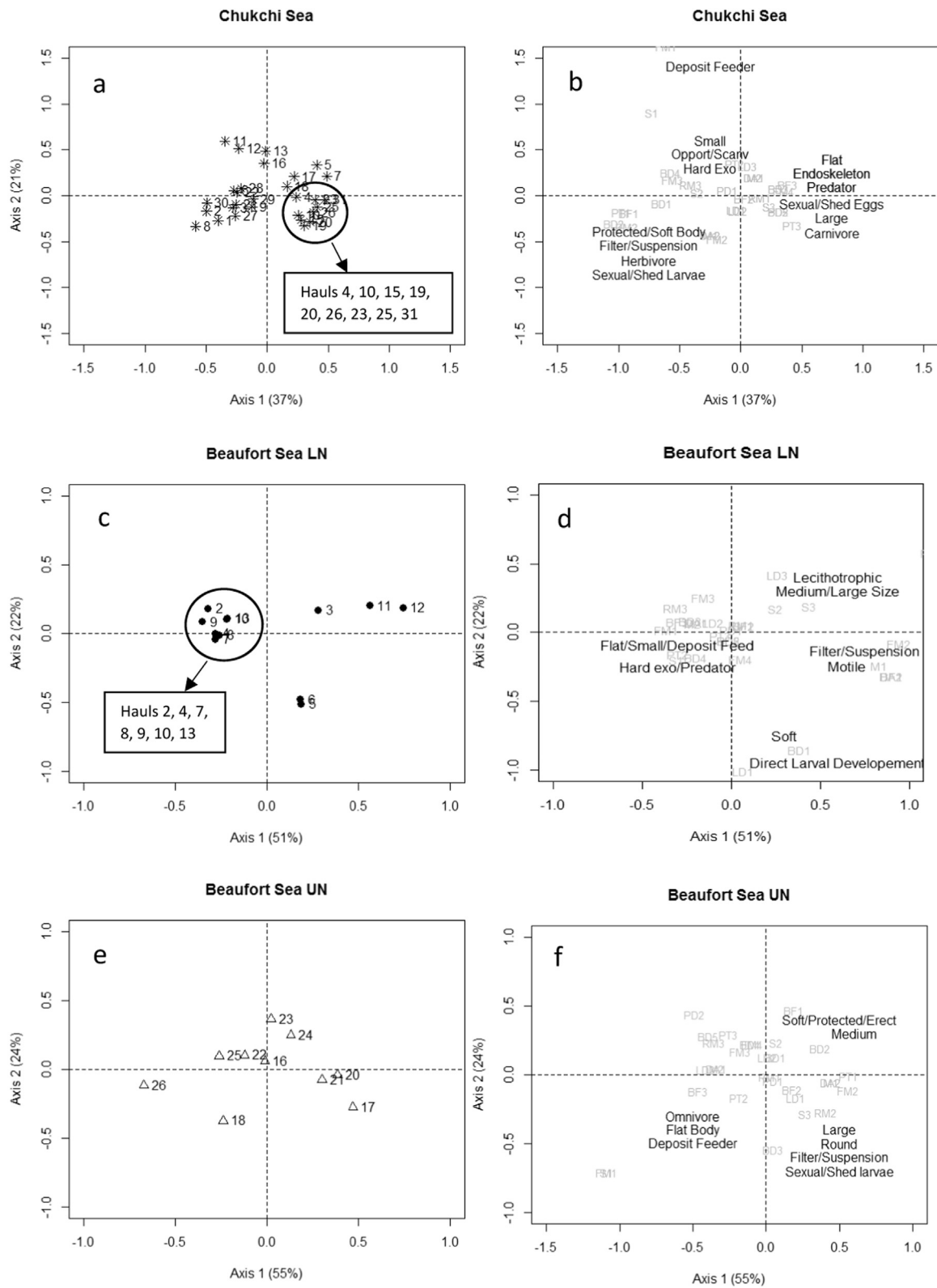
The axis score coordinates for each trait from the FCA analysis were plotted by survey to visualize which trait scores accounted for the most variance in the distribution of hauls (i.e. points located far from the zero coordinate for both axes). For example, the trait modality “small” for both the Chukchi and Beaufort Sea UN surveys showed coordinate scores distant from zero on both axes, which means this trait contributed to the observed variance in the pattern of haul distribution (Fig. 6). In contrast, the variation in the distribution of the trait modality “large” showed little to no variation in trait distribution for all three surveys (i.e. all three points are located at or near the zero coordinate) (Fig. 6). Biological traits and their subsequent modalities, that showed little to no variation in their distribution across hauls, included Degree of Attachment, Mobility, Propagule Dispersal, and Larval Dispersal (Fig. 6). The trait modality “deposit feed” showed large variation in the distribution of the trait both within a survey (e.g. the Chukchi Sea, asterisk) and between surveys (e.g. the three points are widely distributed); however, there was little variation in the distribution both within and between surveys for the other trait modalities within Feeding Mechanism (e.g. “filter/sus”, “opp/scavenger”) (Fig. 6).

There was no significant difference in the variation of biological trait distribution among the three surveys (Chukchi Sea, Beaufort Sea LN, Beaufort Sea UN) based on the results of the Kruskal-Wallis test for significance on the first axis of the FCA ordination ( $p = 0.90$ ).

To further characterize the variation in the distribution of biological traits, we mapped biological traits and the corresponding trait modalities with correlation ratios greater than 0.20 on axis 1 (Body Design, Body Form, General Prey Type, and Feeding Mechanism) (Fig. 7a–d). (Table 4). Correlation ratio scores greater than 0.20 can be considered those traits with the most variable distribution within a survey. The Chukchi and Beaufort Sea LN surveys each had three traits that met this criteria, followed by one trait in the Beaufort Sea UN survey that met this criteria (Fig. 7a–d). The biological traits with ratios  $> 0.2$  showed the highest variation in their distribution within each survey (Fig. 7a–d) (Table 4). There were three biological traits that explained the greatest amount of variation in their distribution on axis 1 and that was Feeding Mechanism (Fig. 7c) in the Beaufort Sea LN and UN surveys and both Body Design and General Prey Type (Figs. 7a and 7d) in the Chukchi and Beaufort Sea LN surveys (Table 4).

In the Chukchi Sea survey, the biological trait Body Design had the highest correlation ratio for axis 1 explaining 23% of the variability among the traits on axis 1, followed by Body Form and General Prey Type (Table 4). In that, the “soft/protected” (Fig. 7a), “erect” (Fig. 7b), and “herbivore” (Fig. 7d) trait modalities occurred in their highest proportion in the western part of the survey area and, in general, these trait modalities did not occur on the southern slope of Barrow Canyon.





**Fig. 5.** Results of the fuzzy correspondence analysis (FCA) on the biological traits for the Chukchi Sea (a and b) (asterisk), Beaufort Sea LN (c and d) (black dots), and Beaufort Sea UN (d and e) (triangles) surveys. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with no net liner. Figs. 5a, 5c, and 5e are the ordination results by haul and Figs. 5b, 5d, and 5f are the ordination results by traits (in light gray text) and aids in the interpretation of the results in the first column. Hauls that are grouped in the black circle indicated significance with bottom hardness in the Chukchi Sea (5a) and hauls > 200 m depth in the Beaufort Sea LN (5c).

**Table 4**

Correlation ratios for the FCA ordination of biological traits. The proportion of variance on each axis that can be explained by the Trait modalities (Table 2) within each Biological Trait. Ratios greater than 20% on axis 1 are in bold and less than 5% on axis 1 in italics. Biological traits that are mapped in Fig. 7 are shown in bold text. The respective eigenvalues for each survey are given for each axis. The total inertia (in parentheses) represents the total variance accounted for in an ordination. The percent of variance that can be explained by each axis is listed by survey and axis.

Survey	Biological traits	Axis 1	Axis 2
Chukchi	Size	0.110	0.070
Chukchi	<b>Body Design</b>	<b>0.237</b>	0.030
Chukchi	<b>Body Form</b>	<b>0.218</b>	0.013
Chukchi	<b>General Prey Type</b>	<b>0.218</b>	0.102
Chukchi	<b>Feeding Mechanism</b>	0.143	0.193
Chukchi	Degree of attachment	0.028	0.083
Chukchi	Mobility	0.028	0.083
Chukchi	<b>Propagule Dispersal</b>	0.033	0.010
Chukchi	Reproductive Mode	0.079	0.007
Chukchi	<b>Larval Development</b>	0.002	0.051
Percent of Variance	(Total Inertia)	37%	21% (0.299)
Eigenvalues		0.109	0.064
Beaufort LN	Size	0.082	0.035
Beaufort LN	<b>Body Design</b>	<b>0.225</b>	0.072
Beaufort LN	<b>Body Form</b>	0.196	0.022
Beaufort LN	<b>General Prey Type</b>	<b>0.207</b>	0.054
Beaufort LN	<b>Feeding Mechanism</b>	<b>0.202</b>	0.025
Beaufort LN	Degree of attachment	0.172	0.022
Beaufort LN	Mobility	0.179	0.015
Beaufort LN	<b>Propagule Dispersal</b>	0.000	0.001
Beaufort LN	Reproductive Mode	0.022	0.130
Beaufort LN	<b>Larval Development</b>	0.021	0.178
Percent of Variance	(Total Inertia)	51%	22% (0.253)
Eigenvalues		0.130	0.055
Beaufort UN	Size	0.141	0.107
Beaufort UN	<b>Body Design</b>	0.067	0.119
Beaufort UN	<b>Body Form</b>	0.084	0.054
Beaufort UN	<b>General Prey Type</b>	0.120	0.036
Beaufort UN	<b>Feeding Mechanism</b>	<b>0.235</b>	0.077
Beaufort UN	Degree of attachment	0.151	0.003
Beaufort UN	Mobility	0.151	0.003
Beaufort UN	<b>Propagule Dispersal</b>	0.025	0.019
Beaufort UN	Reproductive Mode	0.047	0.020
Beaufort UN	<b>Larval Development</b>	0.049	0.018
Percent of Variance	(Total Inertia)	55%	24% (0.193)
Eigenvalues		0.107	0.045

Opposite this result, the southern slope of Barrow Canyon in the Chukchi Sea survey was dominated by “endoskeleton/hard shell” (Fig. 7a), “flat/round” (Fig. 7b), “carnivore/omnivore” (Fig. 7d) trait modalities. In the Beaufort Sea LN survey, Body Design and subsequent modalities also had the highest correlation ratio on axis 1, likely due to the trait modality “soft/protected” only occurring at depths < 200 m, on the Beaufort Sea Shelf (Fig. 7a). Alternatively, the deep slope stations in the Beaufort Sea LN survey showed an absence of the “soft/protected” (Fig. 7a), “erect” (Fig. 7b), “filter/suspension” (Fig. 7c), and “herbivore” (Fig. 7d) trait modalities. The trait modality “deposit feeder” (Fig. 7c) that only occurred in the northeast portion of the Chukchi Sea survey area, was the largest proportion of the Beaufort Sea LN hauls in the deep slope stations. The trait modality “deposit feeders” was also not common on the Beaufort Sea shelf (mostly UN) hauls, which were mostly dominated by “filter/suspension” feeders (Fig. 7c). In the Beaufort Sea UN survey, the biological trait Feeding Mechanism was the only trait > 0.2 with a correlation ratio explaining 23% of the variability on axis 1 (Table 4), likely due to the increased occurrence of the trait modality “deposit feeders” around the 50 m depth contour (Figs. 7c, 3 hauls).

We selected the two biological traits with ratios less than 0.05 on axis 1 (Propagule Dispersal and Larval Development) for all three surveys to further illustrate patterns in trait distribution between regions (Fig. 7e-f) (Table 4). These two biological traits and subsequent trait modalities showed the least variation in their distribution within each

survey. Even though the distribution of trait modalities within a survey was homogenous for these low correlation ratios, the proportion of trait modalities between surveys was quite variable (Fig. 7e-f). Specifically, the biological trait Larval Development had a higher proportion of “planktotrophic” larvae (long pelagic larval durations) in the Beaufort Sea LN survey than the Chukchi Survey based on the pie charts (Fig. 7e). In contrast, the Chukchi survey had a higher proportion of “direct” development (low dispersal potential) and “lecithotrophic” larvae (yolk sack attached as source of nutrition; shorter dispersal range than “planktotrophic”) throughout the survey area compared to lower proportions in waters > 200 m in the Beaufort Sea LN survey (Fig. 7e). In general, the trait modality “direct” was homogeneously distributed and in every haul except one in the Chukchi Sea survey, compared to the other two surveys where the trait is more patchily distributed (e.g. a few hauls in the Beaufort Sea LN and UN surveys have high proportions). The trait modality “substrate” occurs in greater proportions in the Chukchi Sea survey compared to the proportions this trait occurs in both the Beaufort Sea LN and UN surveys (Fig. 7f). In general, the trait modality “pelagic” was dominate in most of the Chukchi survey hauls and dominated all hauls in the Beaufort Sea surveys (Fig. 7f).

## 4. Discussion

### 4.1. Environmental variables and epibenthic invertebrate biomass

The epibenthos in the Arctic's Barrow Canyon are both taxonomically and functionally diverse reflecting the high levels of production and the confluence of three water masses into the canyon. The environmental variables used in this study accounted for a moderate portion of the variance (< 47%) in benthic community structure and these results generally aligned with recent studies in the northeast Chukchi and Beaufort seas. In this study, depth was an important factor in the deeper Beaufort Sea stations (Beaufort UN) in that some of the largest biomass estimates from the Beaufort survey occurred at the deepest depths and this result was not entirely due to gear differences (Rand and Logerwell, 2011). Ravelo et al. (2015) also showed depth was an important factor in structuring the benthic invertebrate community of the Beaufort Sea shelf and the northeastern Chukchi Sea. In addition, previous studies also showed correlative relationships between water depth and temperature and the structuring of benthic communities (Blanchard et al., 2013a; Blanchard and Feder, 2014; Ravelo et al., 2014).

Although bottom hardness measurements were not available for the Beaufort Sea in our study, sediment characteristics are also important factors in structuring the epibenthic communities on the Beaufort Sea shelf (Ravelo et al., 2015) and were influential in the northeast Chukchi Sea, both in our study and Ravelo et al. (2014). In this region, it is well documented that variation in current velocities can act to deposit or carry finer sediments downstream (Darby et al., 2009); in this study, we noted that there was a decrease in bottom hardness on the north part of the Chukchi shelf, suggesting this part of the study area was comprised of finer sediments. This was corroborated by Grebmeier et al., 2015a who reported that sediment becomes finer from the west side of Barrow Canyon, onto the offshore Chukchi (Fig. 8). One of the variables we examined that represented current velocity in our study was “speed (velocity) on the day of sampling” and the results were narrowly insignificant in the Chukchi Study area ( $p = 0.059$ ). In this study area of the Chukchi Sea, current velocity does coincide with the Pacific-origin WW (PWW) that flows from the northeastern shelf of the Chukchi Sea but then shifts from the west side of Barrow Canyon to the eastern side as it heads northward into the Pacific Arctic Basin (Gong and Pickart, 2015). This water mass flow erodes the fine sediment especially in the central Canyon and leaves coarser sediments (Pisareva et al., 2015).

Our analysis for the Chukchi Sea shows that the faunal distribution patterns are in part related to these sediment and associated current velocity patterns, but the moderate to low correlation factors suggest

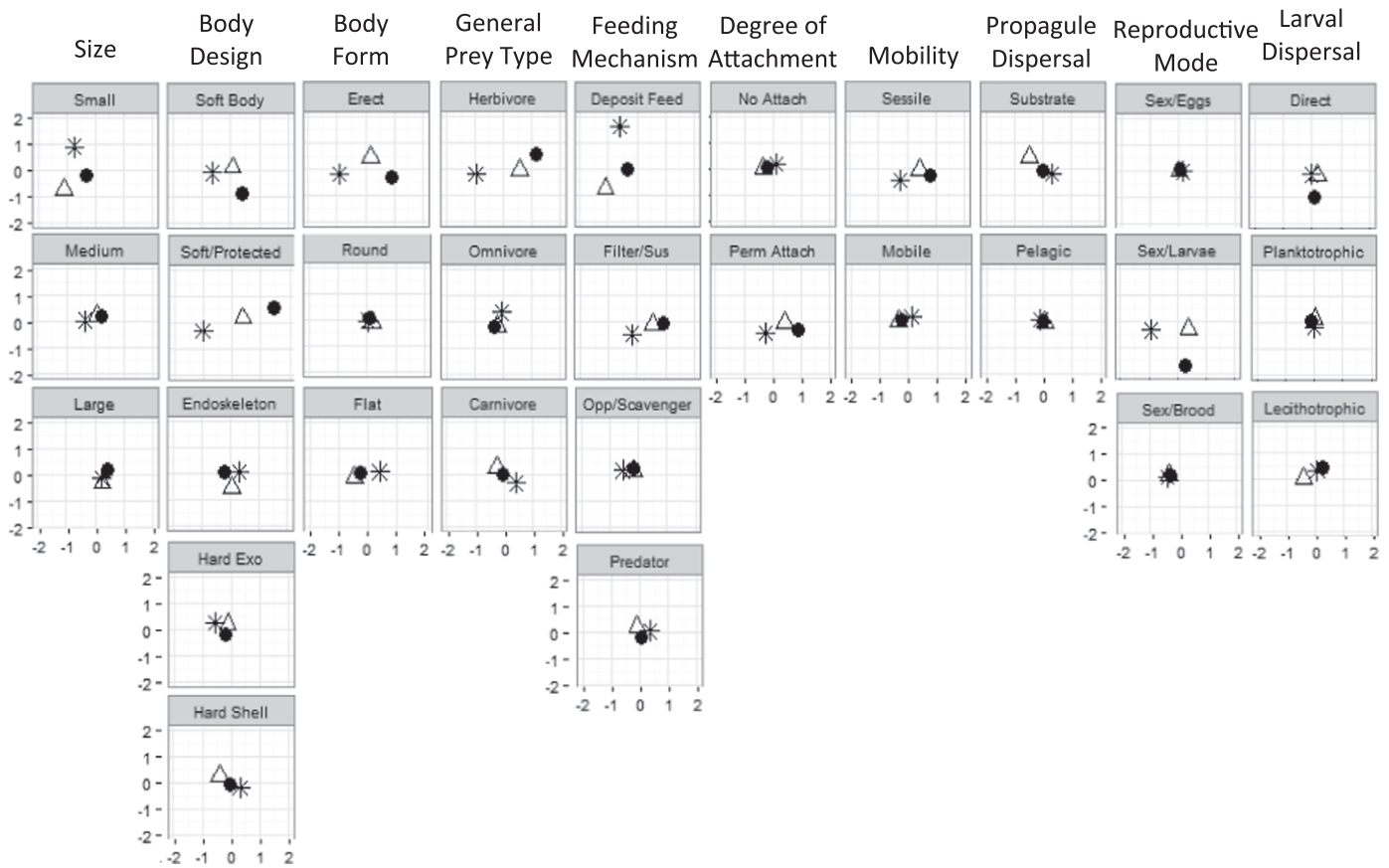
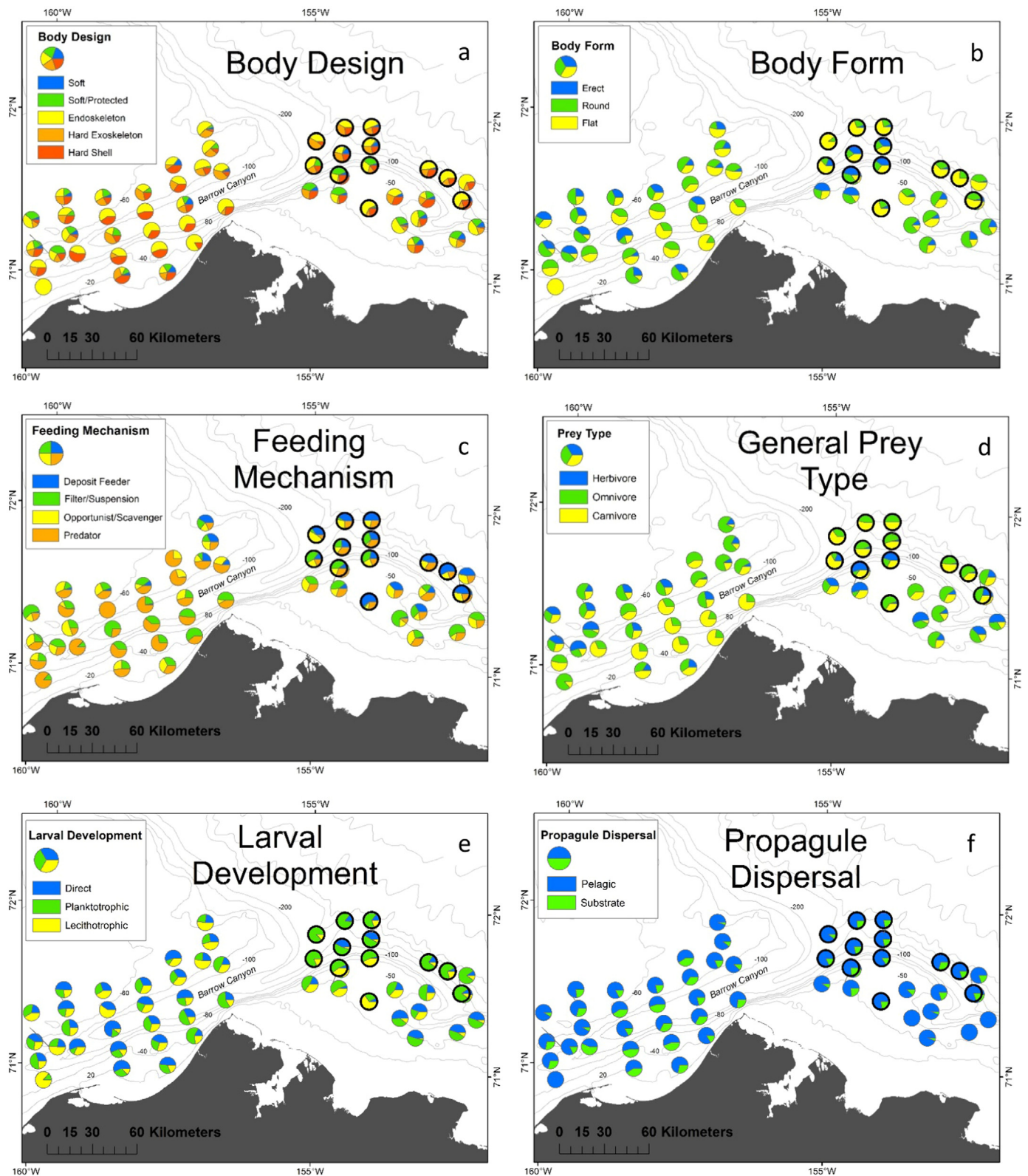


Fig. 6. Traits score results from the fuzzy correspondence analysis (FCA) on the biological traits for the Chukchi Sea (asterisk), Beaufort Sea LN hauls (black dots), and Beaufort Sea UN hauls (triangles) surveys. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with no net liner. This figure is an alternative representation of Figs. 5b, 5d, and 5f and is a visual comparison of the variation for each trait, in each survey, with vertical grouping by the Biological Trait and subsequent Trait Modalities. Note: some trait codes are truncated (e.g., Opp/Scavenger), refer to Table 2 for full listing of traits.

that other factors, such as competitive interactions, may also influence faunal distribution patterns as examples illustrate here. The coarser sediment and higher flow is associated with taxa that are larger bodied such as the basket star, *Gorgonocephalus* spp., gastropods, and sea stars (Asteroidea). The basket star, *Gorgonocephalus* spp., is known to inhabit areas of high current since they filter organisms from the water column (Patent, 1970). In the Chukchi Sea, *Gorgonocephalus* spp., was almost exclusively located in this higher current flow (i.e. bottom hardness and Mean Year Speed were correlated). The dominance of predatory sea stars within this PWW and coarser sediment coincides with both the absence of snow crabs, possibly due to competitive interactions, and a marked increase in nutrient rich waters transported from the Pacific into Barrow Canyon (Grebmeier et al., 2006). Another example of faunal changes with sediment and current velocity patterns is the presence of the filter-feeding sea cucumber, *Psolus peronii*. This species of sea cucumber occurred in high abundances (Figs. 1 and 3) in areas of higher current velocity and increased bottom hardness (Fig. 2). The predatory lyre crab, *Hyas coarctatus*, also occurs primarily west and on the Chukchi Sea Shelf and does not co-occur with the basket star *Gorgonocephalus* spp.; possibly, this may indicate avoidance of sea stars and gastropods due to competition and/or a preference for finer sediment and lower current velocities. Only four hauls captured the deposit feeding mud star, *Ctenodiscus crispatus*, in the northeast corner of the Chukchi Sea study area. This result may indicate that this portion of the Chukchi Sea study area may have the finest sediment and lowest current velocities as supported in Figs. 2 and 8. The brittle star *Ophiura sarsii* occurred in very low numbers in the northeastern Chukchi Sea survey even though it was dominant in several other studies in the

Chukchi Sea (Frost and Lowry, 1983; Ambrose et al., 2001; Feder et al., 2005; Bluhm et al., 2009; Ravelo et al., 2014). This does not appear to be an artifact of the sampling method because this species was captured with the same gear in the Beaufort Sea UN hauls. Possibly, this may be due to competitive interactions between these large, predatory taxa in the central part of Barrow Canyon.

We observed another taxonomic transition between the Barrow Canyon slope in the Beaufort Sea and the Beaufort Sea Shelf. There is higher benthic biomass on the Beaufort Sea slope and a shift in dominant taxa between the Beaufort slope (brittle stars and snow crab) and the Beaufort Shelf (sea cucumbers, mussels, mud stars, etc.). This taxonomic transition coincides with a transition from the PWW and Chukchi summer water (CSW) entering Barrow Canyon in the Chukchi Sea to both the Beaufort shelfbreak jet < 200 m, and the warmer more saline Atlantic water that dominates depths > 200 m along the Beaufort Sea slope (Pickart, 2004; Weingartner et al., 2005b; Gong and Pickart, 2015). Unlike the Chukchi Sea portion of Barrow Canyon, the brittle star *Ophiura sarsii*, and the snow crab, *Chionoecetes opilio*, dominate these deeper depths (> 200 m) that exit Barrow Canyon and lead into the deep Arctic basin. Our results also illustrated an inverse relationship between depth and current velocity in that these deeper basin stations also experience, on average, lower currents than those stations on the Beaufort slope and shelf. Although we do not know the exact mechanism influencing these distributions, they are consistent with previous findings by Frost and Lowry (1983) and Ravelo et al. (2015), and we hypothesize that *O. sarsii* and snow crabs prefer the warmer, slower, and saltier Atlantic influenced water.



**Fig. 7.** Biological traits with correlations ratios above 0.20 (a-d) and correlation ratios below 0.05 (e and f) are shown for hauls in the Chukchi Sea, Beaufort Sea LN (outlined in black), and Beaufort Sea UN surveys. The Beaufort Sea LN refers to hauls sampled with a net liner and UN refers to those hauls sampled with no net liner. Each pie chart represents one haul. Note: to illustrate all hauls on one map some pie charts two hauls from the Beaufort Sea UN survey are slightly displaced from the actual haul location but a line connecting the chart to the location is shown.

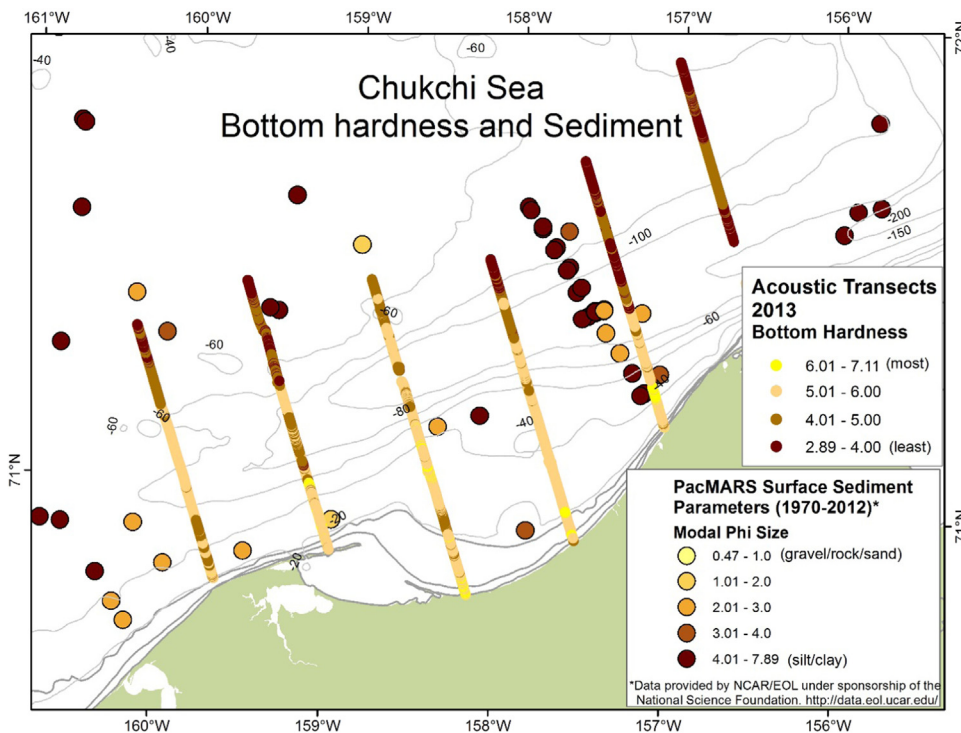


Fig. 8. Map of the Chukchi Sea survey area overlaid with the acoustic transects for bottom hardness and the PacMARS Surface Sediment Parameters (Grebmeier and Cooper, 2016). PacMARS Surface Sediment Parameters. Version 2.0. UCAR/NCAR-Earth Observing Laboratory. <https://doi.org/10.5065/D6416V3G>. The measure of bottom hardness is from vessel acoustics and is unitless; higher values imply harder bottom. “Modal Phi Size” refers to the sediment grain size mode. This figure illustrates the transition from finer to coarser sediment from off-shore (lower current velocity) into Barrow Canyon and onto the shelf, where current velocities are greater.

#### 4.2. Patterns in biological and functional traits

Our two surveys in the Chukchi and Beaufort seas encompass most of Barrow Canyon, sharing some of the hydrographic characteristics, but they only share a portion of the biomass-dominant taxa. Because of this result, we asked if these two study areas were, in fact, functionally different or shared similarities. Although the regional comparison is somewhat biased by the different mesh size in the Beaufort Sea LN survey, we were able to shed light on the variability of the biological traits both within and adjacent to Barrow Canyon. The fact that there was not a biological trait or trait modality exclusive to either system infers that these two systems share similarities in their biological processes which may be surprising given the differences in taxonomy between the two study areas. This is one of the fundamental benefits to a biological traits analysis; even though the taxonomic composition and distribution is different, the underlying functional processes are similar.

Of the ten biological traits examined, however, four traits and their respective trait modalities were considered variable enough within their respective study area to further examine patterns. The four biological traits, Body Design, Body Form, Feeding Mechanism, and General Prey Type share some characteristics. For example, the trait modality “soft/protected” often coincides with the trait modalities “erect”, and “filter/suspension” feeding. Similar to the connection in water masses and taxonomic distribution, the variability we observed in trait distribution can in part be attributed to habitat heterogeneity and transitions (e.g. sediment, hydrography) that occur in this region. The Chukchi Sea survey area contained a high prominence of filter/suspension feeders in line with the convergence of the PWW and increased current velocities as this water mass accelerates north into Barrow Canyon. High current velocities tend to contain high loads of suspended particles that serve as food for these filter feeders. These filter/suspension feeders maintain a presence in Barrow Canyon as it enters into the Beaufort and extends onto the shelf with the PWW transitioning into the Beaufort shelfbreak jet. The filter/suspension feeders do not extend to the Barrow Canyon slope or waters > 200 m where deposit feeders dominate. This is likely related to the lower suspended particle content in slowing waters and the fine-grained, less eroded sediment that is more suitable for deposit feeders. This supports the taxonomic

distribution results and again highlights an important transition zone from the fast flowing Beaufort Sea shelf environment (< 200 m) dominated by filter/suspension traits to one dominated by the deposit feeding trait within the deeper Atlantic water. These relationships between feeding mechanism and flow velocity match results of a study by Pisareva et al. (2015) that used the feeding modes of benthic fauna and sediment characteristics as indicators of hydrographic flow on varying time scales. They also concluded that, in general, benthic suspension feeders were associated with regions of stronger flow and deposit feeders with regions with weaker flow (Pisareva et al., 2015), and that these faunal patterns were reflective of the long-term flow velocities. Further, Pisareva et al. (2015) found that there was a higher proportion of suspension feeding fauna in the central Barrow Canyon and a higher proportion of deposit feeding taxa outside the Canyon based on flow speed and sediment grain size. This shift in both taxa and traits from the head of Barrow Canyon in the Chukchi Sea to the Beaufort Sea shelf occurs within an oceanographically complex region. The hydrography at the head of Barrow Canyon in the Chukchi Sea hosts both vertical and horizontal transition zones that include lateral fronts, vertical stratifications and the influence of swift flows interacting with steep bottom topography gradients (Fig. 2).

Some biological traits had little variability in their distribution within a survey but differed between surveys. For example, those traits representing reproduction modes and early life history stages (Propagule Dispersal and Larval Development) showed little to no variation within a survey. It is possible that these traits are less influenced by currents, water mass properties, and sediment composition than morphological or feeding traits. In contrast to this result, between-survey differences included a high proportion of “direct” development in the Chukchi Sea survey that was observed to a lesser degree in the Beaufort Sea. This trait may contribute to some of the differences we observed in the taxonomy between the Chukchi and Beaufort parts of Barrow Canyon. The retention of “direct” developers (low dispersal) at the head of Barrow Canyon may cause these taxa to remain in the Chukchi Sea and not be advected into the Beaufort Sea. Whether the prominence of taxa with this Larval Development trait at the head of Barrow Canyon are fostered by conditions such as nutrients and upwelling, or whether these differences are driven by competitive

interactions within the community itself, is difficult to determine. Although we do not quantitatively compare the absolute biomass of these traits between surveys (e.g. there is “more” of a trait in a survey), the fact that some of these trait modalities are evenly distributed within a survey is interesting. Life history strategies in marine benthic invertebrates, in particular reproduction, are especially complex processes with multiple tradeoffs that can translate into differences, for example, in fecundity among closely related species inhabiting different habitats (Llodra, 2002). This suggests the possibility that the processes affecting those taxa at the head of Barrow Canyon are not the same as those in the Beaufort Sea side of Barrow Canyon in depths less than 200 m, even though the water mass transport, bathymetry, and current velocities appear to be similar and given these sites are within only 60 km of each other.

#### 4.3. Study limitations and recommendations for future studies

The limitations of our functional traits analysis is that in the Arctic, life history and other information on benthic invertebrates is particularly sparse. In the absence of life history traits for many of these Arctic species, our approach was, therefore, to apply known trait modalities from those species within the same genus or family. Given the lack of species-specific knowledge, we used traits that focused on the general functions of an organism, like Feeding Mechanism, rather than those traits describing complex processes like growth rates. We recommend that future studies on impacts of climate change and other human impacts also include those traits characteristic of Arctic fauna such as (slow) growth rates, (high) longevity and (late) age at maturity. Also, the focus of this study was on the top 90% by biomass of the epibenthic invertebrates; this eliminated 80–90% of the taxa that were captured in the surveys, shifting the focus to organisms that make up the largest biomass and for which information on biological traits could be gathered. The weakness in focusing on only a relatively small number of taxa, in this case < 20 per survey area, is that information was lost on taxa or species that may have been common to all stations but comprised a very small fraction of the total biomass at that station and across the survey area. These taxa or species could be filling a small, but important, ecological niche in the overall function of a local community. The BTA approach could also be refined by using fuzzy instead of binary coding for the traits since many species exhibit more than one trait modality within a trait category. For example, most sea stars were placed in the “predator” modality as their primary method of feeding, but they can also be “opportunistic/scavengers” and “deposit feeders”; fuzzy coding would allow better resolution of the complexity of their functional contributions at the community level.

#### 4.4. Conclusions and monitoring recommendations

It is well documented that the effects of climate change are accelerated in the Arctic (Pithan and Mauritsen, 2014). What remains unclear, is the magnitude in which these rapidly changing conditions will affect marine life in the coming years. For example, Cross et al. (2018) has shown that decreased saturation rates of calcium carbonate (e.g. ocean acidification) from anthropogenic changes in atmospheric carbon dioxide, has fundamentally altered the duration and intensity of the PWW. Both in- and epi- faunal invertebrates are particularly vulnerable to changes in ocean acidification. Since the PWW is the primary source of transport from the Pacific to the Arctic Basin, through Barrow Canyon, a well-documented biological “hotspot” for micro- to macro-fauna (Moore et al., 2010; Moore and Stabeno, 2015; Grebmeier et al., 2015), it is an especially important region of the Pacific Arctic to monitor for the effects of climate change. A traits analysis, along with traditional taxonomic methods, has become a useful tool in ecosystem monitoring and management (Usseglio-Polatera et al., 2000; Doledec et al., 2006; Tomanova et al., 2008). In these studies, researchers used community composition analyses (taxonomic and/or traits) and

changes therein as a direct reflection of ecosystem health. Although changes in taxonomic diversity can be indicative of change that is occurring, extending this to analyzing biological traits makes a direct connection between environmental processes and the ecological functioning of the systems organisms.

This study improved the knowledge of epibenthic communities in the Barrow Canyon area, which has previously not been well resolved nor their connections to the complex regional hydrodynamics. This effort contributes to the baseline data in terms of both species and functional diversity of the epibenthic invertebrate communities within this region. Monitoring the epibenthic invertebrate community at these “hotspots” is in line with the recently established Distributed Biological Observatory (Grebmeier et al., 2010, 2015a), the US-wide Marine Biodiversity Observation Network (MBON) including its Arctic component and the Conservation of Arctic Flora and Fauna’s Circumpolar Biodiversity Monitoring Program. Benthic taxa can be excellent proxies for change over time because they are relatively long lived at high latitudes and can be indicative of changes in sediment characteristics and water mass influences due to warming, acidification, and the loss of sea ice (Kortsch et al., 2012; Grebmeier et al., 2015a; Cross et al., 2018). We recommend biological trait analysis approaches be included in such monitoring efforts.

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