

**CHUKCHI SEA ENVIRONMENTAL STUDIES PROGRAM:
BENTHIC ECOLOGY OF THE NORTHEASTERN CHUKCHI SEA,
2008–2013**

Prepared for

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FINAL REPORT

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EXECUTIVE SUMMARY

ConocoPhillips, Shell Exploration and Production Company, and Statoil USA E&P are supporting the multidisciplinary Chukchi Sea Environmental Studies Program (CSESP) to establish baseline ecological conditions in the northeastern Chukchi Sea. The CSESP has provided information on physical, chemical, and biological oceanographic trends over a period of six years. The Klondike and Burger study areas were first sampled in 2008, and Statoil was added in 2010; sampling at these locations continued through 2013.

Macrofauna (sediment-dwelling organisms retained on a 1.0-mm sieve) and environmental parameters were sampled at 39 stations in 2013, including 15 stations along the CSESP Distributed Biological Observatory (DBO) line. The objectives of the 2013 benthic ecology component were to describe the temporal variability of benthic communities and the environmental and biological characteristics of the CSESP Distributed Biological Observatory (DBO) line.

Benthic macrofauna in the Klondike, Burger, and Statoil study areas were abundant, contained many large animals, and communities were diverse with many species. Spatial differences in community characteristics were apparent, in that Burger had greater average density and biomass than Klondike did and taxon richness in Burger was significantly greater than that in Statoil. Community characteristics in Statoil were similar to that in Klondike in 2013, although biomass was significantly higher in Statoil than in Klondike. In general, Burger had the highest biomass, density, and richness. Spatial variations of macrofaunal community characteristics and structure coincided with water circulation patterns noted by concurrent studies of the physical oceanography.

Significant temporal variability in community parameters (biomass, density, and richness) indicates high ecosystem variability in this high-latitude study area. Significant Year effects as determined by ANOVA and variable bivalve recruitment (as indicated by reduced shell lengths of the bivalve *Ennucula tenuis* in years with higher recruitment, such as 2012 and 2013) all indicate high interannual variability. The significant increases in biomass, density, and richness in all study areas from 2008 to 2013 were large, compared to criterion for community variations in benthic communities. Density and richness were strongly correlated with the Arctic Oscillation (a climate index reflecting sea-level air pressure in the Arctic Ocean) 2008–2012

suggesting that climate-driven variations in water circulation play a significant role in the variability of benthic communities, as found elsewhere in the North Pacific.

Benthic communities along the CESP Distributed Biological Observatory 2013 demonstrated large environmental and biological gradients from the nearshore to offshore stations. Communities graded from disturbance-tolerant species nearshore to amphipods to mixed polychaete and bivalve communities offshore. Stations DF001 and DF002 were closest to the shoreline, had the coarsest sediments, were shallowest (~15–20 m water depth), and were warmest and least saline. *Tecticeps alascensis* is a carnivore known to prey on amphipods, and an early colonizer of disturbed sediments. Presuming that *T. c.f. renoculis* is also a predator and early colonizer, the presence of the isopod reflects the greater disturbance and dynamics in shallower waters, as does the substantial numbers of nematodes. The occurrence of the isopod *Tecticeps c.f. renoculis* is a potential range extension for this intertidal animal. The occurrence of southern fauna in the northeastern Chukchi Sea is common reflecting the advection of benthic larvae northward from North Pacific populations. The paucity of observations for this isopod reflects the low sampling effort in a very heterogeneous environment, and highlights the importance of local knowledge in detailed studies of benthic communities that are key resources for higher trophic level predators. The benthic communities along the DBO line reflected water depth and associated changes in physical dynamics (increased dynamics in shallower waters from storms, etc.), rather than water mass characteristics as drivers, which is a common assumption for the region. The DBO line demonstrated high spatial heterogeneity as environmental characteristics graded from the nearshore (greater physical dynamics) to offshore conditions (less dynamic, more depositional) with associated changes in biological communities.

In summary, the benthic communities in the northeastern Chukchi Sea have high spatial and temporal variability reflecting a very dynamic ecosystem. The benthic communities are a mix of arctic and North Pacific invertebrates resulting from the flow of water northward through Bering Strait to the Arctic Ocean. Environmental gradients associated with seafloor topographic variations (particularly the change in water depth in Burger that is at the head of a submarine valley) are reflected in the spatial characteristics of macrofaunal communities. Seafloor topography driving water currents and other oceanographic characteristics result in changes in water movements, including persistence of cold water over Burger, stagnant water flow, and deposition of organic carbon. The direct and indirect effects of altered water circulation appear to

be key determinants of spatial variability. Temporal variability appears to be correlated with the Arctic Oscillation, presumably reflecting changes in water circulation; we hope that this hypothesis can be tested by future oceanographic studies in the region. Gradients of the macrofaunal community along the CSESP DBO line were strong and resulted from large shifts in environmental characteristics from inshore to offshore areas. As opposed to assumptions that the Chukchi Sea is oceanographically smooth, the 2008–2013 CSESP demonstrates high spatial and temporal variability of environmental and biological characteristics.

BENTHIC ECOLOGY 2008–2013:

Macrofaunal Community Structure in the CSESP Study Areas and the DBO Line

INTRODUCTION

ConocoPhillips Company (COP), Shell Exploration and Production Company (SEPCO), and Statoil USA E&P, Inc., (Statoil) are supporting the multidisciplinary Chukchi Sea Environmental Studies Program (CSESP) to understand current ecological conditions and trends for three study areas in the northeastern Chukchi Sea prior to oil and gas exploration. The Klondike, Burger, and Statoil (2010–2013 only) study areas encompass successful lease bids in the February 2008 Chukchi Sea Lease Sale 193, and are the focus of the CSESP. The CSESP, which was initiated in 2008 and continued in 2009–2013, provides information on physical, chemical, and biological oceanographic trends and the acoustic environment of the Klondike, Burger, and Statoil study areas and the northeastern Chukchi Sea. Results of this 6-year investigation contribute to benchmarks for determining potential changes in the benthos due to environmental fluctuations and to temporal databases for evaluating, with confidence, long-term trends (e.g., repeated sampling at similar locations over space and time while using similar sampling methods) in macrofaunal communities of the northeast Chukchi Sea.

Since the 2008 lease sale, interest in understanding the arctic environment has grown, with regulatory agencies and academia directing efforts toward improving the understanding of the environment, including that of the Chukchi Sea (Hopcroft et al., 2006; Day et al., 2013; Dunton et al., 2014). Resources in the Chukchi Sea are of great importance to a broad variety of stakeholders, including Native subsistence hunters, environmental organizations, and companies interested in extracting and shipping resources of economic value. Biological resources of interest include marine mammals and seabirds, many of which feed on sediment-dwelling organisms (benthic species) such as polychaete worms, amphipods, clams, shrimp, and crabs (Oliver et al., 1983; Moore and Clarke, 1990; Feder et al., 1994, 2005, 2007; Coyle et al., 1997; Green and Mitchell, 1997; Lovvorn et al., 2003; Moore et al., 2003; Grebmeier et al., 2006; Highsmith et al., 2006; Bluhm et al., 2007; Bluhm and Gradinger, 2008). Thus, understanding spatial and temporal dynamics of benthic communities also contributes to understanding the dynamics of essential resources because of linkages as prey to marine mammal populations.

Investigations of carbon cycling in the Chukchi Sea demonstrated strong coupling between primary production and distributions of invertebrate fauna. The large flux of uneaten phytoplankton reaching the bottom results in locally dense and biomass-rich macrofaunal communities (Dunton et al., 2005; Grebmeier et al., 2006). Consequently, large interannual variability in primary production and zooplankton communities (Questel et al., 2013) may be important sources of temporal variability for benthic communities. Production by ice algae contributes to the annual carbon budget for invertebrate communities in arctic waters, but its ecological importance needs to be established for the Chukchi Sea (Ambrose et al., 2001, 2005). The climate and oceanographic variations jointly influencing pelagic and benthic communities are largely unknown but must be understood to model expectations for the changing environment of the Arctic.

The general objectives of the benthic-ecology component of the CSESP were to 1) investigate the spatial and temporal variability in species-composition, density, and biomass of macrofaunal communities within the study areas and 2) determine environmental drivers. The objectives of the 2013 benthic ecology component were to describe the temporal variability of benthic communities and environmental and biological characteristics of the CSESP Distributed Biological Observatory (DBO) line. Tasks included:

- Collection of macrofaunal samples from 39 stations;
- Laboratory analysis and taxonomic determinations of macrofauna;
- Determination of grain-size characteristics, stable-isotope composition, and concentrations of organic carbon in sediments; and
- Determination of the population dynamics of two bivalve species, *Ennucula tenuis* and *Macoma* spp.

STUDY AREA AND ENVIRONMENTAL SETTING

The Chukchi Sea is a shallow body of water influenced by seasonal ice cover and the advection of southern waters from the Pacific Ocean into the Arctic Ocean via Bering Strait (Weingartner et al., 2005). Water masses moving into the region from the south include Anadyr Water in the west, Bering Shelf Water in the central Chukchi, and Alaskan Coastal Water in the east (Coachman, 1987; Weingartner et al., 2005). Interactions between seafloor topography and water masses split the pressure-driven, northward flow into the Alaska Coastal Current (ACC),

Central Channel flow, and Herald Valley Current with water exiting the Chukchi shelf through Herald Valley, the Central Channel, and Barrow Canyon. Interactions between seafloor topography and currents also result in complex circulation patterns around Hanna and Herald shoals (Martin and Drucker, 1997), both of which are dominant features of the seafloor of the northern Chukchi Sea.

Southern water masses advected north contribute to the ecological characteristics of the Chukchi Sea by, but not limited to, importing heat, nutrients, zooplankton, and benthic fauna. Shallow water depths of the Chukchi Shelf (~35 to 45 m) prevent the establishment of *in situ* communities of large grazing zooplankton, which must be advected from the south into the northern Chukchi Sea annually. The mismatch between the timing of seasonal primary production and the arrival and development of the zooplankton community allows much of the annual production to fall to the seafloor unconsumed, supporting abundant and biomass-rich benthic assemblages (Grebmeier et al., 2006). The advection of production in nutrient-rich Bering Sea Water (BSW; a combination of Bering Shelf Water and Anadyr Water) from the south enhances secondary production in the Chukchi (Feder et al., 1994). In contrast, the ACW that is advected northward along the Alaska coastline is considered to be nutrient-poor, although significant benthic biomass may occur under this water mass (Feder et al., 1994, 2005; Codispoti et al., 2005). Sediment grain size and the ratio of sediment organic carbon to nitrogen (C/N) ratio were predictors of benthic community structure in the Chukchi Sea (Feder et al., 1994; Grebmeier et al., 2006). As a predictor, however, sediment granulometry is a proxy for environmental processes associated with or driven by variations in seafloor topography, hydrodynamics (strong currents, storm effects, ice-gouging, etc.), sediment deposition, and proximity to sediment sources. Given that background, Blanchard et al. (2013a) indicated that interactions between water circulation and variations in seafloor topography where topographic changes drive variations in water patterns (topographic control) may be key sources for spatial variations in macrofaunal communities. Large topographic features of the seafloor cause water currents to diverge from expected flows (e.g., causing eddies, gyres, increased flow in canyons, or stagnant water flow) resulting in greater food availability for the benthos. Water-current variations can result in increased deposition of carbon favoring deposit-feeders where currents slow, or greater flows of carbon past suspension-feeding organisms where water flow is high.

General trends in sediment characteristics of the northeastern Chukchi Sea followed the expected increase in depth and percent of mud in sediments with greater distance offshore (Feder et al., 1994; Grebmeier et al., 2006). There was also a trend of increasing percent mud and bottom-water salinity, and decreasing bottom-water temperatures with higher latitude. Feder et al. (1994) discusses the importance of a bottom-water front extending to Point Franklin that aligns closely with the 3°C contour in a geospatial model for bottom-water temperature (Fig. 1). Benthic communities reflected the differences in water masses, possibly due to the advection of production from the south in the BSW, with increased density and biomass north of the front. Though the position and strength of bottom-water fronts will be highly variable from year-to-year, the environmental/biological associations discussed by Feder et al. (1994) align with expectations of effects from differing water masses with lower benthic biomass under the ACW (Grebmeier et al., 2006). Exceptional benthic density and biomass were noted near and in Barrow Canyon due to the advection of carbon past suspension-feeders.

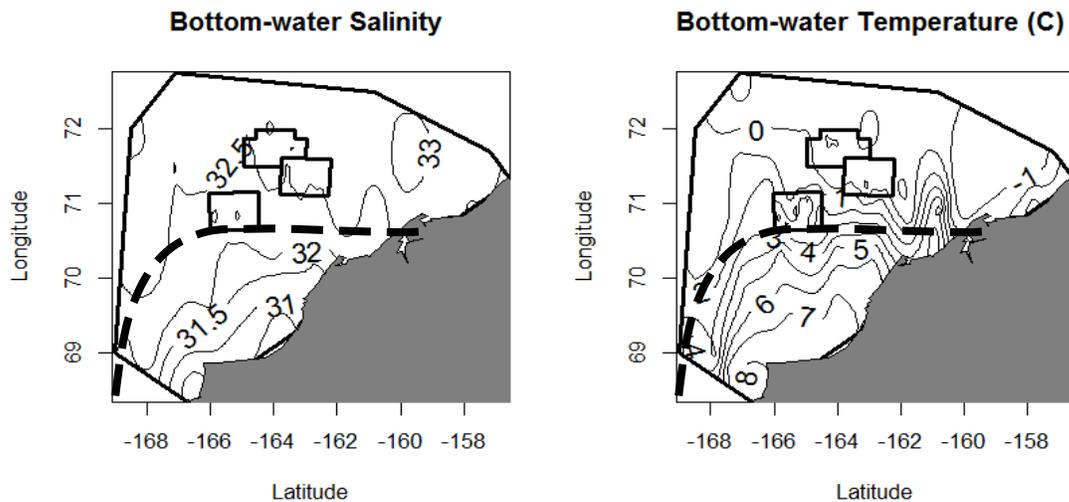


Figure 1. Geospatial models of bottom-water salinity and temperature for the northeastern Chukchi Sea. Data are from 1986 (Feder et al., 1994) and values averaged from 2008–2010 for the CSESP (Blanchard et al., 2013a). The dashed line denotes the bottom-water front discussed by Feder et al. (1994).

The CSESP study area lies 100–200 km northwest of the village of Wainwright, Alaska, on the northwestern coast of Alaska (Fig. 2; Day et al., 2013). Klondike lies along a channel of northward-flowing water (called the Central Channel) and has coarse sediments, whereas Burger

is a depositional area with muddy sediments. Cold, saline winter-water remains longer in Burger than in Klondike. The stagnant water circulation and increased stratification by the persistent winter water would increase the flux of carbon to the sediment surface in Burger. Klondike functions more as a pelagic-dominated system, with more oceanic zooplankton and pelagic-feeding birds, whereas Burger functions more as a benthic-dominated system with more benthic-feeding mammals (Day et al., 2013). The Statoil study area lies northwest of and adjacent to Burger and shares environmental and biological characteristics of both Burger and Klondike.

When discussing topographic control, the phrase “seafloor topography” is used in this report to emphasize the ecological significance of submerged geological features and past geological history for determining present oceanographic characteristics and distributions of benthic fauna (Elias and Brigham-Grette, 2007; Blanchard and Feder, 2014).

METHODS

Sampling

Macrofauna were sampled with the van Veen grab at 39 stations in the three study areas and along the CSESP DBO line (Table 1 and Fig. 2). Sampling occurred from 17 September to 10 October on cruise WWW1304. Macrofauna were sampled with a double van Veen grab with two 0.1-m² adjoining grabs. Three replicate samples were collected at each station. Material was collected from one of the adjoining grabs for macrofauna and was washed on a 1.0-mm stainless steel screen and preserved in a 10% solution of formalin in seawater buffered with hexamine. Benthic organisms were identified to the lowest taxonomic resolution possible, counted, and wet weights measured (following Feder et al, 1994). Sediment samples were also collected from the adjoining grab, frozen on the ship, and sieved in the laboratory to determine the proportion of mud, sand, and gravel (Wentworth, 1922). Sediment samples for carbon concentration were frozen on the ship and processed at the Alaska Stable Isotope Facility (University of Alaska, Fairbanks).

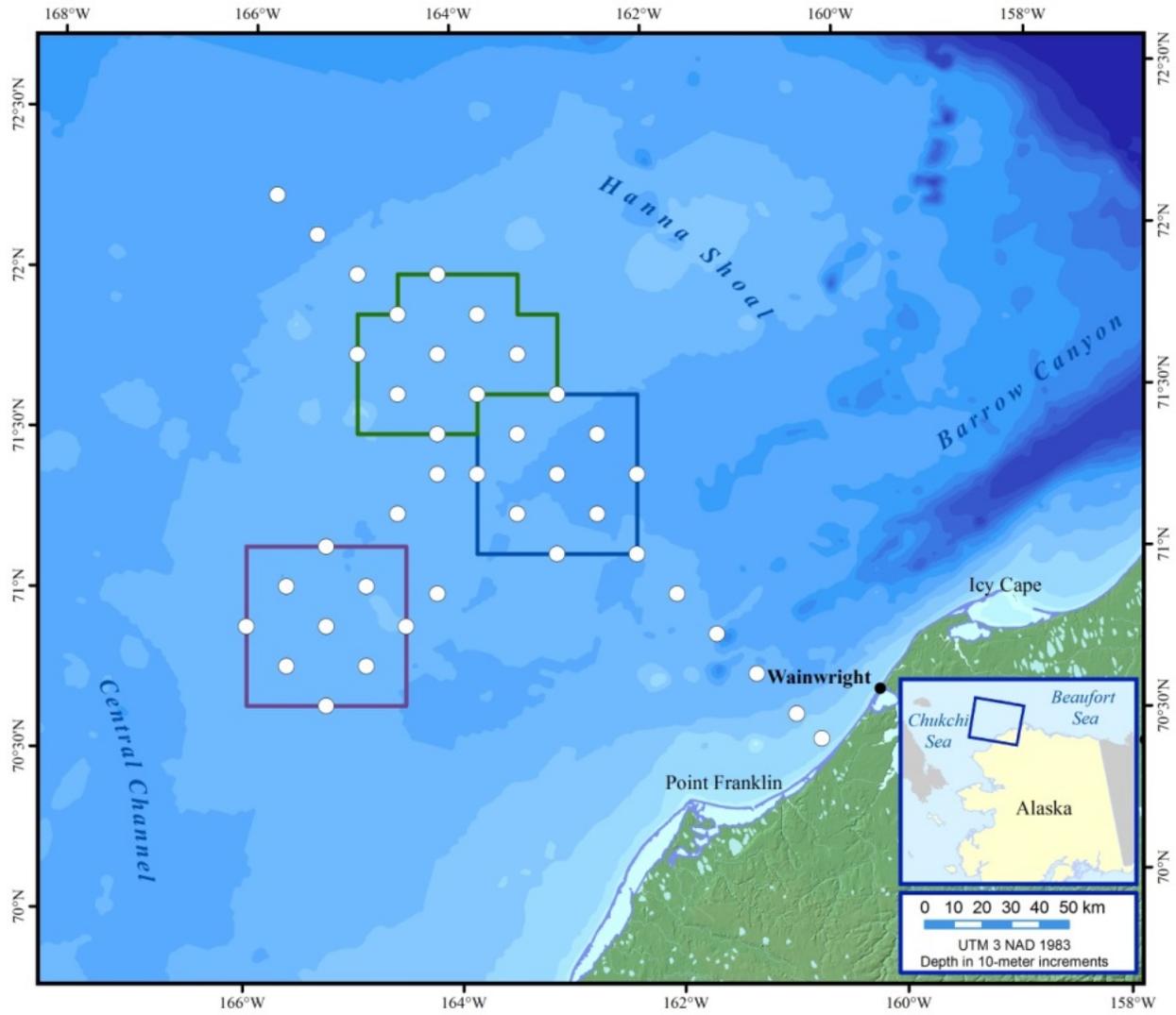


Figure 2. Stations sampled for macrofauna during the 2013 CSESP survey.

Table 1. Coordinates (decimal-degree format) for benthic sampling locations during the 2013 CSESP study. DF = DBO line station, KF = Klondike, BF = Burger, SF = Statoil, TF = transitional station between Burger and Klondike, and HC = Hanna Shoal Central.

Station	Latitude	Longitude	Station	Latitude	Longitude
BF003	71.113371	-163.034704	SF003	71.495641	-164.172060
BF005	71.103710	-162.266597	SF005	71.621472	-164.561049
BF007	71.241507	-163.408919	SF007	71.746502	-164.955468
BF009	71.233368	-162.635541	SF009	71.744678	-164.160893
BF011	71.368893	-163.788076	SF011	71.739575	-163.366621
BF013	71.362297	-163.009414	SF014	71.870527	-164.555229
BF015	71.352499	-162.231449	SF016	71.867040	-163.755778
BF017	71.490482	-163.388290	SF020	71.993710	-164.149687
BF019	71.482225	-162.604905			
BF021	71.617904	-163.772246	DF001	70.495070	-160.621784
BF023	71.611214	-162.983426	DF002	70.578240	-160.838399
KF003	70.648553	-165.251470	DF003	70.710655	-161.188366
KF007	70.772190	-165.630936	DF004	70.842403	-161.542967
KF009	70.773228	-164.875114	DF005	70.973470	-161.902276
KF011	70.895031	-166.015109	DF006	72.119764	-165.359865
KF013	70.897638	-165.254622	DF007	72.243114	-165.770349
KF015	70.897122	-164.494051	HC014	71.995561	-164.954874
KF017	71.021259	-165.638900	TF001	70.997543	-164.193240
KF019	71.022312	-164.873538	TF003	71.247877	-164.569489
KF023	71.146717	-165.257859	TF006	71.371119	-164.177397

Quality-control

The TigerObserver system, an integrated navigational and data-recording system, was developed for the CSESP in 2009 to integrate data collected in the field with the ship's navigation system in real time. This data-recording system allows for geographic coordinates and measurements of oceanographic conditions to be linked with biological data and minimizes transcriptional errors between field notes and databases. Data managers aboard the vessels assisted scientists with onsite quality-control checks to minimize data-input errors. The TigerObserver system transcribed the data into a Microsoft® (MS) Access database. Raw

datasheets from the field and laboratory were archived at the University Of Alaska Fairbanks (UAF) Institute of Marine Science (IMS).

Quality-control procedures were followed in processing macrofaunal samples in the laboratory. The work of the preliminary sorters separating invertebrates from sediment debris was monitored throughout the project by a trained taxonomist. Once fully trained, a minimum of 10% of samples sorted by the preliminary sorters were re-sorted by a trained sorter to be certain that >95% of the organisms in each sample were removed from the sediment debris. All of the work performed by junior taxonomists was checked and verified by a senior taxonomist, with checks and verification tapering off as the junior taxonomists approached the skill level expected of a more experienced taxonomist. Work was verified to ensure that all counts were accurate and all organisms were identified correctly. Fauna identified in 2013 were compared with the voucher collection from the 1986 investigation by Feder et al. (1994) and to current references (e.g., other benthic programs, our work in the same study area throughout the years) to ensure accuracy, consistency among studies, and consistency with currently recognized taxonomy (to the best of our abilities). Consultation with other taxonomic experts provides quality-control checks for taxonomic identifications. Original data forms and MS Access databases will be archived at IMS and delivered to OLF in accordance with prescribed data management protocols.

Representative specimens of each taxon collected during the CSESP were archived at the Institute of Marine Sciences (IMS). These voucher specimens provide records of identification of organisms sampled in the study. Although some archived specimens may be sent to experts for further identification and/or verification, a complete collection will be maintained at IMS.

Prior to analyses of macrofaunal compositional data, the taxonomic information was scrutinized for consistency as a further quality-control check. Pelagic, meiofaunal, and epibenthic taxa (e.g., barnacles, tanaidaceans, benthic copepods, sea stars, crabs) were excluded from analytical data sets for macrofauna.

Statistical analysis

Trends in community composition were evaluated using univariate and multivariate approaches. Descriptive summaries of the data provide insights into study area variability and include average density, biomass, and richness (number of taxa per replicate). Comparisons among years for resampled study areas (Klondike, Burger, and Statoil) were performed using

mixed-model ANOVA methods. Canonical correspondence analysis (CCA) was used to test for associations between community structure of the macrofauna compositional data (species–sample matrix) and environmental predictors. CCA is a direct gradient-analysis tool that presents in an ordination that portion of trend in the biological community that is directly associated with the environmental characteristics. The statistical program R (www.R-project.org) was used for all statistical analyses. The R library “lme4” was used for mixed-model ANOVAs and “vegan” was used for CCA. Note that, to ensure comparability, the 2008–2012 data sets for Klondike, Burger, and Statoil were reduced to the 9 long-term monitoring stations sampled in each study-area box every year; this approach ensures a common sampling design that allows for appropriate inferences. Bottom-water salinity and temperature were provided by the CSESP physical oceanography team. The Arctic Oscillation (AO; <http://jisao.washington.edu/ao/>) is a climate index representing sea-level pressure over the Arctic Ocean. Winter AO values (December–March) are presented and correlated with biological measures, where appropriate.

The 2008–2010 CSESP studies showed significant temporal variability with a sharp decline of macrofaunal density in 2010, but not biomass (Blanchard et al., 2013a). The absence of a decline in biomass led to the hypothesis that larger organisms did not experience declines, but that recruiting individuals faced poor survival in 2010. Bivalves provide an easy means to test such a hypothesis by testing the null hypothesis that shell lengths do not differ among years. The absence of recruiting individuals in any one year will result in a shift in length frequencies towards larger shell lengths whereas high proportions of young-of-the-year bivalves will shift the length frequencies towards smaller bivalves, as will mortality of older bivalves. To test the hypothesis of similar lengths among years (equal recruitment), shell lengths for *Ennucula tenuis* were measured from 2008 to 2013; *Macoma* spp. also were sampled in 2012–2013. Data are presented as bar charts of median shell lengths. Length–frequency histograms for previous years (2008–2012) are presented in Blanchard and Knowlton (2013), and show increasing proportions of young, rather than significant losses of adults. Documenting growth patterns of dominant bivalves has been a common tool in baseline investigations in Alaska, including *E. tenuis*, *Nuculana pernula*, *Macoma calcarea*, and *Yoldia amygdalea* from the Bering Sea (McDonald et al., 1981), *Ciliatocardium ciliatum ciliatum* (formerly *Clinocardium ciliatum*), *M. calcarea*, and *Serripes groenlandicus* from the Bering and Chukchi seas (Stoker, 1978, 1981), and *Mytilus trossulus* from Port Valdez (Blanchard and Feder, 2000).

RESULTS

Temporal Variability

Average macrofaunal density in the long-term monitoring stations in the three study areas 2008–2013 ranged from 771 ind. m⁻² (Klondike 2008) to 6,077 ind. m⁻² (Burger 2013) (Table 2). Biomass ranged from 89.5 g m⁻² (Klondike 2013) to 446.5 g m⁻² (Burger 2013). Average richness ranged from 60 taxon categories sample⁻¹ (0.1-m⁻²; Statoil 2010) to 120 categories sample⁻¹ (Burger 2013). (See Appendix I for a list of macrofaunal species.)

Macrofauna with the highest densities in Klondike from 2008 to 2013 included the bivalve *Ennucula tenuis*; the polychaetes *Barantolla americana*, *Maldane sarsi*, and family Cirratulidae; and the amphipods *Melita* spp. and *Protomedeia* spp. (Table 3). Dominants by density in Burger included the bivalve *E. tenuis*; the polychaetes *M. sarsi* and *Scoletoma* spp.; the amphipod *Photis* sp.; and ostracods. In the Statoil study area, the taxa with highest densities included the bivalves *E. tenuis*, *Macoma* spp., *Yoldia hyperborea*, and *Yoldia* spp. and the polychaetes *M. sarsi* and *Praxillella praetermissa*. Macrofauna with the highest biomass in Klondike included the polychaete *M. sarsi*; the bivalves *Astarte borealis*, *Macoma calcarea*, and *Nuculana pernula*; the brittle star *Ophiura sarsi*; and the sipunculid worm *Golfingia margaritacea*. Animals with greatest biomass in Burger from 2008 to 2013 were the polychaete *M. sarsi*; the bivalves *A. borealis*, and *M. calcarea*; the brittle star *O. sarsi*; and the sipunculid worm *G. margaritacea*. In Statoil, the organisms with the greatest biomass included the bivalves *A. borealis*, *M. calcarea*, and *Y. hyperborea*; the brittle star *O. sarsi*; and the sipunculid worm *G. margaritacea*.

Repeated-measures Analysis of Variance (rm ANOVA) indicates significant differences among study areas and years. The study area and year main effects were significant for biomass and richness whereas there was a significant study area by year interaction for density (Table 4). Klondike had lower density than Burger, with the significant interaction reflecting the much lower density in Burger and Statoil in 2010 than the much smaller decline in Klondike for 2010 (Fig. 3). There was a general increase in density from 2008 to 2013 in all three study areas. Biomass was significantly lower in 2008–2011 and 2013 than in 2012, and biomass in Klondike was consistently lower than Burger or Statoil (Table 4). Burger had significantly greater richness than Statoil and by year, 2010 had lower richness than 2008–2009 and 2011–2013 with richness otherwise significantly increasing from 2008 to 2013.

Table 2. Density (ind. m⁻²), biomass (g m⁻²), and species richness for the study areas sampled for macrofauna during the 2008–2013 CSESP study, by study area and year. SD = standard deviation and CI = confidence interval. This table is based on the new sampling design using the nine stations repeatedly sampled in each focused study area from 2008 to 2013.

Study Area	Year	Density			Biomass			Richness		
		Average	SD	95% CI	Average	SD	95% CI	Average	SD	95% CI
Klondike	2008	771.1	362.8	(529.2, 1,013.0)	155.2	191.2	(27.8, 282.7)	67.1	14.0	(57.8, 76.5)
	2009	1,213.0	973.6	(563.9, 1,862.1)	118.8	59.8	(79.0, 158.7)	76.1	21.8	(61.6, 90.6)
	2010	1,052.2	707.3	(580.7, 1,523.8)	162.9	73.1	(114.1, 211.6)	71.9	25.0	(55.2, 88.5)
	2011	2,005.2	1,336.2	(1,114.4, 2,896.0)	149.4	82.2	(94.6, 204.2)	87.8	21.0	(73.8, 101.8)
	2012	2,579.3	1,278.2	(1,727.1, 3,431.4)	205.4	105.1	(135.3, 275.5)	92.6	25.2	(75.7, 109.4)
	2013	3,070.7	821.9	(2,439.0, 3,702.5)	89.5	44.4	(55.4, 123.7)	105.1	17.8	(91.5, 118.8)
Burger	2008	3,777.0	2,750.3	(1,943.5, 5,610.6)	350.9	107.5	(279.2, 422.5)	89.1	13.2	(80.3, 97.9)
	2009	4,671.1	3,844.1	(2,108.4, 7,233.9)	296.5	99.7	(23.00, 363.0)	96.4	11.6	(88.7, 104.2)
	2010	2,851.9	2,441.9	(1,223.9, 4,479.8)	320.3	92.3	(258.8, 381.8)	76.7	9.8	(70.1, 83.2)
	2011	5,151.9	4,404.6	(2,215.5, 8,088.2)	406.8	154.3	(303.9, 509.6)	100.3	11.4	(92.7, 107.9)
	2012	5,436.3	4,516.0	(2,425.6, 8,447)	438.3	128.9	(352.3, 524.3)	105.2	13.0	(96.6, 113.9)
	2013	6,067.3	3,142.6	(3,651.7, 8,483)	446.5	189.7	(300.6, 592.3)	120.3	13.1	(110.3, 130.3)
Statoil	2010	915.0	493.5	(566.0, 1264.0)	286.6	103.8	(213.2, 360.0)	60.3	19.1	(46.8, 73.7)
	2011	1,184.1	461.5	(876.4, 1,491.7)	279.1	127.7	(194.0, 364.3)	71.3	24.5	(55, 87.7)
	2012	2,818.1	1072.6	(2,103.1, 3,533.2)	385.6	150.4	(285.3, 485.8)	85.2	23.6	(69.5, 101.0)
	2013	4,457.8	1394.7	(3,385.7, 5,529.8)	263.8	125.8	(167.0, 360.5)	100.9	21.0	(84.7, 117.1)

Table 3. Rankings by density (ind. m⁻²) and biomass (g m⁻²) of dominant animals (top three) in Burger, Klondike, and Statoil from the 2008–2013 CSESP study for the reduced sampling design for the long-term monitoring stations.

Study Area	Year	Taxon	Density	Taxon	Biomass
Klondike	2008	<i>Maldane sarsi</i>	71	<i>Maldane sarsi</i>	29.56
		<i>Ennucula tenuis</i>	68	<i>Ophiura sarsi</i>	15.20
		<i>Barantolla americana</i>	44	<i>Golfingia margaritacea</i>	13.55
Klondike	2009	<i>Ennucula tenuis</i>	112	<i>Maldane sarsi</i>	16.21
		Cirratulidae	59	<i>Golfingia margaritacea</i>	10.33
		<i>Maldane sarsi</i>	47	<i>Nuculana pernula</i>	9.77
Klondike	2010	<i>Ennucula tenuis</i> .	90	<i>Golfingia margaritacea</i>	51.51
		<i>Maldane sarsi</i>	78	<i>Maldane sarsi</i>	31.68
		Cirratulidae	65	<i>Astarte borealis</i>	19.12
Klondike	2011	<i>Ennucula tenuis</i>	172	<i>Maldane sarsi</i>	34.36
		Cirratulidae	144	<i>Astarte borealis</i>	23.25
		<i>Melita</i> spp.	92	<i>Macoma calcarea</i>	14.12
Klondike	2012	<i>Ennucula tenuis</i>	304	<i>Golfingia margaritacea</i>	63.76
		<i>Protomedeia</i> spp.	243	<i>Astarte borealis</i>	46.68
		Cirratulidae	159	<i>Maldane sarsi</i>	40.69
Klondike	2013	<i>Ennucula tenuis</i>	471	<i>Maldane sarsi</i>	12.18
		<i>Protomedeia</i> spp.	378	<i>Golfingia margaritacea</i>	11.01
		<i>Melita</i> spp.	218	<i>Nuculana pernula</i>	7.18
Burger	2008	<i>Maldane sarsi</i>	748	<i>Ophiura sarsi</i>	62.23
		Ostracoda	287	<i>Astarte borealis</i>	54.59
		<i>Scoletoma</i> spp.	189	<i>Golfingia margaritacea</i>	38.16
Burger	2009	<i>Maldane sarsi</i>	750	<i>Astarte borealis</i>	57.51
		Ostracoda	289	<i>Macoma calcarea</i>	44.56
		<i>Photis</i> spp.	212	<i>Ennucula tenuis</i>	28.81
Burger	2010	<i>Maldane sarsi</i>	1,085	<i>Golfingia margaritacea</i>	55.62
		Ostracoda	136	<i>Astarte borealis</i>	42.29
		<i>Ennucula tenuis</i>	131	<i>Macoma calcarea</i>	40.10
Burger	2011	<i>Maldane sarsi</i>	1,788	<i>Maldane sarsi</i>	74.44
		Ostracoda	415	<i>Macoma calcarea</i>	61.45
		<i>Ennucula tenuis</i>	312	<i>Golfingia margaritacea</i>	52.65
Burger	2012	<i>Maldane sarsi</i>	1,536	<i>Astarte borealis</i>	82.53
		<i>Ennucula tenuis</i>	343	<i>Macoma calcarea</i>	48.23
		Ostracoda	245	<i>Golfingia margaritacea</i>	46.75
Burger	2013	<i>Maldane sarsi</i>	975	<i>Ophiura sarsi</i>	69.46
		Ostracoda	567	<i>Astarte borealis</i>	62.56
		<i>Ennucula tenuis</i>	386	<i>Golfingia margaritacea</i>	44.34

Table 3. Continued.

Study Area	Year	Taxon	Density	Taxon	Biomass
Statoil	2010	<i>Ennucula tenuis</i>	87	<i>Astarte borealis</i>	88.78
		<i>Yoldia hyperborea</i>	66	<i>Macoma calcarea</i>	42.12
		<i>Praxillella praetermissa</i>	60	<i>Yoldia hyperborea</i>	41.86
Statoil	2011	<i>Ennucula tenuis</i>	153	<i>Macoma calcarea</i>	41.89
		<i>Maldane sarsi</i>	114	<i>Yoldia hyperborea</i>	35.00
		Ostracoda	113	<i>Astarte borealis</i>	32.83
Statoil	2012	<i>Yoldia</i> spp.	486	<i>Astarte borealis</i>	59.83
		<i>Macoma</i> spp.	254	<i>Macoma calcarea</i>	57.74
		<i>Ennucula tenuis</i>	212	<i>Golfingia margaritacea</i>	43.58
Statoil	2013	<i>Yoldia</i> spp.	870	<i>Yoldia hyperborea</i>	43.87
		<i>Macoma</i> spp.	776	<i>Astarte borealis</i>	42.73
		<i>Ennucula tenuis</i>	664	<i>Ophiura sarsi</i>	22.39

Table 4. Repeated-measures Analysis of Variance of density, biomass, and richness for the CSESP study, 2008–2013. Values significant at $\alpha = 0.05$ are in bold type. Tukey multiple comparisons are presented for main effects; see Figure 3 for the patterns defining the significant interaction for density.

Density	F-statistic	P-value	Biomass	F-statistic	P-value
Year	49.18	<0.0001	Year	3.56	0.0053
Study Area	12.90	0.0001	Study Area	27.10	0.0000
Year x Study Area	6.74	0.0000	Year x Study Area	0.76	0.6403

Richness	F-statistic	P-value
Year	17.80	0.0000
Study Area	4.51	0.0219
Year x Study Area	2.00	0.0533

Main effects multiple comparisons

Biomass	Year	2008, 2009, 2010, 2013 < 2012
	Study Area	K < B, S
Richness	Year	2008 < 2009, 2011-2012; 2009 < 2012, 2013; 2010 < 2008-2009, 2011 - 2013; 2011 < 2012, 2013; 2012 < 2013
	Study Area	B > S

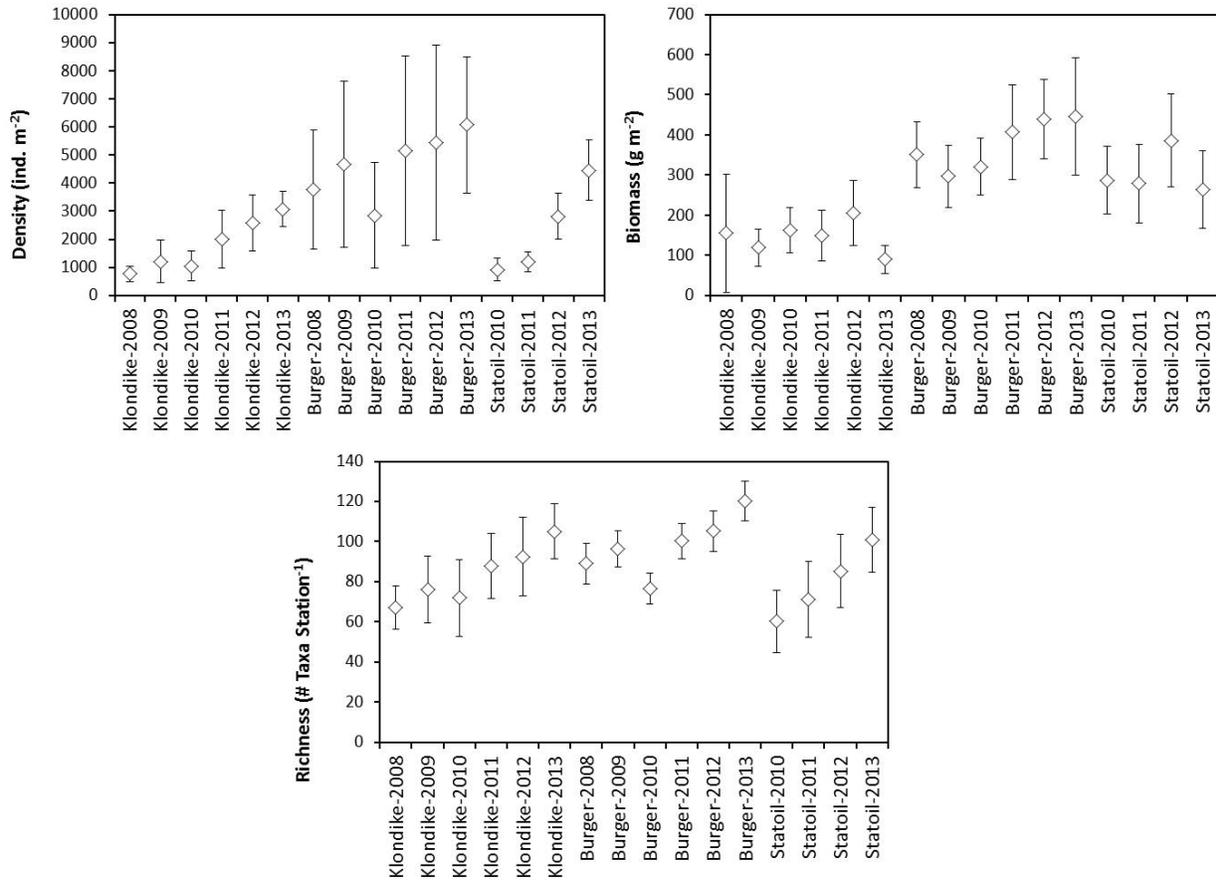


Figure 3. Averages and 95% confidence intervals of density, biomass, and richness for the 2008–2013 CESP study, by study area and year. Values are based on untransformed data.

Multivariate analysis of macrofaunal community composition (density) for all CESP sampling years (2008–2013) indicates a strong separation of stations by study area but weak separation by year (Fig. 4). CCA accounted for a total of 8% of community variability, with water depth, percent mud, and bottom-water temperature having the strongest correlations with Axis 1. Stations in Klondike and Burger were generally well separated, with stations in Statoil overlapping with those in the other two study areas (Fig. 4a). By years, the CCA ordination demonstrates that later years for Klondike cluster to the left, with earlier years for Klondike spread to the right, although years for the other sites overlap substantially (Fig. 4b).

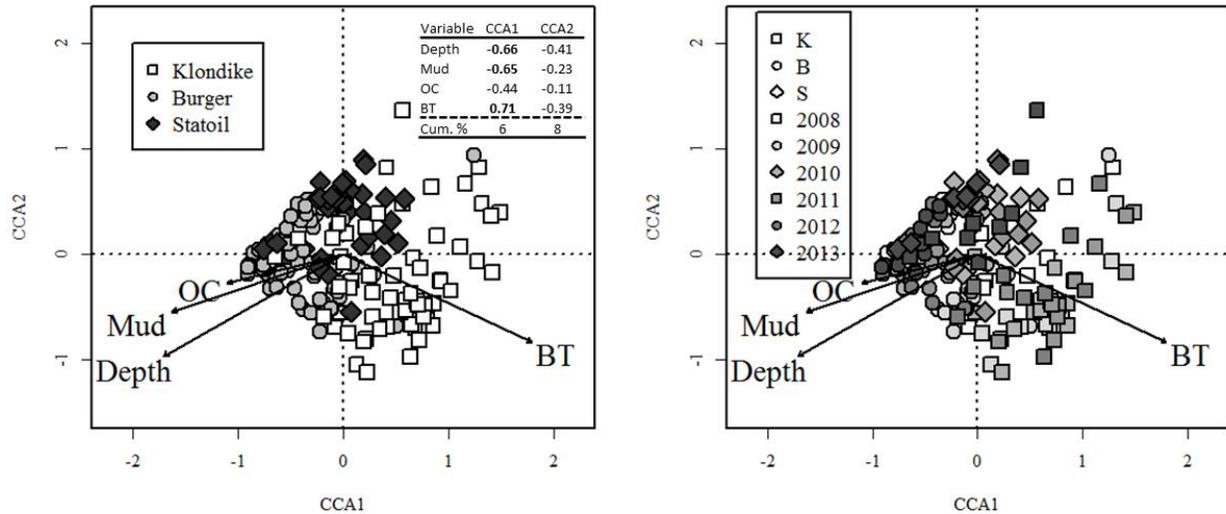


Figure 4. Canonical correspondence analysis of $\ln(X+1)$ -transformed benthic density data from 2008–2013 CSESP study areas. BT = bottom-water temperature and OC = sediment organic carbon.

Benthic density and richness are strongly correlated with the AO from 2008 to 2012 ($r = 0.85$ and $r = 0.78$, respectively). With the addition of the 2013 data, the correlation was much lower for density ($r = 0.15$; Fig 5) and richness ($r = -0.05$). Biomass had weak correlations with the AO ($r \sim 0.20$) for both periods. Variability in correlation coefficients can be very high with small sample sizes with the addition of a single data point, particularly when lag effects from temporal correlations persist among years. Shifts in correlation statistics, such as that for density and richness between 2012 and 2013, can be expected. The high correlations of density and richness with the AO 2008–2012 suggest a strong link between climate variability and benthic communities in the Chukchi Sea, although caution is warranted due to the small sample size, as indicated by the lower correlation values in 2013.

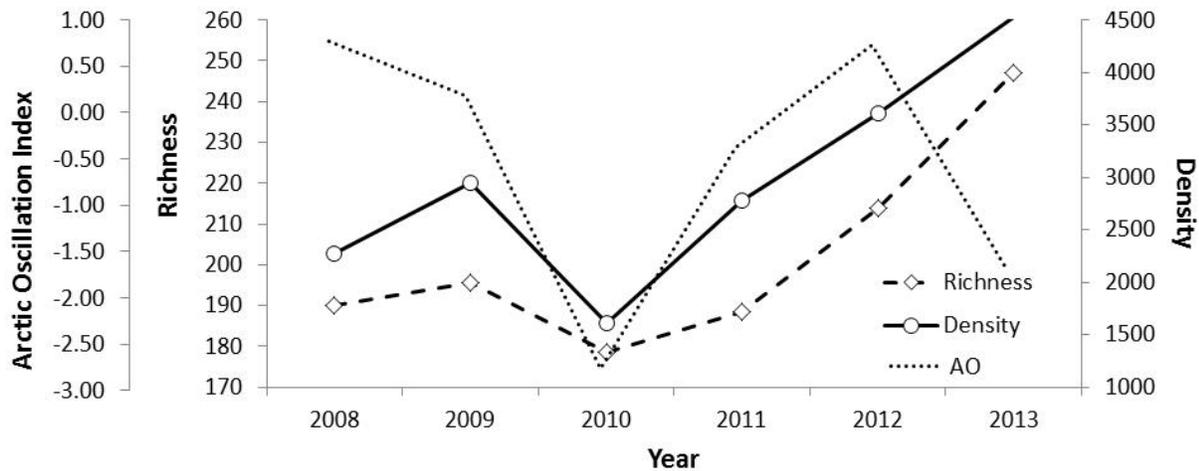


Figure 5. Average benthic density and richness and the winter Arctic Oscillation climate index (averaged from December to March for each winter) for 2008–2013.

Population dynamics of bivalves

Median lengths of *E. tenuis* in Klondike from 2008–2013 (medians ranged from a minimum of 2.45 to a maximum of 4.93 mm) were smaller than those found in Burger (3.68–8.01 mm) and Statoil (2.31–7.38 mm; Table 5). Median lengths declined in all study areas from 2008 to 2013 and for all study areas combined, median lengths declined over time from 6.55 mm in 2008 to 2.64 mm in 2013 (Fig. 6). (Maximum shell lengths are not presented here but Blanchard and Knowlton (2013) demonstrate no evidence for unusual declines in larger (older) age classes.) The biomass: density ratio for *E. tenuis* (B/D ratio; average biomass/average density X 100) provides insights into population-level variations as increases in the density of small organisms (in this case, increased density result in a decline in the B/D ratio. The declining B/D ratio from 2008 to 2013 correlates with the declining trend observed in the median lengths of *E. tenuis* over time, again suggesting increasing recruitment over the time period. Yearly median lengths of *E. tenuis* were strongly correlated with the prior years' winter AO ($r = 0.72$).

Median lengths of *Macoma* spp. in Klondike (4.81 and 3.93 mm) and Burger (4.62 and 3.39 mm) were larger than those found in Statoil (2.74 and 2.56 mm; Table 5). Across all sites in 2012, median length was 3.70 mm but lower in 2013 with a median of 3.10 mm. Median lengths were also significantly lower in 2013 at Klondike and Burger than in 2012 (Fig. 6).

Table 5. Median lengths and 95% confidence intervals (CI) for *Ennucula tenuis*. Med = median lengths and “–” = no data collected.

Year	Klondike		Burger		Statoil		All	
	Med	95% CI	Med	95% CI	Med	95% CI	Med	95% CI
2008	4.93	(4.36, 5.46)	7.39	(6.93, 7.83)	–	–	6.55	(6.15, 6.95)
2009	3.05	(2.89, 3.33)	8.01	(7.34, 8.63)	–	–	5.66	(5.16, 6.03)
2010	3.31	(3.12, 3.45)	7.32	(6.88, 7.88)	7.38	(6.12, 8.17)	5.34	(4.95, 5.79)
2011	3.07	(2.65, 3.92)	6.38	(5.13, 7.77)	2.70	(2.55, 2.89)	3.73	(3.40, 4.19)
2012	2.65	(2.57, 2.74)	4.78	(4.31, 5.00)	2.38	(2.25, 2.44)	3.08	(2.94, 3.19)
2013	2.45	(2.36, 2.53)	3.68	(3.38, 4.09)	2.31	(2.24, 2.38)	2.64	(2.52, 2.73)

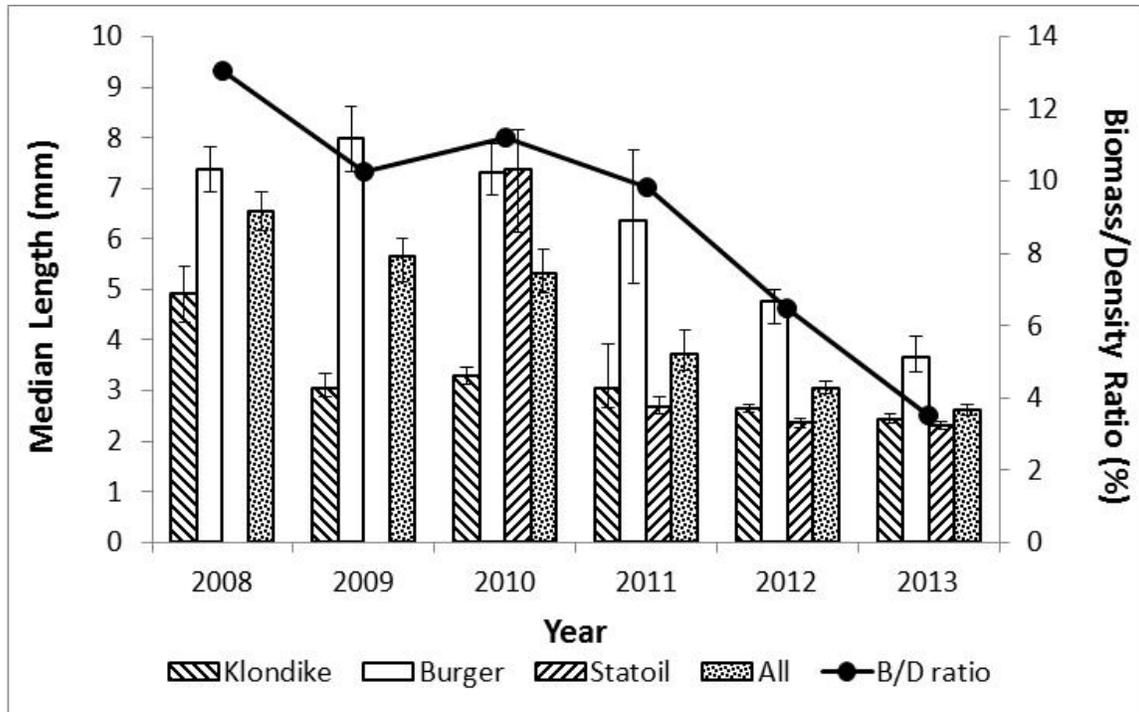


Figure 6. Median lengths of *Ennucula tenuis* with 95% confidence intervals and the biomass: density ratio for the Klondike, Burger, and Statoil study areas during the 2008–2013 CSESP study.

Table 6. Median lengths and 95% confidence intervals (CI) for *Macoma* spp. Med = median lengths and “–” = no data collected.

Year	Klondike		Burger		Statoil		All	
	Med	95% CI	Med	95% CI	Med	95% CI	Med	95% CI
2012	4.81	(4.52, 5.03)	4.62	(4.62, 4.44)	2.74	(2.61, 2.84)	3.70	(3.53, 3.85)
2013	3.93	(3.71, 4.23)	3.39	(3.15, 3.91)	2.56	(2.48, 2.66)	3.10	(2.96, 3.19)

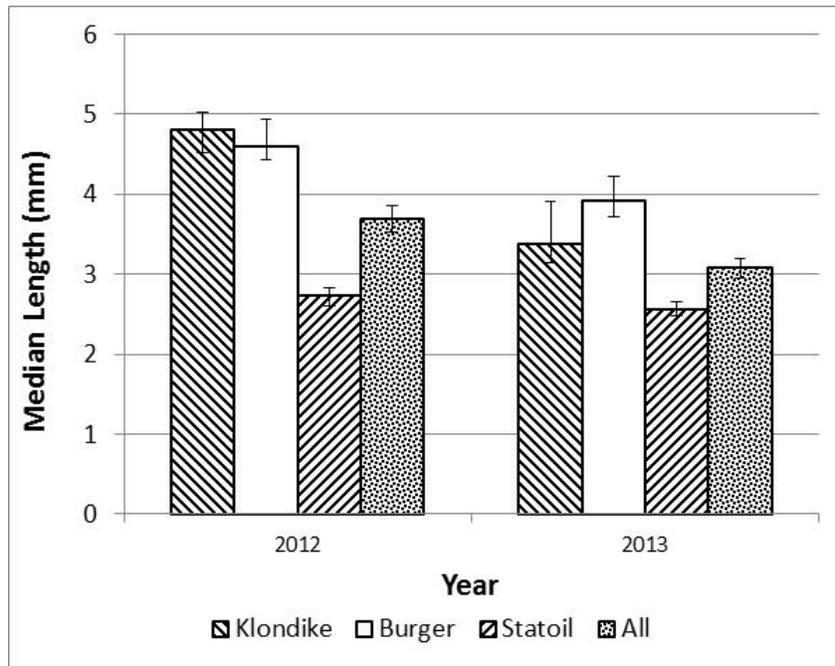


Figure 7. Median lengths of *Macoma* spp. with 95% confidence intervals for the Klondike, Burger, and Statoil study areas during the 2012–2013 CSESP study.

The CSESP Distributed Biological Observatory line

The CSESP Distributed Biological Observatory (DBO) line included 15 stations in 2013 encompassing a gradient from nearshore shallow waters to offshore waters in the Central Channel (Table 1). Sediment characteristics of stations on the DBO line changed with distance from shore (Fig. 8). The most eastern stations (DF001 and DF002; closest to shore and to the right in the plot) were in shallower water and had coarser substrates than did stations farther offshore (to the left in the plot); in contrast, the percent mud increased with water depth and

distance from shore. The average carbon-isotope ratio reflected the inshore–offshore gradient with lower values along the eastern end of the DBO line (Stations DF001–DF005; $\delta^{13}\text{C} = -24.6 \pm 0.65$; 95% CI) than among the Burger stations (BF005–BF021; $\delta^{13}\text{C} = -22.4 \pm 0.73$) or the western end (SF009–DF007; $\delta^{13}\text{C} = -22.0 \pm 1.03$).

Strong biological trends were apparent along the DBO line. Biomass and density demonstrated spatial trends with peak values occurring in the middle of the DBO line (Fig. 8). Peak biomass and density occurred at Station BF013 and declined toward either end of the DBO line; these values also increased at the most offshore stations (DF006 and DF007). Both biomass and density were low at the shallow, inshore stations (DF001 and DF002). The density of amphipods was proportionally greater inshore, declined in an offshore direction, and was lowest at Stations BF013 and DF007. The density of bivalves was proportionally higher offshore. The proportion of polychaete density was highest at the Burger stations and peaked at BF013. Amphipods comprised a small amount of benthic biomass, and bivalves were proportionally the most dominant macrofaunal group by biomass, ranging from about 10% of total biomass at Station DF001 to >60% at Stations DF002 and DF006. The biomass of echinoderms (especially ophiuroids) was highest at Burger stations, with maximal proportions of ~20% at Station BF009, whereas polychaetes constituted up to nearly 50% of biomass in offshore areas, with a maximal proportion recorded at Station SF014 (47%).

Characteristic taxa shifted from intertidal and disturbance-tolerant species (e.g., isopods and nematodes) at the most inshore stations DF001 and DF002 to high densities of amphipods comprising a spectrum of niches (*Ampelisca* spp., *Melita* spp., *Photis* spp., and *Protomedea* spp.) at stations DF003 to BF005 (Table 7). Deposit-feeding polychaetes and suspension-feeding bivalves were more numerous and had greater biomass at Burger stations, with a predominance of the polychaete *Maldane sarsi*. The bivalves *E. tenuis*, *Macoma* spp., and *N. pernula* were more numerous at the western end of the DBO line (station DF007). Overall, large bivalves, including *A. borealis*, *A. montagui*, *M. calcarea*, and *Y. hyperborea*, comprised the bulk of biomass at DBO stations with the brittle star *O. sarsi* and the peanut worm *G. margaritacea* also occurring with high biomass in some stations. Mean density and biomass were greater at station BF013 due to extremely high densities of *M. sarsi*.

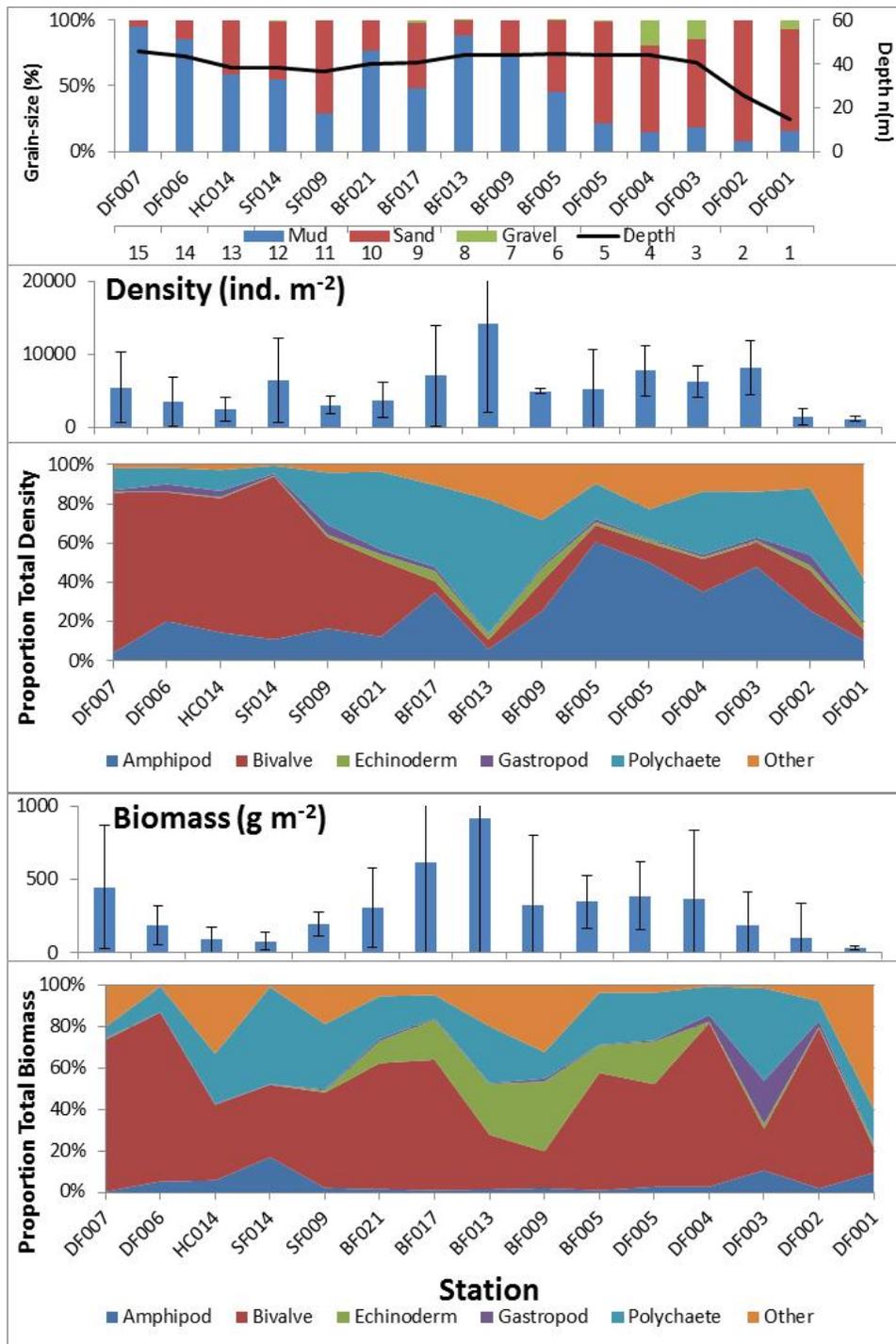


Figure 8. Environmental characteristics (grain-size (%) and water depth (m)), benthic macrofaunal density (ind. m⁻²), and proportion of total density for key taxonomic categories (%), biomass (g m⁻²), and proportion total biomass of key categories along the CESP Distributed Biological Observatory line, 2013. The position of stations along the horizontal axis reflects the spatial orientation of the DBO line with the most eastern station (DF001) on the right and the most western station (DF007) on the left.

Table 7. Ranking of dominant taxa (first three) by density (ind. m⁻²) and biomass (g m⁻²) for stations along the CSESP Distributed Biological Observatory line, 2013.

Station	Taxon	Density	Taxon	Biomass
DF001	<i>Tecticeps</i> spp.*	577	<i>Tecticeps</i> spp.*	17.34
	<i>Praxillella praetermissa</i>	53	<i>Ampelisca eschrichti</i>	2.44
	<i>Ampelisca eschrichti</i>	53	<i>Astarte borealis</i>	2.14
DF002	Nematoda	133	<i>Cyclocardia crassidens</i>	48.42
	<i>Ampelisca macrocephala</i>	100	<i>Serripes groenlandicus</i>	8.79
	<i>Mysella planata</i>	83	<i>Yoldia hyperborea</i>	7.76
DF003	<i>Ampelisca birulai</i>	730	<i>Nephtys caeca</i>	38.98
	<i>Ampelisca macrocephala</i>	673	<i>Limneria undata</i>	33.93
	Nematoda	557	<i>Ennucula tenuis</i>	17.01
DF004	<i>Ennucula tenuis</i>	607	<i>Astarte borealis</i>	200.89
	<i>Ampelisca macrocephala</i>	507	<i>Astarte montagui</i>	30.82
	<i>Rhodine bitorquata</i>	280	<i>Cyclocardia crebricostata</i>	19.07
DF005	<i>Protomedeia</i> spp.	2,440	<i>Astarte borealis</i>	128.22
	<i>Ektondiastylis robusta</i>	880	<i>Ophiura sarsi</i>	75.94
	<i>Ennucula tenuis</i>	533	<i>Astarte montagui</i>	34.75
BF005	<i>Photis</i> spp.	2,393	<i>Astarte borealis</i>	153.87
	<i>Paraphoxus</i> spp.	253	<i>Ophiura sarsi</i>	45.48
	<i>Ennucula tenuis</i>	247	<i>Axiothella catenata</i>	24.89
BF009	Ostracoda	923	<i>Ophiura sarsi</i>	108.06
	<i>Photis</i> spp.	613	<i>Golfingia margaritacea</i>	99.10
	<i>Ennucula tenuis</i>	530	<i>Ennucula tenuis</i>	23.91
BF013	<i>Maldane sarsi</i>	7,773	<i>Maldane sarsi</i>	105.12
	Ostracoda	1,707	<i>Ophiura sarsi</i>	99.28
	<i>Ennucula tenuis</i>	413	<i>Golfingia margaritacea</i>	77.53
BF017	<i>Paraphoxus</i> spp.	1,003	<i>Astarte borealis</i>	247.47
	<i>Ampharete</i> spp.	590	<i>Ophiura sarsi</i>	83.92
	Caprellidae	570	<i>Astarte montagui</i>	39.08
BF021	<i>Yoldia hyperborea</i>	870	<i>Yoldia hyperborea</i>	72.13
	<i>Paraphoxus</i> spp.	270	<i>Ennucula tenuis</i>	37.67
	<i>Terebellides</i> spp.	257	<i>Ophiura sarsi</i>	32.41
SF009	<i>Ennucula tenuis</i>	517	<i>Astarte borealis</i>	76.11
	<i>Macoma</i> spp.	420	<i>Golfingia margaritacea</i>	33.64
	<i>Byblis</i> spp. + <i>Protomedeia</i> spp.	127	<i>Axiothella catenata</i>	16.29
SF014	<i>Yoldia</i> spp.	1,867	<i>Melita</i> spp.	10.97
	<i>Macoma</i> spp.	1,627	<i>Yoldia</i> spp.	6.66
	<i>Ennucula tenuis</i>	1,313	<i>Terebellides stroemi</i>	6.43

* A mixture of *T. alascensis* (1 specimen) and *T. c.f. renoculis* (~ 99% of density).

Table 7. Continued.

Station	Taxon	Density	Taxon	Biomass
HC014	<i>Ennucula tenuis</i>	730	<i>Golfingia margaritacea</i>	28.97
	<i>Macoma</i> spp.	363	<i>Yoldia hyperborea</i>	19.53
	<i>Nuculana pernula</i>	297	<i>Axiothella catenata</i>	6.70
DF006	<i>Ennucula tenuis</i>	920	<i>Yoldia hyperborea</i>	87.31
	<i>Macoma</i> spp.	643	<i>Astarte borealis</i>	25.32
	<i>Nuculana pernula</i>	590	<i>Macoma calcarea</i>	14.23
DF007	<i>Nuculana pernula</i>	2,810	<i>Serripes groenlandicus</i>	123.92
	<i>Macoma</i> spp.	753	<i>Golfingia margaritacea</i>	87.10
	<i>Ennucula tenuis</i>	593	<i>Nuculana pernula</i>	86.93

DISCUSSION

Benthic fauna of Klondike, Burger, and Statoil are diverse, abundant, and representative of northern Pacific benthic assemblages found throughout the Bering and Chukchi Seas (Feder et al., 1994, 2005, 2007; Blanchard et al., 2011, 2013a, b). Fauna within the study area include all major groups found in Alaskan waters and are dominated by polychaetes and bivalves (Feder et al., 1994; Blanchard and Feder, 2014). The high density and biomass of the communities reflect strong pelagic-benthic coupling where large amounts of annual production reaches the benthos within the CSESP study area. Benthic communities in Burger had higher density and biomass than Klondike did and had higher richness than Statoil. Density and richness in Klondike were similar to that of Statoil, although biomass was lower in Klondike than in Statoil, which had substantial biomass in large clams. Bottom-water temperature, percent mud, and water depth were associated with community structure in the multivariate analysis, and there was a strong spatial separation of sites and a weaker separation by years.

Temporal variability of benthic macrofauna in the northeastern Chukchi Sea

Temporally, benthic communities demonstrated significant variations with biomass, density, and richness increasing over time 2008–2013. Fifty percent changes in average station biomass and density are common in benthic systems, with larger variations often indicative of environmental stress (see discussion in Blanchard et al., 2002). In the presence of stress, opportunistic fauna (such as capitellid and cirratulid polychaetes) become important components

of the community with high density and low biomass (Jewett et al., 1999; Blanchard and Feder, 2003, Blanchard et al., 2003, 2011). Fluctuations of benthic-community parameters in the present study are large ranging from 146% to 229% increases in biomass (maximum/minimum biomass*100) and 160% to 487% increases in density. Variations in richness were less with maximum richness representing ~150% of minimum richness among all study areas. In spite of the high temporal variability, the distributions of macrofauna appear spatially and temporally stable (Feder et al., 1994; Blanchard et al., 2013a; Blanchard and Feder 2014); opportunists did not replace other community members, dominants were persistent among years, and richness varied within reasonable bounds. The high variability thus, reflects ecosystem dynamics at high latitudes in the presence of ecosystem changes (Grebmeier et al., 2010).

Large-scale climatic variations appear to play a role in temporal changes of benthic communities through water circulation. In the North Pacific, the Pacific Decadal Oscillation (an index reflecting sea-water temperature co-varying with patterns in water circulation) is associated with long-term variations in benthic community density and richness in San Francisco Bay, California and Port Valdez, Alaska (Blanchard et al., 2010; Cloern et al., 2010). Coyle et al. (2007) also noted an association between benthic community characteristics and the AO for macrofauna in the eastern Bering Sea with higher biomass in the negative phase of the AO. Likewise, the strong correlations between the Arctic Oscillation (AO) Index and benthic-community characteristics for the first 5 years of the present study suggest potentially strong environmental influences. Negative AO values (high atmospheric pressure at sea level) in winter are associated with strengthened circulation of the Beaufort Gyre and stormy weather in lower latitudes (Thompson and Wallace, 1998; Stroeve et al., 2011). The lack of correlation with the addition of the 6th year in the present study is expected; correlations are quite variable with small sample sizes and lag effects (the carryover of a trend from prior years into the present) may be present. Nevertheless, the increasing density and richness over time in the CSESP study areas suggest that increased circulation across the Chukchi Shelf in winter may be dispersing and sustaining new recruits resulting in the observed increased density and richness, as suggested for the North Pacific. Declines in median shell lengths of *Ennucula tenuis* indicate increased numbers of juveniles in the population, also suggesting the presence of strong temporal changes in environmental conditions.

It is not yet understood how the AO might influence benthic communities in the Chukchi Sea, but climate variations in the North Pacific are associated with ecosystem-wide effects that influence the density and richness of benthic communities (Blanchard et al., 2010; Cloern et al., 2010). The hypothesis that covariance of benthic-community parameters with the AO is caused by interannual variations in water circulation provides a direction for future research, since the actual pathways driving the relationship remain to be determined.

Median lengths of *E. tenuis* varied by study area and declined over time. For each year, median lengths of *E. tenuis* in the Klondike study area were smaller than median lengths of *E. tenuis* in Burger and Statoil. The lower medians reflect a smaller proportion of large bivalves in Klondike and, in association with the very limited occurrences of larger lengths in Klondike, suggest lower survival of this clam in Klondike than in Burger or Statoil (Blanchard and Knowlton, 2013). In the present study, the decline in median shell lengths continued through 2013 with an associated decline in the biomass/density (B/D) ratio. Smaller B/D ratios indicate the presence of more small, lighter animals whereas greater B/D ratio values indicate the presence of larger animals. Thus, the declining shell lengths and B/D ratios demonstrate a shift towards smaller bivalves. Blanchard and Knowlton (2013) demonstrated no decline in maximum shell lengths or unusual loss of larger bivalves (adults), indicating increased proportions of recruiting individuals. The correlation of median shell length of all sites with the AO lagged by one year (the prior year's winter AO) suggests oceanographic drivers for the dynamics of the *E. tenuis* populations in the CSESP study area. Use of a lagged AO value is biologically reasonable in this case because, if spawning occurs in the spring and summer, it probably takes one year for many bivalves to grow large enough to be retained on a 1.0-mm-mesh sieve.

The CSESP Distributed Biological Observatory line

A strong association of the faunal gradient with sediment grain-size and water depth from inshore to offshore was expected in 2012, the first year of the CSESP Distributed Biological Observatory (DBO) line, but the observed trends were less clear than anticipated in that year (Blanchard and Knowlton, 2013). In 2013, sampling of the full CSESP DBO line (15 stations) provided greater insights into biological changes along the environmental gradients captured by this transect. Sediment grain-size decreased as water depth increased with greater distance

offshore. The lower $\delta^{13}\text{C}$ values in the eastern portion of the CESP DBO line indicate terrestrial carbon sources near the coast with marine sources offshore. Stations DF001–DF003 are under the warmer, less saline Alaska Coastal Water (ACW), whereas stations DF004–DF007 are under the more saline, colder, and nutrient-enriched Bering Sea Water (BSW; Fig 9).

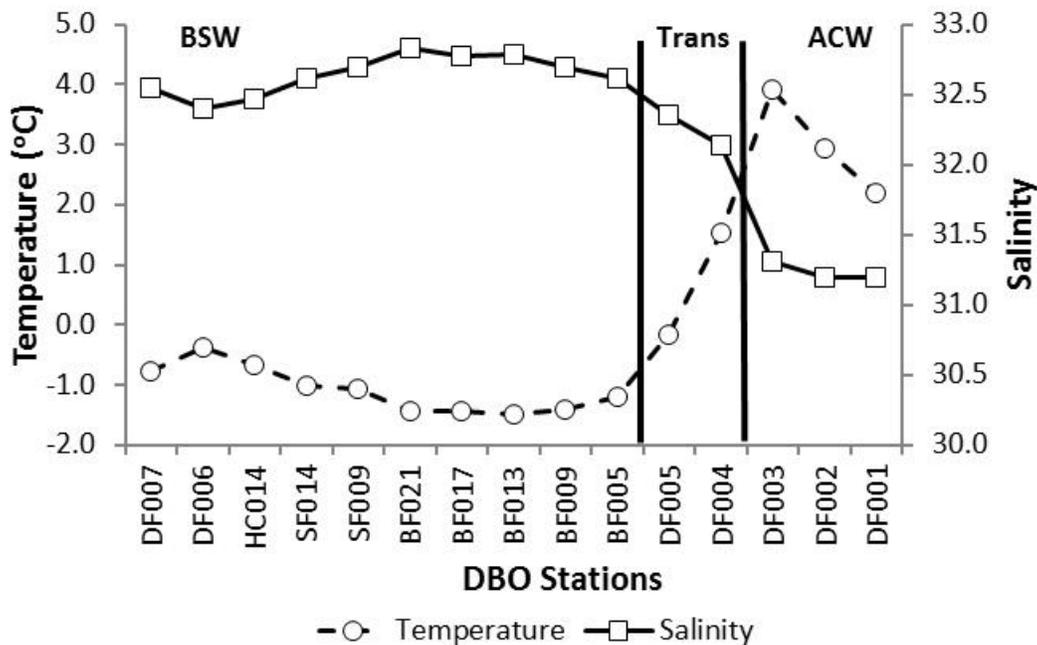


Figure 9. Bottom-water temperature and salinity along the CESP Distributed Biological Observatory Line, 2013. ACW = Alaska Coastal Water; BSW = Bering Sea Water; Trans = Transitional Water. The position of stations along the horizontal axis reflects the spatial orientation of the DBO line with the most eastern station (DF001) on the right and the most western station (DF007) on the left.

Spatial gradients in benthic community characteristics reflected distance offshore and water depth. Biomass and density were low at the inshore stations and increased to peak values at station BF013 in the middle of the DBO line. Biomass and density declined to the west but with increased values at the west end of the DBO line. Characteristic fauna shifted from crustaceans inshore to polychaetes and bivalves offshore with large bivalves having the greatest biomass at most stations, although 3 stations followed different biomass patterns. Nematodes are poorly represented in grab samples and historically have been excluded from macrofaunal data sets in the Chukchi Sea (see Methods section; Feder et al., 1994, 2007), but data exploration in

the present study led to their inclusion because of their ecological importance in the density ranking. As common responders to physical disturbance and their possible roles as detritivores (Jensen, 1987), the relatively high proportion of total density comprised by nematodes at stations DF002 and DF003 suggests different dynamics at the nearshore sites.

The influence of advected nutrients and particulate organic carbon (POC) in the BSW on secondary productivity in sediments was noted by Feder et al. (1994). Grebmeier et al. (1988) proposed that lower benthic productivity and biomass occurred under the ACW (with lower nutrient quality) than under the BSW (with higher quality nutrients), although Feder et al. (1994, 2005, 2007) found this pattern to be inconsistent in some areas. Feder et al. (1994, 2007) suggested that mixing of water masses and northward advection of carbon may subsidize areas of high productivity in the Chukchi Sea. The low biomass and density nearshore in the present study reflect covariance with water depth and greater dynamics (exposure to storms and disturbance from ice gouging) in shallow arctic sediments. Although biomass and density were low at stations SF001 and DF002, values at stations DF003, DF004, and DF005 were comparable to other stations along the CSESP DBO line and under BSW, with the exception of BF013 which has exceptionally high biomass and density. Support for the hypothesis that benthic biomass is lower under ACW is not fully supported by the present study; increased physical dynamics in shallower water depth provide a more reasonable explanation for biomass and density patterns in this case (see also Hunt et al., 2013). Transitioning to the Burger study area, temperature and salinity values shift from those characteristic of the ACW (warmer and fresher) to those of BSW (cold, saline waters; Fig. 9). Biomass and density values increase in Burger and then decline again at Statoil, suggesting that the oceanographic characteristics that define communities at Burger (stagnant water increasing POC flux to the bottom; Blanchard et al., 2013a) do not occur at Statoil. At station DF007, however, biomass and density again increase and dominance by bivalves suggest increased suspension feeding activity pointing towards increased deposition/water flow in the Central Channel.

Finding the intertidal isopods *Tecticeps alascensis* and *T. c.f. renoculis* as the most numerous taxon at station DF001 is a curiosity. Very little ecological information is recorded for *T. renoculis* although more is known for *T. alascensis* in the area. The depth range for *T. alascensis* (found from 20m to 200m; Richardson, 1905; Carlton, 2007) is greater than that for *T. renoculis* (found to 20m; Richardson, 1909), although too little distribution information is

available to *T. renoculis* to conclude a limitation to shallow subtidal sites. Diet studies of *T. alascensis* determined that it was a scavenging predator, colonizing gray whale feeding pits along with ampeliscid amphipods (Thomson and Martin, 1984). The ecology of *Tecticeps renoculis* has similarities to *T. convexus* from southern waters of the U.S. coastline. *Tecticeps convexus* is intertidal to shallow subtidal and found on sands where it can blend in. *Tecticeps convexus* curls up and protrudes its sharp uropods into a defensive position when threatened, as does *T. renoculis* (Richardson, 1909; Pavlovskii, 1955; Carlton, 2007). *Tecticeps renoculis* is known as a cold-water isopod from the Sea of Okhotsk (~ Latitude 48.725° N), but few published records are available, so its eastward distribution is unknown. Morphometrically, *T. c.f. renoculis* from the DBO line fits the original description by Richardson (1909) but the absence of observations for this species between the Sea of Okhotsk and the northeastern Chukchi Sea is problematic. *Tecticeps c.f. renoculis* in the Chukchi Sea thus, represents either a significant range extension or a previously unrecognized species.

The extension of southern intertidal organisms into the northeastern Chukchi Sea is a result of the northward transport of benthic fauna from the North Pacific and is very common. Many species occur across broad temperature ranges along the North Pacific coasts and into the Arctic including the mussel *Mytilus trossulus* and the barnacle *Semibalanus balanoides*. *Tecticeps alascensis* was noted by Thomson and Martin (1984) and Feder et al. (2007) in the southeastern Chukchi Sea and more recently in the northeastern Chukchi Sea by the Alaska Monitoring and Assessment Program (M. K. Hoberg, personal observations). Since the genera is known from the area, the occurrence of *Tecticeps c.f. renoculis* in the study area, and absence of records otherwise, reflects the lack of sampling effort for this isopod's preferred habitat, rather than a new species introduction. Since species in the study area are advected north from southern macrofauna populations, this isopod must have a much greater geographic distribution than currently described.

In contrast to the 2013 CSESP DBO line, prior sampling nearshore at marine-mammal feeding areas in the Chukchi Sea indicated high benthic biomass and density, as also observed adjacent to Barrow Canyon (Feder et al., 1994; Blanchard and Feder, 2014). The effect of increased water flow into marine canyons is to increase the flow of POC past suspension-feeders, enhancing benthic productivity, even if the benthic communities lie under otherwise carbon-depleted waters, such as under the ACW in Barrow Canyon and its proximity (Feder et al., 1994;

De Leo et al., 2010; Schonberg et al., 2014). Feder et al. (1994, 2005, 2007) also identified several locations where biomass and/or density were high underneath the ACW; all were associated with variations in water circulation (e.g., polynyas, convergences, canyons; Blanchard and Feder, 2014). At least some of these areas of high biomass under the ACW are associated with key vertebrate resources, including eider ducks and gray whales.

Spatial heterogeneity of benthic habitats in the northeastern Chukchi Sea is high among stations on the CSESP DBO line. Benthic habitats in the more nearshore habitats investigated by the CSESP are very heterogeneous in both sediment composition and depth. Sediments generally become finer in marine systems with distance offshore and greater water depth, and with the exception of the Burger study area, this general pattern does occur in the Chukchi Sea (Feder et al., 1994). Nearshore, the low biomass and density of amphipods in the CSESP DBO station DF003, which is in close proximity to the CSESP mammal-feeding sampling locations, reflects the high spatial variability of habitats and large changes in environmental conditions. Against the pattern of the general increase in fine sediments with distance offshore, the offshore habitats are also highly variable with sharply changing habitats among the three study areas and highly variable benthic communities.

Links with CSESP Investigations:

Physical oceanographic studies from 2008–2013 provide evidence for the topographic control of water circulation that then plays a defining role in the characteristics of benthic communities. A portion of the Burger study area lays in a trough (a submerged watershed) draining toward Barrow Canyon to the south of Hanna Shoal with Klondike stations to the southwest. Weingartner et al. (2013) demonstrated colder water and higher salinity in the trough in Burger, reflecting the persistence of winter water. The complexity of water circulation around Hanna Shoal is not fully known (see Faulkner et al., 1994; Weingartner et al., 2005, 2013), but the stagnant water flow caused by the interaction between seafloor topography and circulation appears to be ecologically significant as it is the site of high bivalve biomass and intensive feeding by walrus (Feder et al., 1994; Blanchard et al., 2013a, b). The persistent cold water pool at Burger may have direct ecological effects through influences on biological processes and distributions of benthic and pelagic fauna, in addition to indirect effects from stagnant water flow. Oceanographic surveys continue to investigate spatial and temporal variations in water

flow and will provide further insights into how interactions between geomorphology and currents affect differences in available organic carbon (food) sources and local deposition (Weingartner et al., 2013).

The mismatch between the development of the zooplankton community and the phytoplankton bloom, in association with the low density of zooplankton in the Chukchi Sea, results in a large flux of unconsumed primary production to the benthos, enhancing benthic community growth (Grebmeier et al., 1988; Grebmeier et al., 2006). The timing of the phytoplankton bloom is controlled by melting sea ice that stratifies the water-column, creating the necessary conditions for primary production (Questel et al., 2013). Recent oceanographic variations driving large shifts in seasonal production and zooplankton community characteristics would be expected to influence benthic communities as well (Blanchard et al., 2013 b; Questel et al., 2013). The role of production by phytoplankton within sea-ice in the Chukchi Sea is unknown but may be a significant source of carbon for benthic fauna, although isotopic studies point to pelagic producers as the primary food sources (Tu, 2013). Advection of particulate organic carbon from the rich blooms of the northern Bering and southern Chukchi Seas is thought to contribute to maintenance of high benthic biomass in the northeastern Chukchi Sea as well (Feder et al., 1994; Grebmeier et al., 2006). As a result of the tight linkage of benthic community biomass to seasonal production, variations in oceanographic conditions shifting the timing of biological processes that control pelagic-benthic coupling will be crucial for maintenance and long-term variability of benthic communities.

Investigations of fish ecology during the 2009–2010 CSESP studies demonstrated the high diversity of benthic organisms preyed upon by benthic fishes (Norcross et al., 2013; see also Barber et al., 1997). Diets of five fish species included macrofaunal organisms, primarily polychaete worms (Norcross et al., 2013; see also Coyle et al., 1997; Green and Mitchell, 1997). High densities of benthic fishes in summer do not, however, overlap with the area of high macrobenthic biomass in the CSESP study area, possibly due to habitat preferences (e.g., sediment grain-size and water temperature) of fishes (Day et al., 2013; Norcross et al., 2013).

Collectively, walrus may consume up to ~3 million tons of benthic biomass and disturb sediments over thousands of kilometers per year from the Bering to the northeastern Chukchi Sea (Ray et al., 2006; Krupnik and Ray, 2007). Fay (1982) and Sheffield et al. (2001) demonstrated that walrus in the Bering and Chukchi Seas feed on a wide array of organisms, including soft-

bodied benthic worms, all of which are components of the benthic community in the CSESP study area. Likewise, bearded seals also feed on an array of megafaunal and larger macrofaunal organisms and fishes as well, like those found in the CSESP study area (Lowry et al., 1980). The areas of high overall benthic biomass and, more specifically, bivalve biomass in the CSESP study area coincide with areas of high feeding activity by walrus in the summer and a substantial part of the at-sea distribution of bearded seals (Aerts et al., 2013; Blanchard and Knowlton, 2013; Hannay et al., 2013, Schonberg et al., 2014). Although biomass resources necessary to support benthic-feeding predators in the offshore Chukchi Sea have not been discovered, Blanchard and Knowlton (2012) found that the biomass of *Macoma calcaria* nearly doubled the bivalve biomass at some stations, with the biomass of *G. margaritacea* increasing up to seven-fold when sampling to 26cm depth in the sediments.

Gray whales feed primarily in the northern Bering and southern Chukchi seas, but some also feed in the northeastern Chukchi and western Beaufort seas (Moore and Clark, 1990; Feder et al., 1994; Highsmith et al., 2006). Gray whales suck sediment into their mouths to capture amphipods and other macrofauna and favor sediments with dense beds of ampeliscid amphipods (Highsmith and Coyle, 1992; Nelson et al., 1994; Bluhm and Gradinger, 2008). Although amphipods are an important component of the macrofaunal community within the present study area, their numbers were lower in the CSESP study area than in areas where gray whales feed (Highsmith and Coyle, 1992; Nelson et al., 1994; Bluhm and Gradinger, 2008; Blanchard et al., 2013a; Schonberg et al., 2014), suggesting that the feeding habitat farther offshore is suboptimal for gray whales. Biomass and densities of amphipods in the CSESP DBO line were also too low to support gray whale feeding, although much higher densities occur nearby (Feder et al., 1994; Blanchard et al., 2013a; Blanchard and Feder, 2014).

CONCLUSIONS

As in prior years, benthic communities in the Klondike, Burger, and Statoil study areas reflect the high quantity of annual primary production reaching the benthos in the relatively shallow water of the Chukchi Sea. The macrofaunal assemblages of 2008–2013 were characteristic of species found throughout the Bering and Chukchi seas and were similar to those found in 1986 in the northeastern Chukchi Sea by Feder et al. (1994). Although the average

density of macrofauna was higher in Burger than in Klondike and Statoil, the assemblages at all study areas were generally similar (they contained most of the same species), and community variations reflect local environmental gradients co-varying with bottom-water temperature, sediment grain-size characteristics, and water depths (Blanchard and Knowlton, 2012, 2013). Spatial drivers of benthic community characteristics appear to be related largely to water circulation and larger oceanographic characteristics of the area.

Significant increases in biomass, density, and richness reflect an ecosystem in flux at the northern edge of the Chukchi Shelf. Temporal variations in benthic communities may be associated with the water circulation via ecosystem-level variations related to the Arctic Oscillation. Water circulation variations, stratification, and shifts in flow patterns can have significant and large effects on benthic fauna, including anoxia and loss of benthic communities under low flow conditions. The water circulation changes may control to some extent, larval survival and recruitment. Additionally, macrofauna communities in ecosystems with such large interannual variability in physical and biological processes as the Chukchi Sea can be expected to also demonstrate high variability in unexpected ways. For example, while patches of anoxic sediments can always be expected in benthic systems, reduced water flow can force large reductions in benthic communities with cascading effects to higher trophic levels, especially after a large build-up of benthic communities like in the present study. Long-term studies relying on repeated measurements at the same locations provide the means for understanding ecosystem variability, and the importance of long-term sampling becomes increasingly important in areas of high variability and of ecological importance.

High spatial heterogeneity in environmental and biological characteristics was apparent along the CSESP DBO line in 2013. The shift from terrestrial carbon in nearshore waters to marine sources offshore and the transition from disturbance-tolerant intertidal organisms to amphipods to bivalves in the western end of the DBO line covaried with sediment grain-size and water depth. Effects of water mass characteristics (ACW v. BSW) were unclear as benthic biomass and diversity of stations under ACW were comparable to those under BSW, except for the shallowest stations and BF013 which appears to be a site with high carbon deposition. Stations DF001 and DF002 were exposed to greater physical dynamics due to their very shallow water depths (~ 15m). The high biomass and density of benthic amphipods found in nearby sediments were not apparent in the DBO line reflecting the high environmental variability and

dynamics of the nearshore region. Earlier studies have assumed that the northeastern Chukchi Sea is oceanographically smooth with comparatively smooth changes in macrofauna communities. In contrast, the 2008–2013 CSESP demonstrates high spatial and temporal variability of environmental and biological characteristics.

Interactions between water circulation, climatic and physical controls, and benthic communities are largely unknown, but must be understood to understand future changes in the study area. At the regional scale, northward advected larvae provide the basis for benthic populations and are critical for the ecology of the northeastern Chukchi Sea. At smaller scales, local variations in topography and water circulation increase the spatial variability of communities. Additionally, greater variance requires greater sampling efforts to maintain a constant statistical power. More importantly, sampling efforts must match the scales of gradients to describe environmental and biological interactions adequately (Feder et al., 1994; Blanchard and Feder, 2014). The limited sampling of the DBO line in 2012 was not adequate to fully describe the joint gradients among environmental features, oceanographic characteristics, and benthic fauna, whereas sampling in 2013 was. It appears then, that the spacing of sampling points in the DBO line in 2013 is a minimum for demonstrating environmental/biological interactions and ecologically-relevant gradients in the northeastern Chukchi Sea.

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APPENDIX I

PRELIMINARY LIST OF MACROFAUNAL TAXA COLLECTED, 2008 – 2013

PORIFERA

CNIDARIA

Hydrozoa

Anthozoa

Actiniidae

Edwardsiidae

Edwardsia spp.

Halcampoididae

Haloclavidae

Halcampidae

Halcompa crypta

Nephtheidae

Gersemia rubiformis

NEMERTEA

ANNELIDA

POLYCHAETA

Polynoidae

Bylgides sarsi

Bylgides promamme

Arcteobia anticostiensis

Enipo canadensis

Enipo chuckchi

Enipo gracilis

Enipo torelli

Eunoe spp.

Eunoe nodosa

Eunoe oerstedii

Eunoe clarki

Gattyana spp.

Gattyana amondseni

Gattyana ciliata

Gattyana cirrhosa

Harmothoe spp.

Harmothoe beringiana

Harmothoe extenuata

Harmothoe imbricata

Hesperonoe adventor

Parahalosydna krassini

Pholoidae/Sigalionidae

Pholoe minuta

Phyllodocidae

Phyllodoce groenlandica

Eteone spp.

Eteone flava

Eteone longa

Eteone pacifica

Eteone spetsbergensis

Hesionidae

Nereimya aphroditoides

Syllidae

Proceraea cornuta

Syllis spp.

Typosyllis spp.

Typosyllis alternata
Typosyllis pigmentata
Exogone spp.
Exogone naidina

Nephtyidae

Nephtys spp.
Nephtys ciliata
Nephtys caeca
Nephtys punctata
Nephtys longosetosa
Nephtys paradoxa

Sphaerodoridae

Sphaerodorum papillifer
Sphaerodoropsis spp.
Sphaerodoropsis minuta
Sphaerodoropsis sphaerulifer

Glyceridae

Glycera capitata

Goniadidae

Glycinde wireni

Onuphidae

Paradiopatra parva

Eunicidae

Lumbrineridae

Scoletoma spp.
Scoletoma fragilis

Arabellidae

Drilonereis spp.

Dorvilleidae

Orbiniidae

Scoloplos armiger
Leitoscoloplos pugettensis

Paraonidae

Aricidea spp.
Levinsenia gracilis

Apistobranchidae

Apistobranchus ornatus

Spionidae

Dipolydora spp.
Prionospio steenstrupi
Spio cirrifera
Spiophanes bombyx
Pygospio elegans
Marenzelleria wireni

Magelonidae

Magelona longicornis

Trochochaetidae

Trochochaeta spp.
Trochochaeta carica
Trochochaeta multisetosa

Chaetopteridae

Phyllochaetopterus spp.

Cirratulidae

Cirratulus cirratus
Chaetozone setosa
 Cossuridae
Cossura pygodactylata
 Flabelligeridae
Brada spp.
Brada inhabilis
Brada villosa
Brada nuda
Flabelligera spp.
Flabelligera affinis
Flabelligera mastigophora
Diplocirrus longisetosus
 Scalibregmatidae
Scalibregma californicum
Scalibregma inflatum
 Opheliidae
Travisia forbesi
Travisia pupa
Ophelia limacina
Ophelina groenlandica
Ophelina acuminata
 Sternaspidae
Sternaspis scutata
 Capitellidae
Capitella capitata
Heteromastus filiformis
Notomastus spp.
Notomastus latericeus
Mediomastus spp.
Barantolla americana
 Maldanidae
Maldane sarsi
Nicomache spp.
Nicomache lumbricalis
Petaloproctus spp.
Petaloproctus borealis
Petaloproctus tenuis
Axiothella catenata
Praxillella gracilis
Praxillella praetermissa
Rhodine spp.
Rhodine bitorquata
Rhodine loveni
 Oweniidae
Owenia fusiformis
Myriochele heeri
Galathowenia oculata
 Sabellariidae
Idanthysus saxicavus
 Pectinariidae
Pectinaria spp.
Pectinaria granulata

Pectinaria hyperborea

Ampharetidae

Amage spp.

Ampharete spp.

Ampharete goesi

Ampharete acutifrons

Ampharete crassiseta

Ampharete finmarchica

Ampharete vega

Lysippe labiata

Asabellides sibirica

Terebellidae

Amphitrite cirrata

Neoamphitrite groenlandica

Nicolea zostericola

Thelepus spp.

Thelepus cincinnatus

Thelepus setosus

Artacama proboscidea

Lanassa nordenskioldi

Lanassa venusta venusta

Lysilla loveni

Axionice maculata

Laphania boeckii

Proclea spp.

Proclea emmi

Proclea graffii

Trichobranchidae

Terebellides spp.

Terebellides kobei

Terebellides reishi

Terebellides stroemi

Trichobranchus glacialis

Sabellidae

Chone spp.

Chone infundibuliformes

Chone duneri

Chone magna

Chone mollis

Euchone spp.

Euchone analis

Euchone incolor

Bispira crassicornis

Laonome kroeyeri

Serpulidae

OLIGOCHAETA

MOLLUSCA

GASTROPODA

Lepetidae

Lepeta caeca

Trochidae

Margarites spp.

Margarites giganteus

Margarites costalis
Solariella spp.
Solariella obscura
Solariella varicosa

Turbinidae
Moelleria costulata

Rissoidae
Alvania spp. (possibly *Frigidoalvania cruenta*)
Cingula spp.

Turritellidae
Tachyrhynchus spp.
Tachyrhynchus erosus
Tachyrhynchus reticulatis

Trichotropidae
Trichotropis spp.
Ariadnaria borealis
Neophinoe kroyeri
Neophinoe coronata

Velutinidae
Limneria undata

Capulidae

Naticidae
Cryptonatica affinis
Lunatia pallida

Muricidae
Boreotrophon spp.
Boreotrophon clathratus
Boreotrophon truncatus
Nodulotrophon coronatus

Buccinidae
Aulacofusus brevicauda
Aulacofusus herendeenii
Buccinum spp.
Buccinum plectrum
Buccinum polare
Colus spp.
Liomesus spp.
Neptunea spp.
Neptunea ventricosa
Neptunea communis
Neptunea borealis
Neptunea heros
Plicifusus kroeyeri
Pyrulofusus deformis
Retifusus roseus
Volutopsius spp.

Cancellariidae
Admete spp.
Admete solida
Admete viridula

Conidae (Mangelidae)
Oenopota spp.
Oenopota elegans

Oenopota excurvatas
Oenopota impressa
Oenopota pyramidilis
Obesotoma simplex
Propebela spp.
Propebela turricula
Propebela arctica
Propebela nobilis
Curtitoma incisula
Curtitoma novajasemljensis

Pyramidellidae

Odostomia spp.

Cylichnidae

Cylichna spp.
Cylichna occulta
Cylichna alba

Diaphanidae

Diaphana minuta

Haminoeidae

Haminoea vesicula

Retusidae

Retusa obtusa

NUDIBRANCHIA

OPISTHOBRANCHIA

POLYPLACOPHORA

Leptochitonidae

Leptochiton spp.

Ischnochitonidae

Stenosemus albus

Mopaliidae

Amicula vestita

BIVALVIA

Nuculidae

Ennucula tenuis
Nuculana spp.
Nuculana pernula
Nuculana minuta
Portlandia spp.

Yoldiidae

Yoldia spp.
Yoldia hyperborea
Yoldia myalis
Yoldia seminuda

Mytilidae

Crenella decussata
Musculus spp.
Musculus niger
Musculus discors
Musculus glacialis

Pectinidae

Chlamys behringiana

Lucinidae

Parvilucina tenuisculpta

Thyasiridae
Adontorhina cyclia
Axinopsida serricata
Thyasira flexuosa

Lasaeidae
Neaeromya compressa
Mysella planata
Kurtiella tumida

Carditidae
Cyclocardia spp.
Cyclocardia crebricostata
Cyclocardia crassidens
Cyclocardia ovata

Astartidae
Astarte spp.
Astarte montagui
Astarte borealis

Cardiidae
Ciliatocardium ciliatum ciliatum
Serripes spp.
Serripes groenlandicus
Serripes laperousii

Tellinidae
Macoma spp.
Macoma calcarea
Macoma brota
Macoma moesta

Veneridae
Liocyma fluctuosa

Myidae
Mya spp.
Mya arenaria
Mya psuedoarenaria
Mya truncata

Hiatellidae
Hiatella arctica

Pandoridae
Pandora glacialis

Lyonsiidae
Lyonsia arenosa

Periplomatidae
Periploma aleuticum

Thraciidae
Thracia spp.
Lampeia adamsi

ARTHROPODA

PYCNOGONIDA

CRUSTACEA

OSTRACODA

CUMACEA

Lampropidae

Lamprops quadriplicata

Leuconidae

Leucon spp.
Eudorella spp.
Eudorella emarginata
Eudorella groenlandica
Eudorellopsis spp.
Eudorellopsis integra
Eudorellopsis biplicata

Diastylidae

Diastylis spp.
Diastylis bidentata
Diastylis paraspinulosa
Ektondiastylis robusta

Nannastacidae

Campylaspis spp.
Campylaspis papillata
Cumella spp.

TANAIDACEA

ISOPODA

Antarcturidae

Pleuoprion murdochi

Idoteidae

Synidotea spp.
Synidotea bicuspidata
Synidotea muricata

Tecticepidae

Tecticeps spp.
Tecticeps alascensis
Tecticeps c.f. *renoculis*

Munnidae

Munna spp.

AMPHIPODA

Odiidae

Odius spp.
Odius carinatus

Ampeliscidae

Ampelisca spp.
Ampelisca macrocephala
Ampelisca birulai
Ampelisca eschrichti
Byblis spp.
Byblis gaimardi
Byblis robusta
Byblis frigidis
Byblis pearcyi
Byblis breviramas
Haploops laevis

Argissidae

Argissa hamatipes

Corophiidae

Crassikorophium spp.
Crassikorophium crassicorne

Ischyroceridae

Erichthonius spp.
 Dexaminidae
 Guernea nordenskioldi
 Eusiridae
 Eusirus cuspidatus
 Pontogeneia spp.
 Rhachotropis spp.
 Rhachotropis oculata
 Gammaridae
 Maera loveni
 Melita spp.
 Melita dentata
 Uniciolidae
 Uniciola leucopis
 Haustoriidae
 Eohaustorius eous
 Pontoporeiidae
 Monoporeia affinis
 Pontoporeia femorata
 Priscillina armata
 Isaeidae
 Photis spp.
 Photis vinogradovi
 Protomedeia spp.
 Ischyroceridae
 Ischyrocerus spp.
 Lysianassidae
 Anonyx spp.
 Hippomedon spp.
 Guernea nordenskioldi
 Orchomene spp.
 Paratryphosites abyssii
 Uristidae
 Centromedon spp.
 Melphidippidae
 Oedicerotidae
 Aceroides latipes
 Bathymedon spp.
 Monoculodes spp.
 Westwoodilla caecula
 Epimeriidae
 Paramphithoe polyacantha
 Phoxocephalidae
 Harpiniopsis spp.
 Harpiniopsis kobjakovae
 Harpiniopsis gurjanovae
 Paraphoxus spp.
 Paraphoxus oculatus
 Grandifoxus spp.
 Grandifoxus acanthinus
 Grandifoxus vulpinus
 Grandifoxus nasuta
 Pleustidae

Pleustes panoplus
Pleustomesus spp.
Pleustomesus medius
Podoceridae
Dyopedos arcticus
Stenothoidae
Synopiidae
Syrrhoe crenulata
Tiron bioculata
Caprellidae
BRACHYURA
Pinnotheridae
Pinnixa spp.
SIPUNCULA
Golfingiidae
Golfingia margaritacea
Phascoliidae
Phascolion strombus
ECHIURA
Echiuridae
Echiurus echiurus alaskanus
CEPHALORHYNCHA
PRIAPULIDAE
Priapulus caudatus
BRACHIOPODA
ECHINODERMATA
Holothuroidea
Myriotrochidae
Myriotrochus rinkii
Ophiuroidea
Ophiuridae
Ophiura sarsi
Stegophiura nodosa
Amphiuridae
Amphiodia craterodmeta
Amphiura sundevalli
Gorgonocephalidae
Gorgonocephalus spp.