CHUKCHI SEA ENVIRONMENTAL STUDIES PROGRAM 2008–2012: BENTHIC ECOLOGY OF THE NORTHEASTERN CHUKCHI SEA

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 a multi-disciplinary environmental studies program to establish baseline ecological conditions in the northeastern Chukchi Sea. The Chukchi Sea Environmental Studies Program (CSESP) is managed by Olgoonik-Fairweather LLC. The overall field program will provide information on physical, chemical, and biological (including zooplankton and benthic ecology), and oceanographic baseline trends. The study was initiated in 2008 and sampling continued in 2009 – 2012. The Klondike and Burger study areas were first sampled in 2008 and Statoil was added in 2010; sampling at these locations continued through 2012. The Greater Hanna Shoal study area encompasses Klondike, Burger, and Statoil, and was the focus of the CSESP in 2011 – 2012.

Objectives of the 2011 – 2012 benthic ecology component were to document macrofaunal community structure within the Greater Hanna Shoal study area, determine associations of macrofaunal community structure with environmental factors, evaluate meiofaunal communities, and investigate benthic food webs through caloric contents of macrofauna. For the first discipline within the benthic ecology study, macrofauna (sediment-dwelling organisms retained on a 1.0-mm sieve) and environmental parameters were sampled at 101 stations in 2011–2012 including four additional stations sampled along the CSESP Distributed Biological Observatory (DBO) line in 2012. The benthic ecology component also included two small studies to investigate meiofauna and macrofaunal caloric content. Meiofauna (smaller invertebrate organisms passing through a 1.0-mm sieve but retained on a 0.064-mm sieve) and caloric content samples were analyzed for 31 – 34 stations. Additional tasks include determination of sediment grain-size characteristics, sediment stable isotope composition, concentrations of organic carbon, and population dynamics of two bivalves.

Environmental characteristics reflected interactions between the pressure-driven northward flow of water and topographic deviations of the submerged continental shelf. Northward-flowing water enters the study area through the Central Channel which lies on the western margin of the study area. A branch of the water in the Central Channel breaks off and flows east across Klondike and Statoil. The northward flowing water also circulates around the northern edge of Hanna Shoal, some of which moves south and then westward along the shoal’s southern edge. This clockwise circulation of water around Hanna Shoal brings winter water back into Burger and then converges with the eastward flow coming from the Central Channel. The convergence causes water that circulated around the shoal to diverge back to the east. Additionally, the persistence of a cold water pool in Burger would increase water column stratification thus favoring greater primary production in that area. The convergence of water currents occurs over and to the north and east of Burger. At the regional scale, water depth is greatest in Burger and along the margins of the Hanna Shoal study area. Deeper water depths are associated with greater proportions of mud and concentrations of organic carbon while salinity increases and temperature decreases with increasing latitude. Presumably, the interactions between topography and water currents create the opportunity for bottom water fronts, gyres, and other complex patterns to increase availability of food to the benthos. The potential increase in seasonal production resulting from greater stratification in Burger (caused by the cold pool) could be a significant source of carbon in the area. The greater production combined with the stagnant water flow (allowing greater deposition of particulates) may be major factors contributing to the greater benthic production at Burger. Thus, the complex flows resulting from topographic control over water movements appear to be the drivers for the coinciding environmental and biological differences observed.

Benthic macrofauna in the Klondike, Burger, and Statoil study areas were abundant, contained many animals with high biomass, and comprised diverse communities. Significant differences in community characteristics were apparent as Burger had greater average density, biomass, and number of taxa than Klondike. Statoil was intermediate along the gradient between Klondike and Burger. Multivariate analyses of the repeatedly sampled stations also indicated separation of macrofaunal communities by study area but no clear separation by year. The declines in density and number of taxa observed in 2010 were reversed in 2011 and 2012.

At the regional level, the 2011 – 2012 Greater Hanna Shoal study area was broken into four strata: South (encompassing Klondike), Central A (encompassing Burger), Central B (encompassing Statoil), and North. Expansion of the CSESP study to the larger study area in 2011 and 2012 provided a better opportunity to understand the overall ecology of the region, and place Klondike, Burger, and Statoil in the context of the larger environmental and biological trends. The much deeper insights provided by the funding of the larger study area sampled in 2011 – 2012 are of great value.

Meiofauna were abundant and included both permanent and temporary members. Permanent members include harpacticoid copepods, nematodes, and protozoans of the order Foraminifera. Temporary members include juvenile macrofaunal species such as bivalves and polychaetes. As with the macrofaunal community, meiofaunal densities were lower in the North stratum. Nematodes were the dominant meiofauna followed by copepods, forams, and polychaetes. There were weak to moderate associations between measured environmental variables and the meiofaunal community structure.

Energy content of faunal species demonstrated that the main prey items of marine mammals had the highest energy content, as would be expected. Spatial variations in the energy content of the polychaete family Maldanidae and the bivalves *Macoma* spp. were related to percent mud and bottom-water temperatures, respectively. Spatial variations in the energy content per gram of tissue of Maldanidae and the amphipod family Ampeliscidae demonstrate higher energy content in areas favorable to the feeding modes of these groups. Maldanidae have higher energy content in muddier sediments favoring deposit feeding and Ampeliscidae have higher energy content in Klondike where currents may favor suspension feeding.

Overall, there was a trend of declining density, biomass, and diversity of benthic organisms (meiofauna, macrofauna, and megafauna captured in van Veen grabs) from the South to the North stratum. Community structure was correlated with water depth, percent mud, bottom-water temperature, and sediment organic carbon concentration reflecting the influences of topography, water currents, and resulting geologic and oceanographic differences among the strata. Communities in the study area were dominated by bivalves and polychaetes which were particularly abundance in the Central A and B strata. Common trends in geostatistical and multivariate analyses integrating the environmental and meio-, macro-, and megafaunal data highlight the joint spatial variability among the physical parameters and the benthic assemblages and energy flow.

In summary, trends in the benthic assemblages indicate that oceanographic and topographic characteristics of the study area are important determinants of benthic community composition and energy flow. The benthic communities are a mix of Arctic and North Pacific invertebrates resulting from the flow of water northward through the Bering Strait to the Arctic Ocean importing heat, nutrients, and larvae to the Chukchi Sea. Communities are comprised of numerous, large animals with diverse composition reflecting the flux of unconsumed ice algae and phytoplankton production. The large body size and known habits of all animals found in the study area (including marine mammals) indicate a high level of biological activity within the sediment column (bioturbation) and interactions among animals (e.g., predator/prey relationships). As a result, biological interactions are important in maintaining the structure and diversity of benthic fauna in the study area. Environmental gradients appear to be associated with topographic variations, particularly the change in water depth in Burger which is at the head of a submarine valley. The change in topography interacting with water currents and other oceanographic variables drives a number of changes in water movements including stagnant water flow, increased stratification, and deposition of organic carbon. These latter characteristics result in greater food deposition (primary production) in Burger resulting in greater density and biomass of animals.

CHAPTER 1
GENERAL INTRODUCTION

ConocoPhillips Company (COP), Shell Exploration and Production Company (SEPCO), and Statoil USA E&P, Inc. are supporting a multi-disciplinary environmental studies program to understand baseline conditions for three study areas in the northeastern Chukchi Sea prior to oil and gas exploration. The project is managed by Olgoonik-Fairweather LLC (OLF). The study areas are Klondike, Burger, and Statoil (2010–2012 only) where successful lease bids were made in the February 2008 Chukchi Sea Lease Sale 193. The Chukchi Sea Environmental Studies Program (CSESP) was initiated in 2008 and has continued annually through 2012. The study area was expanded in 2011 and 2012 to include a region from Klondike to Hanna Shoal. The overall research program will provide information on physical, chemical, biological (including zooplankton and benthic ecology) oceanographic baseline trends and the acoustic environment for the Klondike, Burger, and Statoil study areas.

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 the Chukchi Sea (Hopcroft et al., 2006). 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. In the Chukchi Sea, 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, crabs) (Lovvorn et al., 2003; Feder et al., 2005; Grebmeier et al., 2006; Feder et al., 2007). Benthic organisms in the northern Bering and Chukchi seas are important food resources for higher trophic level organisms such as demersal fishes, various seals, walrus, and gray whales (e.g. Oliver et al., 1983; Moore and Clarke, 1990; Feder et al., 1994, 2005, and 2007; Coyle et al., 1997; Green and Mitchell, 1997; Moore et al., 2003; Highsmith et al., 2006; Bluhm et al., 2007; Bluhm and Gradinger, 2008).

Scientific studies conducted intermittently over the last 37 years provide a basis for understanding the ecology of offshore benthic communities in the northeastern Chukchi Sea. The first study of macrofaunal community structure was in 1971 to 1974 by Stoker (1978 and 1981). This was followed in 1986 and 1987 by investigations of the benthos/environmental interactions by Feder et al. (1994). Following the latter study, Grebmeier et al. (1988) documented the strong association between annual pelagic production reaching the seafloor and the benthic communities (pelagic-benthic coupling) in the southeastern Chukchi Sea. The macrofauna of the Chukchi Sea are abundant and biomass locally high due to the comparatively high quantities of unconsumed primary production (from pelagic and ice-algae production) reaching the benthos in some areas (Grebmeier et al., 2006; Blanchard et al., 2013a). A rich megafaunal community (larger animals residing on the sediment surface) is also present in the Chukchi Sea, including numerous mollusks, crabs, and echinoderms (e.g., Feder et al., 1994, 2005; Ambrose et al., 2001; Bluhm et al., 2009 Blanchard et al., 2013b). Recent and on-going investigations in the northeastern Chukchi Sea include the Shelf-Basin interaction study (SBI; http://sbi.utk.edu; Grebmeier et al., 2009), the Russian-American Long-term Census of the Arctic (RUSALCA), and the Bureau of Ocean Energy Management's (BOEM) Chukchi Sea Offshore Monitoring in Drilling Area (COMIDA) program. All of the latter programs focus on broad-scale sampling throughout the Chukchi Sea with SBI having focused on processes along the northern continental margin, RUSALCA encompassing the northern Chukchi Sea, and the COMIDA program focusing on the US offshore Lease Sale Planning area. These studies will contribute to building baseline databases adequate for evaluating, with confidence, long-term trends (e.g., repeated sampling at similar locations over space and time using similar sampling methods) in macrofaunal communities of the northeast Chukchi Sea.

The multi-year, COP/SEPCO/Statoil-sponsored CSESP initiated in 2008 and continued in 2009–2012 will contribute to understanding the benthic ecology within the region. Overall, benthic communities in Burger and Klondike sampled in 2008 – 2010 were diverse and fauna abundant, comparable to those found in prior research and trends were related to apparent environmental gradients (Feder et al., 1994; Blanchard et al., 2013 a and b). The combined results from the 2011 and 2012 investigations will allow for assessment of short-term temporal trends in addition to the evaluation of spatial trends over the larger, regional study area. Results of this five-year investigation in the northeastern Chukchi Sea will contribute to benchmarks for determining potential changes in the benthos due to climate change or other natural environmental fluctuations.

This general introduction describes the overall sampling plans, details on annual variations to the sampling plan, and station coordinates for the 2008–2012 CSESP.

OBJECTIVES

Objectives of the benthic ecology component of the 2012 CSESP were to investigate the benthic ecology of a Chukchi regional study area surrounding Hanna Shoal and temporal variations in the three main study areas. The specific objectives were to:

- Sample macrofaunal organisms within the Klondike, Burger, Statoil, and the larger regional study area (Hanna South, Central, and North) to document macrofaunal community structure;
- Evaluate spatial and temporal variability of macrofauna density and biomass within the three main study areas over 2008–2012;
- Assess macrofaunal species composition, density, and biomass of benthic communities within the regional study area in 2011-–2012 and determine associations of community structures with environmental factors;
- Assess meiofaunal species composition and density within the 2012 study area and determine associations of community structures with environmental factors;
- Determine caloric content of macrofaunal marine-mammal prey items within the 2012 study area;
- Determine sediment grain-size, sediment isotope composition, sediment organic carbon concentrations, and sediment chlorophyll concentrations; and
- Determine shell length frequencies of the mollusks *Ennucula tenuis* and *Macoma* spp.

METHODS

Nomenclature for the 2008–2012 Sampling Cruises

Ships were identified by a unique letter code. The *M/V Bluefin* (BLF) was used for sampling in 2008. The *R/V Westward Wind* (WWW) was used for sampling in 2009 through 2012.

Cruises are identified by the ship letter code, year of sampling, and the number by which cruises are ordered within each year. Cruise designations are: BLF0803 for benthic sampling in 2008 which occurred from August 21 to September 25. In 2009, three benthic cruises were accomplished and named WWW0902, WWW0903, and WWW0904 with megafaunal sampling occurring on WWW0902 (August 14-29) and WWW0904 (September 25 - October 10) and macrofaunal sampling on cruise WWW0903 (September 5-19). Macrofauna were sampled on cruise WWW1002 (August 5-19) in 2010 and megafauna on cruise WWW1003 (September 1-18). Macrofauna were sampled on a larger, regional scale in 2011 during cruises WWW1102 (August 3-24) and WWW1104 (August 31 to October 5, 2011). In 2012, benthic fauna were sampled on cruises WWW1203 (September 1 to September 16) and WWW1204 (September 17 to October 3, 2012).

The study areas were identified with a one character code for the three areas, Klondike (K), Burger (B), and Statoil (S), a one character code for the type of station sampled as fixed (F) or random (R), and lastly, the station number. Stations at which mammals were known to feed were given the character code TM and the Transitional stations were coded as TF. Samples from the regional study were identified as Hanna South (HS), Hanna Central (HC), and Hanna North (HN).

Sampling in 2012 included 60 benthic stations in the regional study area encompassing Klondike, Burger, and Statoil, the regional study area, and 4 stations on the CSESP 2012 Distributed Biological Observatory (DBO) line. Within the CSESP regional study area, a total of 97 individual stations were sampled in 2011 and 2012, plus the 4 DBO stations, representing one statistical "panel" for monitoring, or one temporal group of stations (i.e., the averaged 2011 and 2012 data represent one "sample" of the regional area).

General Sampling Methods

The term "macrofauna" is herein limited to invertebrate animals residing in sediments and retained on a 1.0-mm mesh screen. Meiofauna, as defined in this report, are limited to the invertebrate animals and other organisms found within sediments captured using a 64µm mesh screen. The typical meiofaunal community is comprised of "transitory" species, or juvenile and larval stages from the larger macrofaunal community, as well as "permanent" species, such as nematodes and harpacticoid copepods. The term "megafauna", for the purposes of this report is limited to larger invertebrate animals residing on the sediment or closely associated with the sediment surface (e.g., upright organisms or large clams near the surface). Megafauna are traditionally those animals represented in trawl samples such sea squirts, sea stars, and scallops.

Macrofauna were sampled at 60 stations in 2012 using a double van Veen grab with two 0.1 m^2 adjoining grabs to collect sediments for analyzing sediment grain-size and organic carbon content, as well as for taxonomic determination and caloric content. Three replicate grabs were collected at each station (Table 1-1, Fig. 1-1). The first few centimeters of sediment were collected from the side of the van Veen grab not used for taxonomic purposes, to determine sediment grain-size and organic carbon concentrations.

Meiofauna were collected at each station using a van Veen grab (Table 1 and Fig. 1). Samples were collected using a 7 cm diameter by 1 cm depth plastic ring (hereafter called "shallow core") from the surface layer of the grab sample. A piece of plexiglass was slid underneath the shallow core to lift the sample. Further details for meiofaunal sampling and laboratory methods are given in Chapter 2. Samples from 31 of the 60 stations were analyzed; the rest were archived and may be donated to an ongoing study of the meiofauna of the Beaufort and Chukchi seas.

In 2012, macrofaunal organisms were also frozen for determination of caloric content. The analysis of invertebrate tissues provides insight into the energy content of the benthic communities utilized as food resources by higher trophic level organisms such as fishes and marine mammals. Further methods for the caloric content study are detailed in Chapter 4. Samples from 34 of the 60 stations were completed for this report; the rest were archived.

Macrofaunal sampling has occurred from August to October from 2008 to 2012. The most common dates encompass September. Timing could be a critical factor as recruitment of juveniles into the macrofauna could inflate density estimates. Thus, the consistency of sampling around September (with some deviations), helps to limit seasonal changes in the macrofaunal density estimates.

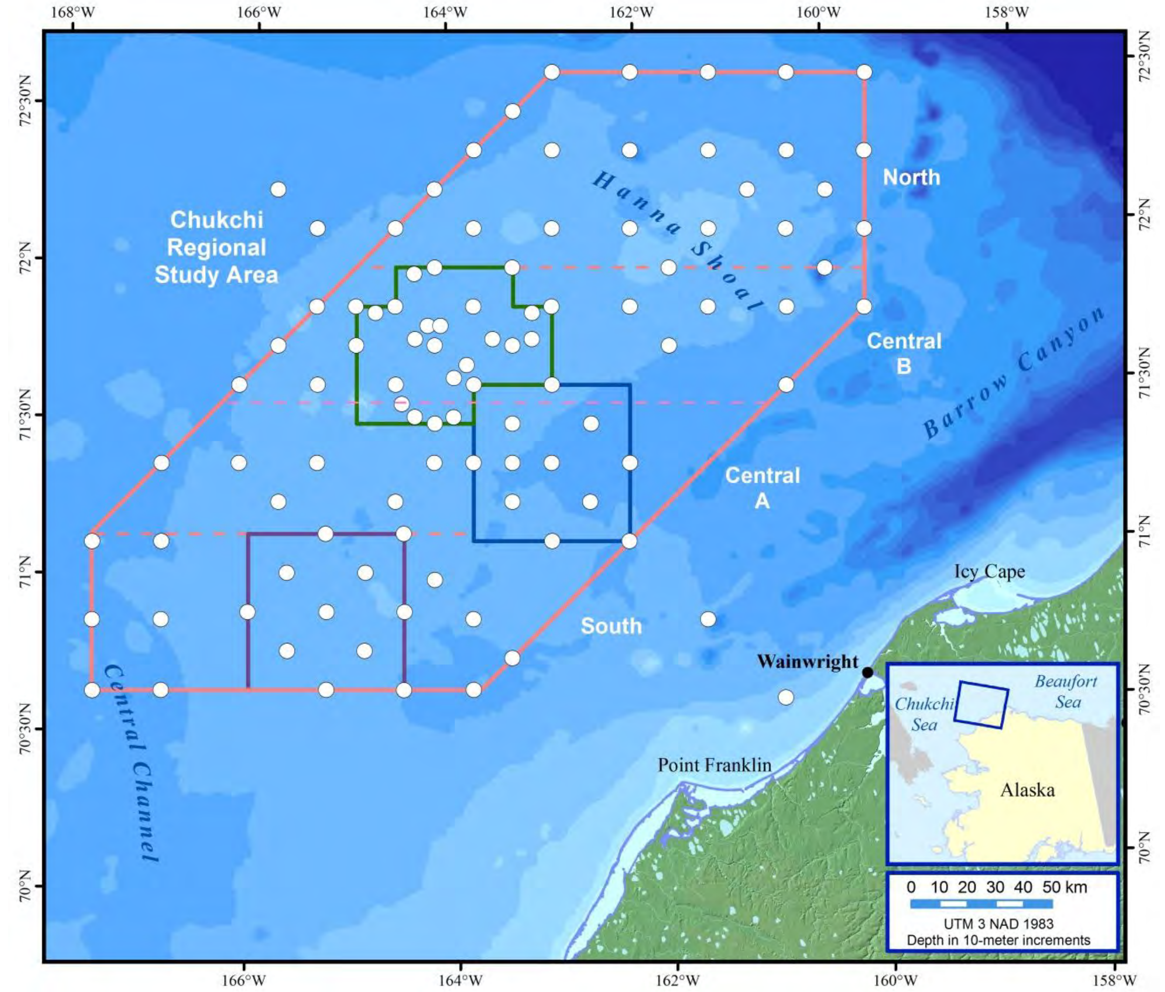

Figure 1-1. Map of all benthic stations sampled during the 2011 and 2012 CSESP benthic surveys.

Table 1-1. Station information for all benthic sampling during the 2011 – 2012 CSESP study. Intended positions (decimal degree format) and sampling strata are given. D = DBO line station, K = Klondike, B = Burger, S = Statoil, T = transitional station between Burger and Klondike, F = fixed station, R = random station, H = Hanna Shoal, C = central, N = north, and S = south.

Station	2011	2012	Latitude	Longitude	Strata	Substrata
DF002		X	70.5782	-160.84	DBO	DBO
DF004		X	70.8424	-161.54	DBO	DBO
DF006		X	72.1198	-165.36	DBO	DBO
DF007		X	72.2431	-165.77	DBO	DBO
BF003	X	X	71.1134	-163.03	South	South
BF005		X	71.1037	-162.27	Central	Central A
BF007	X	X	71.2415	-163.41	Central	Central A
BF009	X	X	71.2334	-162.64	Central	Central A
BF011	X	X	71.3689	-163.79	Central	Central A
BF012	X		71.366	-163.4	Central	Central A
BF013	X	X	71.3623	-163.01	Central	Central A
BF015	X	X	71.3525	-162.23	Central	Central A
BF017	X	X	71.4905	-163.39	Central	Central A
BF019	X	X	71.4822	-162.6	Central	Central A
BF021	X	X	71.6179	-163.77	Central	Central B
BF023	X	X	71.6112	-162.98	Central	Central B
HC003	X	X	71.247	-165.73	Central	Central A
HC005		X	71.3633	-166.9	Central	Central A
HC006	X	X	71.3696	-166.13	Central	Central A
HC007		X	71.3726	-165.35	Central	Central A
HC010		X	71.6186	-166.14	Central	Central B
HC011	X		71.6217	-165.35	Central	Central B
HC012	X		71.7451	-165.75	Central	Central B
HC013		X	71.8707	-165.36	Central	Central B
HC020	X	X	71.5718	-160.62	Central	Central B
HC022	X		71.7196	-161.78	Central	Central B
HC025	X	X	71.8502	-162.16	Central	Central B
HC026	X		71.8368	-161.36	Central	Central B
HC027	X		71.8201	-160.56	Central	Central B
HC028	X	X	71.8002	-159.77	Central	Central B
HC030		X	71.9682	-161.74	Central	Central B
HC032	X		71.9346	-160.14	Central	Central B
HN001		X	72.1196	-164.55	North	North
HN002	X		72.116	-163.74	North	North

Table 1-1. Continued.

Station	2011	2012	Latitude	Longitude	Strata	Substrata
HN003		X	72.1091	-162.93	North	North
HN004	X		72.0989	-162.12	North	North
HN005	X	X	72.0853	-161.31	North	North
HN006	X		72.0684	-160.51	North	North
HN007	X		72.0482	-159.7	North	North
HN008	X		72.2427	-164.14	North	North
HN012	X		72.2015	-160.88	North	North
HN013	X		72.1828	-160.07	North	North
HN014	X	X	72.365	-163.72	North	North
HN015		X	72.358	-162.9	North	North
HN016	X	X	72.3476	-162.08	North	North
HN017	X		72.3339	-161.26	North	North
HN018	X	X	72.3167	-160.44	North	North
HN019	X		72.2962	-159.63	North	North
HN020	X		72.4864	-163.3	North	North
HN025	X	X	72.6069	-162.87	North	North
HN026	X		72.5964	-162.04	North	North
HN027		X	72.5824	-161.21	North	North
HN028	X		72.5649	-160.38	North	North
HN029		X	72.5441	-159.55	North	North
HS001		X	70.6316	-167.5	South	South
HS002	X		70.6395	-166.84	South	South
HS005	X		70.8574	-167.53	South	South
HS006		X	70.8654	-166.86	South	South
HS009		X	71.1063	-167.56	South	South
HS010	X		71.1144	-166.88	South	South
HS011		X	70.645	-163.83	South	South
HS013	X		70.7437	-163.45	South	South
HS014	X		70.871	-163.82	South	South
KF003	X	X	70.6486	-165.25	South	South
KF005		X	70.648	-164.5	South	South
KF007	X	X	70.7722	-165.63	South	South
KF009	X	X	70.7732	-164.88	South	South
KF011	X	X	70.895	-166.02	South	South
KF013	X	X	70.8976	-165.25	South	South
KF015	X	X	70.8971	-164.49	South	South
KF017	X	X	71.0213	-165.64	South	South
KF019	X	X	71.0223	-164.87	South	South

Table 1-1. Continued.

Station	2011	2012	Latitude	Longitude	Strata	Substrata
KF023	X	X	71.1467	-165.26	South	South
KF025		X	71.1462	-164.49	South	South
SF003	X	X	71.4956	-164.17	Central	Central A
SF005	X	X	71.6215	-164.56	Central	Central B
SF007	X	X	71.7465	-164.96	Central	Central B
SF009	X	X	71.7447	-164.16	Central	Central B
SF011	X	X	71.7396	-163.37	Central	Central B
SF013	X		71.871	-164.96	Central	Central B
SF014	X	X	71.8705	-164.56	Central	Central B
SF016	X	X	71.867	-163.76	Central	Central B
SF018	X	X	71.8603	-162.96	Central	Central B
SF020	X	X	71.9937	-164.15	Central	Central B
SF022	X		71.9885	-163.35	Central	Central B
SR005	X		71.5174	-164.37	Central	Central B
SR008	X		71.5157	-163.98	Central	Central B
SR013	X		71.5593	-164.5	Central	Central B
SR035	X		71.6402	-163.97	Central	Central B
SR051	X		71.681	-163.84	Central	Central B
SR077	X		71.7665	-164.36	Central	Central B
SR083	X		71.7622	-163.57	Central	Central B
SR086	X		71.7588	-163.17	Central	Central B
SR093	X		71.8075	-164.23	Central	Central B
SR094	X		71.8069	-164.1	Central	Central B
SR104	X		71.8504	-164.76	Central	Central B
SR116	X		71.8418	-163.16	Central	Central B
SR137	X		71.974	-164.36	Central	Central B
TF001	X		70.9975	-164.19	Central	Central A
TF003	X	X	71.2479	-164.57	Central	Central A
TF006	X		71.3711	-164.18	Central	Central A

Quality Assurance Procedures

The TigerObserver system, an integrated navigational and data collection system, was developed for the CSESP in 2009 to integrate data collection in the field with the ship's navigation system, in real time. This allows for geographic coordinates and oceanographic conditions to be linked with biological data and minimizes transcriptional errors between field notes and databases. Data managers onboard 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).

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

Quality control procedures were followed in processing macrofaunal samples in the laboratory. The work of sorters was monitored throughout the project by a trained taxonomist. Once fully trained, a minimum of 10% of samples sorted by student employees were re-sorted to be certain that greater than 95% of the organisms in each sample were removed. All of the work performed by junior taxonomists was checked and verified by a senior taxonomist, with verification tapering off as they approached the skill level expected for a more experienced taxonomist. Work was verified to ensure that all counts were accurate and all organisms were correctly identified. Fauna identified in the 2012 CSESP were compared to the voucher collection from the 1986 investigation by Feder et al. (1994) and to current references (e.g., other benthic programs and our work in the same study area throughout the years) to ensure accuracy, consistency between studies and, to the best of our abilities, consistency with currently recognized taxonomic status. After one year from the date of collection, the sorted debris (considered nonhazardous after rinsing and removal of biological tissues) will be discarded, following protocols determined by UAF Risk Management. Original data forms and MS Access databases will be archived at IMS and delivered to OLF, in accordance with prescribed data management protocols.

Prior to analyses of macrofaunal data sets, taxonomic information was scrutinized for consistency, as a further quality control check. Pelagic, meiofauna, and epibenthic taxa (i.e., barnacles, tanaidaceans, benthic copepods, brittle stars, sea stars, crabs, etc.) were excluded from analytical data sets for macrofauna. Taxonomic information of megafaunal data sets was also scrutinized for consistency and pelagic and obvious macrofaunal taxa were excluded from the data analyses. Megafaunal information collected from grab samples in 2011 – 2012 were analyzed separately, as part of the general benthic ecology section.

STUDY AREA AND ENVIRONMENTAL SETTING

The Chukchi Sea is a shallow body of water influenced by seasonal ice cover and by advection of southern waters derived from the Pacific Ocean entering into the Arctic Ocean through the Bering Strait (Weingartner et al., 2005). Feder et al. (1994) discusses in detail relevant oceanographic characteristics influencing benthic fauna. Briefly, water-masses moving into the region from the south include the Anadyr Water, Bering Shelf Water, and Alaskan Coastal Water (Weingartner et al., 2005). The northward current flow is derived from differences in sea-level height between the Pacific and Arctic oceans; water transits the Chukchi Shelf exiting through the Herald Valley, the Central Channel, and Barrow Canyon. The water-masses from the south advect heat, nutrients, zooplankton and larvae of benthic fauna into the region, contributing to the ecological characteristics of the Chukchi Sea. The shallow waters of the Chukchi Shelf (~35 to 45 m) prevent establishment of *in situ* communities of large copepod grazers, and they must be advected to the area from the south. The mismatch in time between the arrival and development of the zooplankton community and the timing of robust seasonal primary production allows much of this production to fall to the seafloor unconsumed, supporting very abundant and biomass-rich benthic assemblages (Grebmeier et al., 2006). The combined effects of seasonal ice cover, shallow water depths, and the influx of warmer, nutrient-rich water through the Bering Strait are major contributors to the ecological balance of the Chukchi Sea (Grebmeier et al., 2006).

The Chukchi Sea overlies Beringia (the Bering Land Bridge) that was not submerged during the last glacial period. Beringia emerges and submerges with variations in glacial cycles as water contained in melting glaciers increases sea level enough to submerge the shelf. When exposed, Beringia is a grassland steppe with low relief. It provides a land connection between Alaska and eastern Siberia. When submerged, Bering Strait connects water flowing northward from the Pacific Ocean with the Arctic Ocean. Topographic variations interacting with water masses split the pressure-driven, northward flow into three major branches; the Alaska Coastal, Central, and Herald Valley branches (Weingartner et al., 2005). Topographic and current interactions also result in complex circulation patterns around Hanna and Herald shoals (Martin and Drucker, 1997), both of which are dominant topographic features on the northern Chukchi Sea seafloor.

Historical sampling in 1986 was conducted to determine broad-scale ecological conditions. Sampling stations were dispersed across the northeastern Chukchi Sea (Fig. 1-2; Feder et al., 1994). Sampling locations were selected based on known variations in sediment types, bathymetry, and mean summer ice position. General trends of sediment characteristics in the northeastern Chukchi Sea followed the expected increase in depth and associated increase in percent of mud in sediments with greater distance offshore. There was also a trend of increasing percent mud, increasing bottom-water salinity, and decreasing bottom-water temperatures with increasing latitude. Feder et al. (1994) observed a bottom-water front extending to Point Franklin that aligns closely with the 3°C contour in the geospatial model for bottom-water temperature (Fig. 1-2). Benthic communities reflected the change in water masses, possibly due to advection of production from the south, with increased density and biomass north of the front.

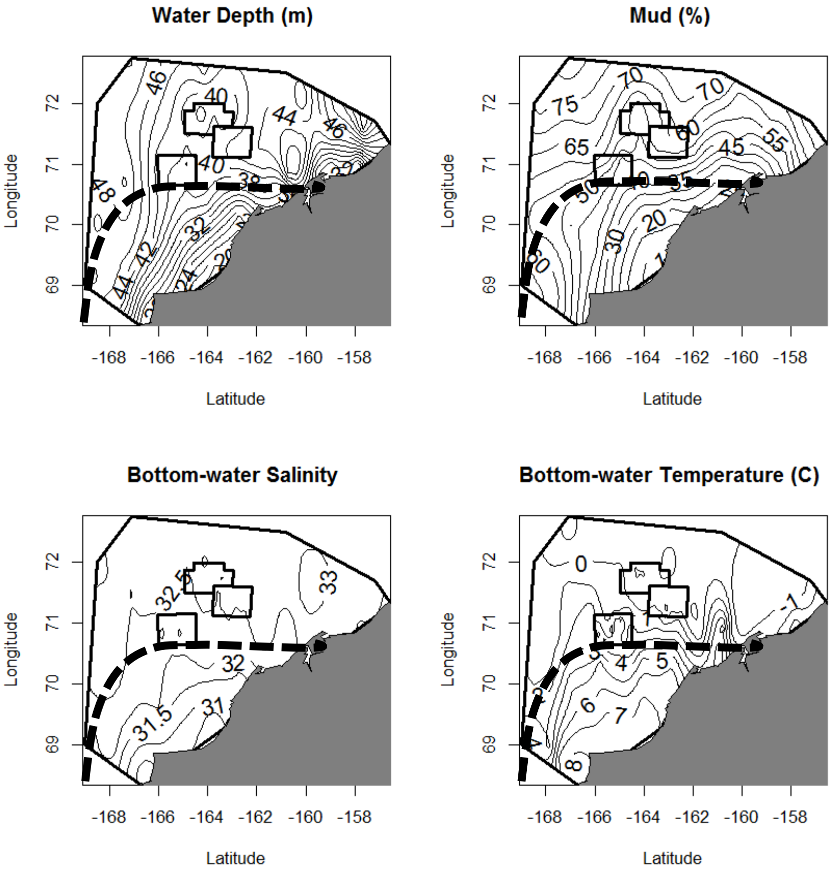

Figure 1-2. Geospatial models of water depth, percent mud, and bottom-water salinity and temperature for the northeastern Chukchi Sea. Data are from 1986 (Feder et al., 1994) and values averaged from 2008–2010 for the CSESP (Blanchard et al., 2013). The dashed line denotes the bottom-water front identified by Feder et al. (1994).

The CSESP study area lies 100 to 200 km west of the village of Wainwright, Alaska, on the northwestern coast of Alaska along the northeastern Chukchi Sea (Fig. 1-1; Day et al., 2013). The 2008–2010 study region encompassed three focused study areas, Klondike, Burger, and Statoil, where successful lease bids were made during the February 2008 Chukchi Sea Lease Sale 193 (Blanchard et al., 2013 a and b). The 2011–2012 study areas encompassed a larger region from Klondike to slightly north of Hanna Shoal. Environmental characteristics within the Klondike, Burger, and Statoil study areas change sharply over a small distance due to interactions between topographic changes and oceanographic features. 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, reflecting complex water movement in the former area. The persistence of the cold water increases stratification that would maintain conditions favorable for seasonal production to continue. The stagnant water circulation, increased stratification, and potentially greater proportions of seasonal production would increase the flux of carbon to the sediment surface in Burger. Klondike functions more as a pelagic-dominated system with more 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 is northwest of and adjacent to Burger and shares environmental and biological characteristics of both Burger and Klondike. Transitional stations are situated along the environmental gradient between Klondike and Burger.

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CHAPTER 2

BENTHIC ECOLOGY 2008–2012:

Association of Macrofaunal Community Structure with Environmental Variables

By Arny L. Blanchard and Ann L. Knowlton

INTRODUCTION

The northeastern Chukchi Sea is a productive shallow body of water influenced by advective processes (Grebmeier et al., 2006). Water masses moving into the region include Bering Shelf water and Alaska Coastal water (e.g., Coachman, 1987). Bering Shelf water has relatively high nutrient concentrations, derived in part from water from the Gulf of Anadyr off the coast of Russia, that enhance benthic biomass in the south. Advection of production in nutrient-rich waters from the south may enhance secondary production in the northern regions (Feder et al., 1994). In contrast, the Alaska Coastal water is considered to be comparatively nutrient poor (Feder et al., 1994; Codispoti et al., 2005; Grebmeier et al., 2006). Differences among water masses are associated with substantial differences in benthic community structure in broad-scale studies (Feder et al., 1994; Grebmeier et al., 2006; Blanchard and Feder, in press). Additional factors identified as important predictors of benthic community structure in the Chukchi Sea include sediment granulometry (e.g., percent gravel, sand, or mud) and the ratio of sediment organic carbon to nitrogen (C/N ratio) (Feder et al., 1994). Sediment granulometry reflects a number of environmental features and processes, such as seafloor topography, hydrodynamics (strong currents, storm effects, ice gouging, etc.), sediment deposition, and proximity to sediment sources. Topographic control over water circulation may be a key source for spatial variations of macrofaunal communities as circulation divergences can result in greater food availability via increased deposition for deposit-feeders, or within the water column for suspension feeders (Blanchard et al., 2013 a).

Investigations of carbon cycling in the Chukchi Sea demonstrated strong linkages between primary production and distributions of invertebrate fauna. The reduced numbers of pelagic (water-column) grazers drives strong pelagic-benthic coupling because of the large flux of uneaten phytoplankton reaching the benthos, resulting in a very abundant and diverse macrofaunal community (Dunton et al., 2005; Grebmeier et al., 2006). Consequently, interannual variability in primary production and zooplankton communities (Questel et al., 2013) may be an important source of temporal variability for benthic communities. Ice algae production 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).

Benthic communities are often categorized by size, life-habits, and sampling gear. Large, mobile animals captured by trawling are considered megafauna or epifauna and generally live on the sediment surface. The macrofauna, also called infauna, includes smaller animals on the sediment surface and those living in the sediments; macrofaunal organisms are sampled with a grab or coring device. These are the animals retained on a 0.5- or 1.0-mm mesh sieve. Meiofauna are smaller animals passing through the 0.5-mm mesh but retained on smaller sieves such as a 64-µm mesh. Smaller-sized organisms are preyed upon by larger organisms throughout the community linking meiofaunal, macrofaunal, and megafaunal communities. Megafauna and macrofauna have been studied in the Beaufort and Chukchi seas but little work has gone into investigations of the meiofauna. Although an ecologically-significant part of the sediment ecosystem, meiofauna are often overlooked, due in part to the difficulty of sampling and identification.

The broad objectives of this portion of the benthic ecology component of the CSESP were to document species composition, density, and biomass of macrofaunal communities within the study areas, and determine associations of communities with environmental characteristics. Specific objectives of the benthic ecology component of the 2011 – 2012 CSESP were:

1) To determine sediment grain-size, isotope composition, and organic carbon concentrations and describe environmental gradients over the regional study area;
2) To test the hypothesis that there is significant temporal variability in summary measures;
3) To test the hypothesis that spatial variability of faunal communities over the regional study area is associated with measured environmental variables;
4) To document meiofaunal species present and test the hypothesis that meiofaunal densities covary across the study area with environmental characteristics (Chapter 3);
5) To evaluate spatial variations in energy content of macrofaunal organisms (Chapter 4); and

6) Determine shell length frequencies for *Ennucula tenuis* and *Macoma* spp.

METHODS

Macrofaunal Sampling Methods

Sampling for macrofauna with the van Veen grab in 2011 – 2012 included 97 stations from the regional study area (Fig. 2-1). In 2011, benthic fauna were sampled on cruises WWW1102 (August 3-24) and WWW1104 (August 31 to October 5, 2011). Sampling occurred from September 1 to October 2 in 2012 (cruises WWW1203 and WWW1204). Eleven fixed stations were sampled in Klondike, 12 in Burger, 24 in Statoil, 3 in the Transitional area, and 47 stations were visited interspersed within the regional sampling area. An additional 4 stations were sampled along the CSESP 2012 Distributed Biological Observatory in 2012. The study design for the larger regional studies in 2011 and 2012 included three strata; Hanna South (South), Hanna Central (Central), and Hanna North (North). The central study region was further divided into two substrata for benthic ecology, Central A and Central B, to better match the scale of benthic biological and environmental processes in the study region. See Blanchard et al. (2011, 2013a) for details of sampling cruises from 2008–2010. Data for 2011 – 2012 were averaged across the two years for regional analyses.

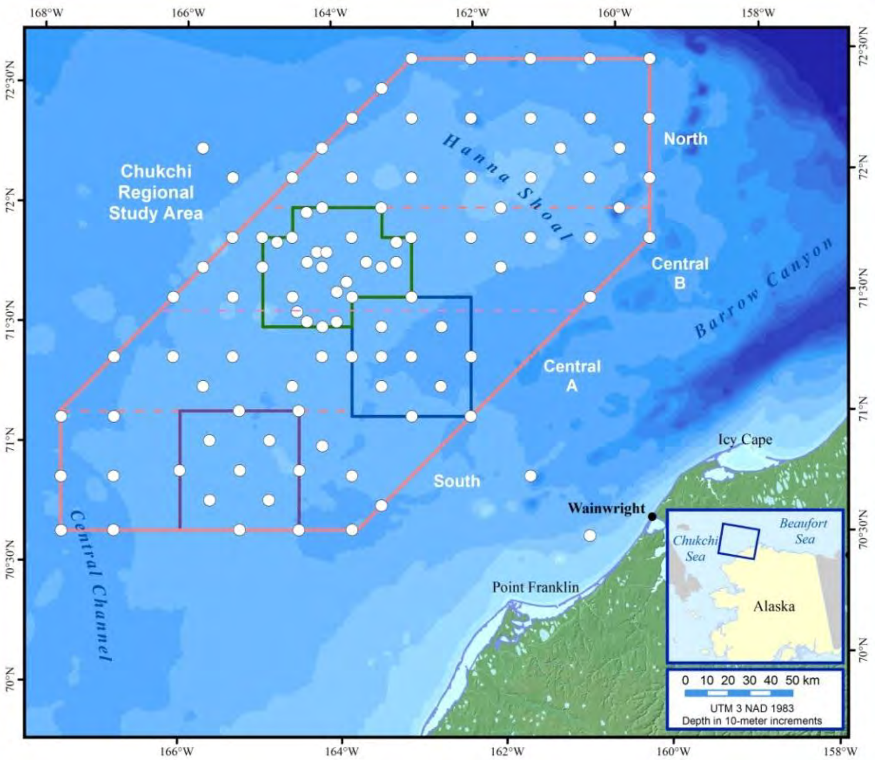


Figure 2-1. Map of stations sampled for macrofauna during 2011 and 2012 CSESP surveys.

Macrofauna were sampled using a double van Veen grab with two 0.1 m^2 adjoining grabs to collect sediments for analyzing sediment grain-size, sediment carbon concentrations, and macrofauna. Three replicate samples were collected at each station. Material collected from each grab for macrofauna was washed on a 1.0-mm stainless steel screen and preserved in 10% formalin-seawater buffered with hexamine. Benthic organisms were identified to the lowest taxonomic resolution possible, counted and wet weight was measured (protocol according to Feder et al, 1994). Sediment samples were also collected from van Veen grab samples and sieved in the laboratory to determine the proportion of mud, sand, and gravel (Wentworth, 1922). Sediment samples for carbon concentration were frozen shipboard, and processed at the Alaska Stable Isotope Facility (University of Alaska Fairbanks).

Documenting growth patterns of dominant bivalves has been a common tool in baseline investigations in Alaska. Length-growth and age-length relationships can be a useful means of documenting the influence of environmental change and such measurements are generally possible only for mollusks (with shells). Baseline investigations in Alaska have evaluated the growth of *Ennucula tenuis*, *Nuculana pernula*, *Macoma calcarea*, and *Yoldia amygdalea* from the Bering Sea (McDonald et al., 1981), *Clinocardium ciliatum*, *Macoma calcarea*, and *Serripes groenlandicus* from the Bering and Chukchi seas (Stoker, 1978), and *Mytilus trossulus* from Port Valdez (Blanchard and Feder, 2000).

The 2008-2010 CSESP studies showed significant temporal variability with a sharp decline of macrofaunal density (Blanchard et al., 2013a). The decline in density but not in biomass led to the hypothesis that larger organisms did not experience declines. The environmental variations and associated differences in faunal summary statistics led to the null hypothesis that populations of *Ennucula tenuis* were not affected by the shifting environmental conditions of 2008-2010. This hypothesis was tested by measuring shell lengths for *E. tenuis* from 2008 to 2011 to develop length-frequency distributions (as histograms). Descriptive statistics of the length distributions are presented. The resulting measurements provide insights into the survival, recruitment, and dynamics of this bivalve population and how dynamics change spatially and temporally. Length data were used to determine relative length-frequency distributions of *E. tenuis* in the study areas. Histograms created from these data present the counts (distributions) per size bin divided by the total number of bivalves and are useful for inferences among data sets of different sizes. Length measurements were also recorded for *Macoma* spp. due to the high biomass of these bivalves in the 2011 – 2012 study area.

Statistical Methods

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 number of taxa (sample number of taxa: average of replicates). Diversity measures presented include the richness (total number of taxon categories identified), Simpson evenness, and Shannon Diversity (Magurran, 2004). Comparisons among years for resampled study areas (Klondike, Burger, and Statoil) were performed using ANOVA with the statistical program Statistica (Statsoft, Tulsa, OK). Non-metric multidimensional scaling (MDS) was applied to determine community structure and spatial and temporal variability of communities using PRIMER (www.primer-e.com). The SIMPER routine of PRIMER is used to evaluate the taxa contributing to each group based on similarity of the benthic community for the multi-year analysis. Associations of community structure were evaluated by correlating the environmental variables with biotic community structure and presented using the BIOENV routine with the MDS ordination. Geostatistical analysis was performed to understand the spatial distribution of environmental and biological variables with the statistical program R (www.r-project.org) and the library geoR.

Animals represented in trawls of past years (the megafauna, animals captured by trawling) are regularly captured in van Veen grabs (e.g., Blanchard et al., 2013b), although their distributions are poorly represented. For example, barnacles can be numerous but counts of juvenile barnacles can excessively inflate variance estimates of macrofaunal parameters, and barnacles as a whole, are sessile filter feeders generally outside of the soft-sediment food web. Upright and colonial organisms occur irregularly, and the diversity of such organisms is best calculated at the regional scale to account for their rare occurrences in grab samples. Additionally, inclusion of large colonial organisms and tunicates can skew biomass estimates from grab samples. Thus, descriptive statistics for animals discussed as megafauna in previous studies are presented separately here.

Brittle stars are more difficult to categorize. Although generally represented in trawl studies as megafauna, they are in fact, macrofauna. It was decided in 2008 to consider them as megafauna in preparation for the trawling started in 2009, as it was desirable to separate the communities so there was less overlap among ongoing investigations (Blanchard et al., 2013 a and b). Blanchard and Knowlton (2013) demonstrate that brittle stars are best estimated by van Veen grabs, as they do appear to move deep into sediments. In keeping with the prior studies, however, data on brittle stars are included with the other megafaunal species.

RESULTS

Environmental Characteristics

Evaluation of environmental characteristics demonstrated varying gradients across the sampling region. Water depth was significantly deeper in Central A than in the Central B stratum (Table 2-1 and Fig. 2-2). Contour plots indicate that water depth is greatest along the margins of the study area with deeper water depths in Burger (Fig. 2-3). Sediment organic carbon concentrations were higher in Central A than in South (Table 2-1 and Fig. 2-2). The spatial model for organic carbon demonstrates an increase with greater distance north (Fig. 2-3). No significant differences among regions were apparent for percent sand; values vary by station with no spatial trend (Table 2-1 and Figs. 2-2 and 2-3). Significant differences were apparent for percent mud, which was significantly greater in Central A than in the South stratum for 2011. Percent mud is higher along the western margin of the study region. Salinity was lowest and temperature highest in the South than in the Central A, Central B, or North strata (Table 2-1 and Fig. 2-2). Salinity increased and temperature declined with increasing distance from the southwest to the northeast corner of the regional study area (Fig. 2-3).

Table 2-1. Summary of environmental characteristics for the strata sampled for macrofauna during the 2011 – 2012 CSESP study. Sediment organic carbon is in mg g^{-1}, bottom-water temperature is in degrees C, and water depth is in meters.

	South				Central A			
Variable	Ave.	SD	n	95% CI	Ave.	SD	n	95% CI
Organic Carbon	8.54	3.03	21	(7.16, 9.91)	12.9	5.24	20	(10.45, 15.36)
Water Depth	41.21	4.03	15	(38.98, 43.44)	42.65	1.95	15	(41.57, 43.73)
% Sand	48.6	15.71	15	(39.9, 57.3)	32.55	20.42	15	(21.24, 43.86)
% Mud	46.08	18.87	15	(35.63, 56.53)	67.08	20.45	15	(55.75, 78.4)
Temperature	1.69	1.12	15	(1.08, 2.31)	-0.33	0.88	15	(-0.82, 0.15)
Salinity	32.56	0.13	15	(32.49, 32.63)	32.84	0.18	15	(32.73, 32.94)

	Central B				North			
Variable	Ave.	SD	n	95% CI	Ave.	SD	n	95% CI
Organic Carbon	9.98	4.31	33	(8.45, 11.51)	12.67	6.6	21	(9.67, 15.68)
Water Depth	39.88	3.98	16	(37.77, 42)	40.1	6.49	10	(35.45, 44.74)
% Sand	34.37	20.09	16	(24.06, 45.46)	36.92	29.12	10	(16.08, 57.75)
% Mud	62.06	20.07	16	(51.36, 72.76)	59.78	31.89	10	(36.96, 82.59)
Temperature	-1.19	0.43	16	(-1.42, -0.96)	-1.29	0.26	10	(-1.48, -1.1)
Salinity	33.08	0.15	16	(33, 33.16)	33.03	0.15	10	(32.92, 33.13)

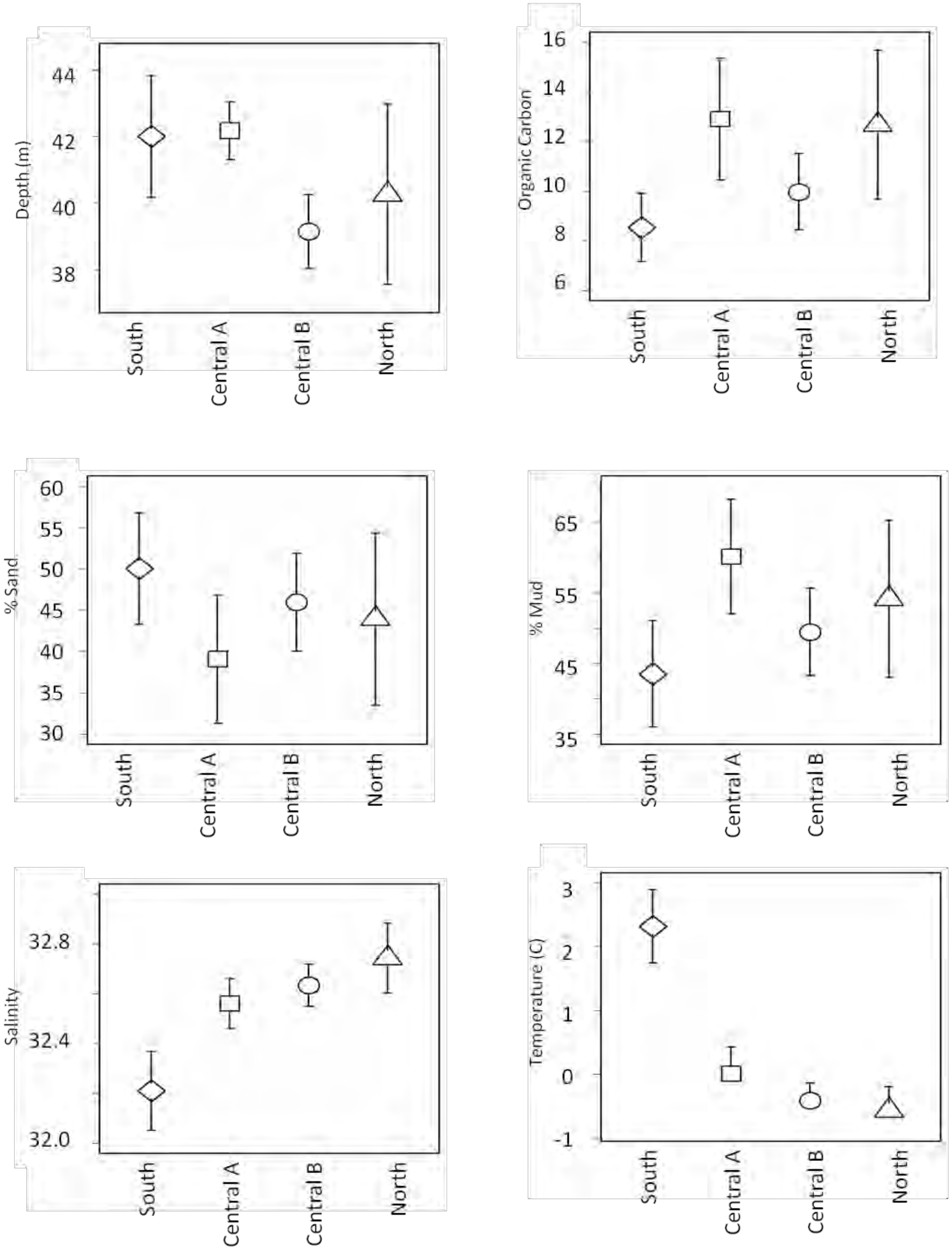


Figure 2-2. Whisker plots of environmental variables by sampling region of the 2011 – 2012 CSESP.

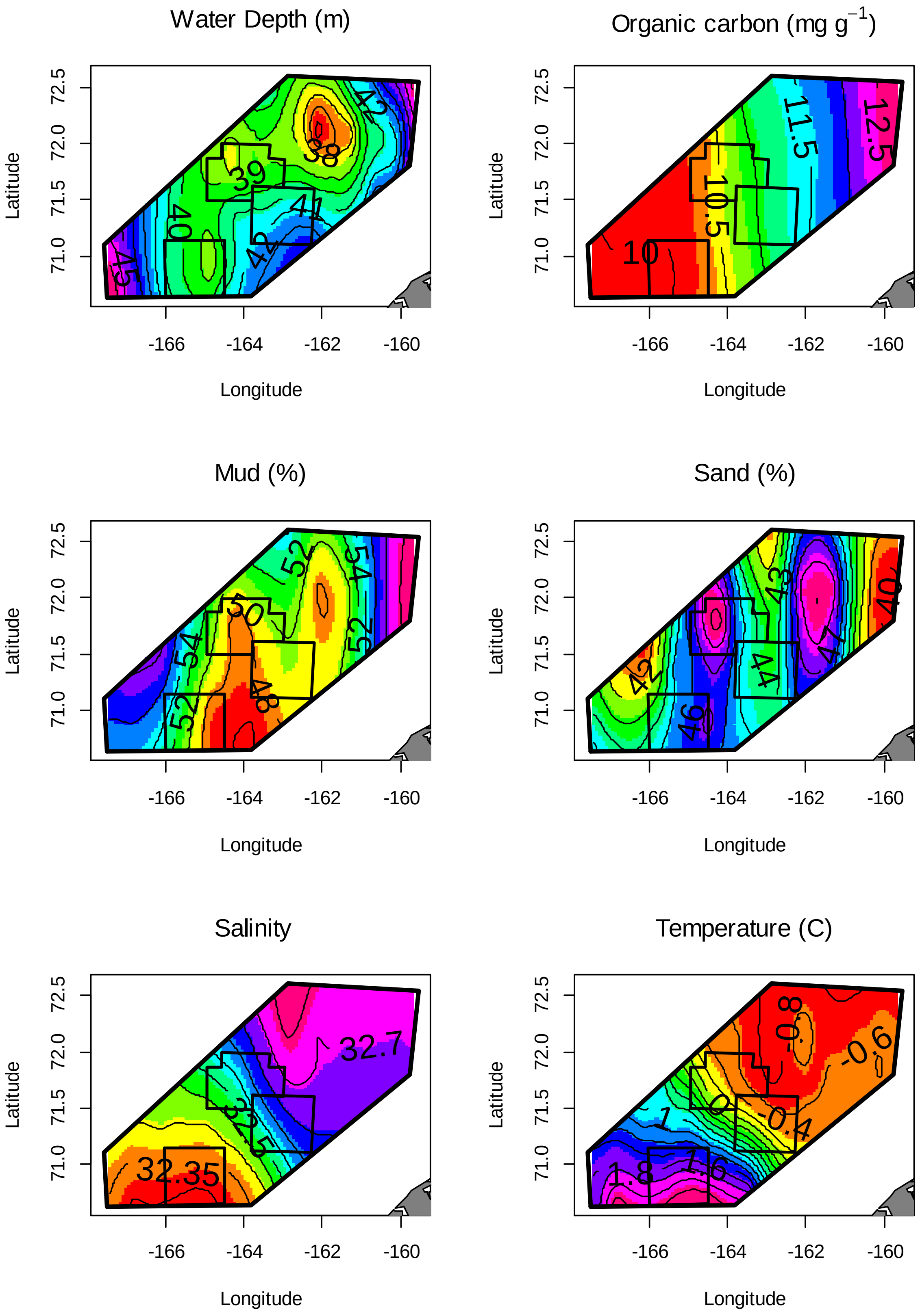


Figure 2-3. Spatial models of environmental variables sampled during the 2011 – 2012 CSESP.

Temporal Variability of Macrofauna, 2008 – 2012

Average macrofaunal density (ind. m^{-2}) in the main study areas from 2008 – 2012 ranged from 794 (Klondike 2008) to 5,169 (Burger 2012) (Table 2-2). Biomass (g m^{-2}) ranged from 115.0 (Klondike 2009) to 427.7 (Burger 2012). The total number of taxonomic categories identified ranged from 159 for Statoil stations in 2012 to 288 for Klondike in 2009 with no temporal trend (see Appendix I for a list of macrofaunal species). The total number of taxonomic categories identified for Burger stations indicate a decrease in number of taxa since 2008, from 268 categories to 196 different taxonomic categories in 2012. The total number of taxonomic categories for Statoil stations also declined from 2010 with 220 taxa categories, 219 categories in 2011, and 159 in 2012. The lower number of taxonomic categories in 2011 and 2012 reflect the decreases in number stations sampled in the last two years of the CSESP.

Shannon diversity and Simpson's evenness were similar for Klondike and Burger in 2008 and 2009 ranging from 4.90 to 5.18 reflecting small differences in diversity. In 2010, diversity increased slightly in Klondike to 5.35 and decreased in Burger to 4.66 creating a larger difference between the two. Simpson's evenness decreased slightly in Burger in 2010 as well from 0.98 to 0.96 and did not change in Klondike which had a value of 0.99 for all years. Statoil was intermediate between Klondike and Burger with a diversity value of 5.1 and evenness of 0.99 (Table 2-2). In 2011, Shannon diversity and Simpson's evenness decreased among all study areas. Diversity in Klondike decreased from the previous year to 4.22, with an evenness of 0.92. The Burger study area experienced a greater decrease in diversity, falling to 3.05 with an evenness of 0.84. Statoil evenness dropped from 0.98 to 0.96, with a decline in diversity from 5.13 in 2010 to 3.95 in 2011 (Table 2-2). Diversity measures dropped in 2012, in part due to changes in the number of stations sampled and variations in taxonomic designations. Shannon diversity ranged from 3.01 to 3.88 in 2012 and Simpson's evenness ranged from 0.83 to 0.95, and both ranges were lower than in prior years.

Animals with highest density in Klondike include the bivalve *Ennucula tenuis*, polychaetes of the family Cirratulidae, and the amphipod *Protomedeia* spp. (Table 2-3). Dominants in Burger include the bivalve *Ennucula tenuis*, the polychaete *Maldane sarsi*, and ostracods. Statoil had *Macoma* spp., *Yoldia* spp., and *E. tenuis* as numerical dominants. By biomass, the numerical dominants in Klondike and Burger include *M. sarsi*, the bivalve *Astarte* *borealis*, and the sipunculid worm *Golfingia margaritacea*. Biomass in Statoil includes the bivalves *A. borealis* and *Macoma calcarea*, and *G. margaritacea*.

Comparisons of biological measures indicate significant differences among study areas from 2008 to 2012. Repeated measures analysis of variance (rm ANOVA) of data from Klondike and Burger 2008 – 2012 indicated significant study area and year main effects for density and biomass and a significant study area by year interaction for the sample number of taxa (Table 2-4). Tukey multiple comparisons demonstrated that density was significantly lower in 2008 and 2010 than in 2011 and 2012, and Klondike had significantly lower density than Burger. Biomass was significantly lower in 2009 than in 2012 and Klondike was lower than Burger (Table 2-4 and Fig. 2-4). Multiple comparisons for the number of taxa indicated that overall, Klondike 2009 and 2010 and Burger 2010 were significantly lower than Klondike and Burger in 2011 and 2012.

Analysis of density of the major taxonomic groups, amphipods, bivalves, gastropods, and polychaetes, by rm ANOVA for Burger and Klondike 2008 – 2012 indicated significant study area effects for Gastropoda and Polychaeta, a year effect for Gastropoda, and study area by year interaction effects for Amphipoda and Bivalvia (Table 2-4 and Fig. 2-5). Overall, Klondike 2008, 2009, and 2010, and Burger 2010 were significantly lower than Klondike and Burger in 2011 and 2012 and Burger 2008 and 2009 for amphipods and bivalves. Gastropods had lower densities in 2008–2010 than in 2011 and 2012, and Burger had lower densities than Klondike. Densities of polychaetes were significantly lower in Klondike than in Burger.

Table 2-2. Summaries of biotic variables for the study areas sampled for macrofauna during the 2008 – 2012 CSESP. Ave. = average, SD = standard deviation, Sample # Taxon = average number of taxonomic categories, Total # Taxon = number of taxonomic categories found in each study area, -- = not calculated, and ns = not sampled. Density was in ind. m^{-2} and biomass was in g m^{-2}.

2008	Klondike		Burger		Statoil	
Variable	Ave.	SD	Ave.	SD	Ave.	SD
Density	794	334	2,784	1,608	ns	ns
Biomass	179	175	333	177	ns	ns
Sample # Taxa	34	10	52	9	ns	ns
Total # Taxa	273	--	268	--	ns	ns
Shannon Diversity	5.18	--	4.90	--	ns	ns
Simpson's Evenness	0.99	--	0.98	--	ns	ns
2009	Ave.	SD	Ave.	SD	Ave.	SD
Density	1,120	686	3,979	2,724	ns	ns
Biomass	115.0	63.1	283.7	109.5	ns	ns
Sample # Taxa	41.4	13.5	58.3	7.6	ns	ns
Total # Taxa	288	--	260	--	ns	ns
Shannon Diversity	5.18	--	4.90	--	ns	ns
Simpson's Evenness	0.99	--	0.98	--	ns	ns
2010	Ave.	SD	Ave.	SD	Ave.	SD
Density	917	559	2,447	2,496	1,050	579
Biomass	192	105	285	86	355	287
Sample # Taxa	36	13	40	8	33	10
Total # Taxa	275	--	239	--	220	--
Shannon Diversity	5.35	--	4.66	--	5.13	--
Simpson's Evenness	0.99	--	0.96	--	0.99	--
2011	Ave.	SD	Ave.	SD	Ave.	SD
Density	2029	1,420	4,659	4,331	1,360	859
Biomass	158	84	389	143	260	194
Sample # Taxa	51	14	56	9	37	10
Total # Taxa	210	--	212	--	219	--
Shannon Diversity	4.22	--	3.05	--	3.95	--
Simpson's Evenness	0.97	--	0.84	--	0.96	--

Table 2-2. (cont'd)

2012	Klondike		Burger		Statoil	
Variable	Ave.	SD	Ave.	SD	Ave.	SD
Density	2,570	1,248	5,169	4,094	2,490	793
Biomass	256	160	428	126	372	141
Sample # Taxa	55	14	59	6	47	14
Total # Taxa	229	--	196	--	159	--
Shannon Diversity	3.88	--	3.01	--	3.38	--
Simpson's Evenness	0.95	--	0.83	--	0.92	--

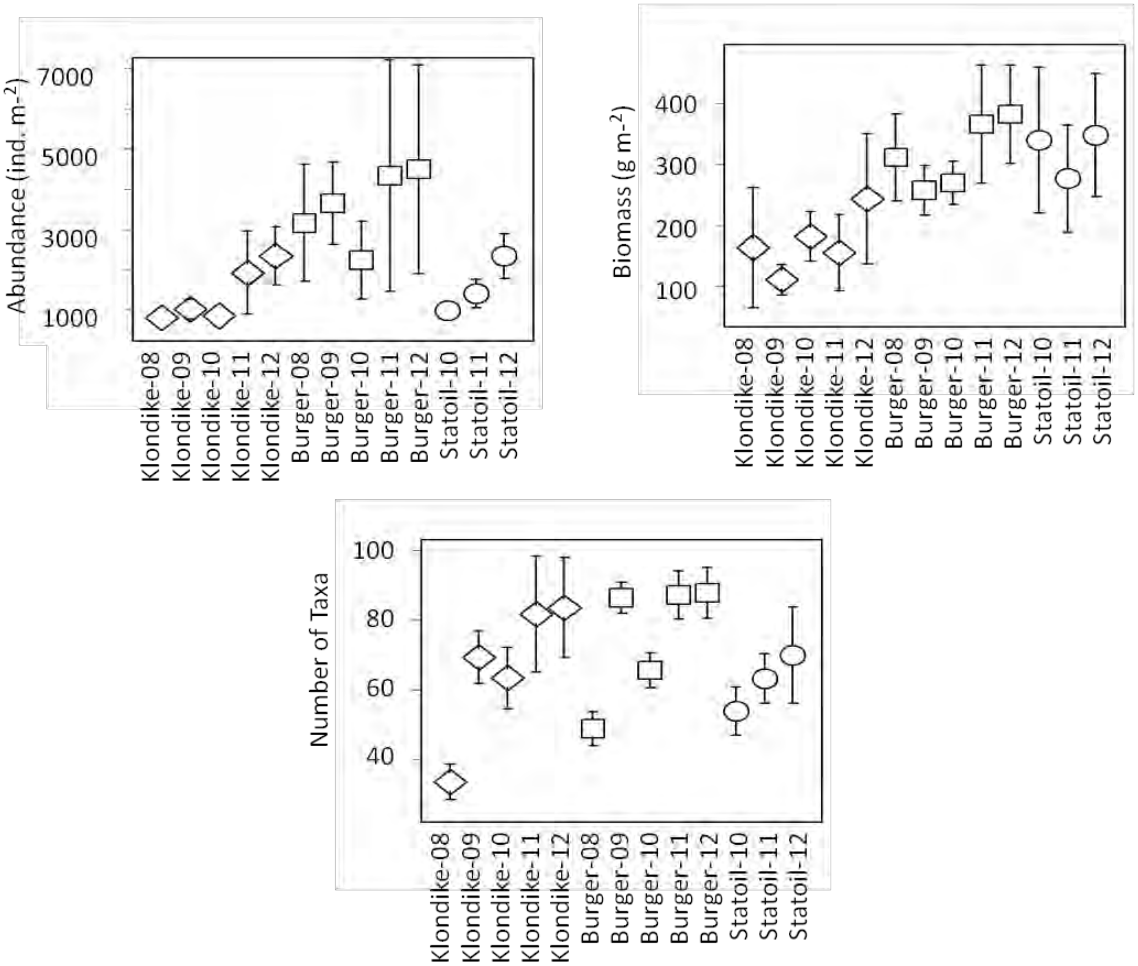


Figure 2-4. Plots of means and 95% confidence intervals based on the raw data for biological summary measures in study areas over the 2008 – 2012 CSESP study.

Table 2-3. Rankings by density and biomass of dominant animals (top ten) in Burger, Klondike, and Statoil from the 2011 – 2012 CSESP.

Study Area	Taxon	Density	Taxon	Biomass
Klondike	*Ennucula tenuis*	304	*Golfingia margaritacea*	48.2
	Protomedeia spp.	243	*Maldane sarsi*	30.6
	Cirratulidae	159	*Astarte borealis*	23.3
	Macoma spp.	126	Maldanidae	5.0
	Nuculana spp.	93	*Ennucula tenuis*	5.0
	Melita spp.	92	*Axiothella catenata*	4.2
	Capitellidae	90	*Proclea emmi*	3.9
	Maldane sarsi	85	*Praxillella praetermissa*	3.8
	Barantolla americana	74	*Nephtys caeca*	3.6
	Praxillella praetermissa	53	Polychaeta	3.5
Burger	*Maldane sarsi*	1536	*Golfingia margaritacea*	63.7
	Ennucula tenuis	343	*Astarte borealis*	46.7
	Ostracoda	245	*Maldane sarsi*	40.7
	Paraphoxus spp.	224	*Axiothella catenata*	8.4
	Macoma spp.	166	*Ennucula tenuis*	7.0
	Photis spp.	117	Maldanidae	6.0
	Cirratulidae	114	*Macoma calcarea*	5.5
	Yoldia spp.	113	*Praxillella praetermissa*	4.4
	Sabellidae	102	*Neoamphitrite groenlandica*	3.3
	Capitellidae	79	*Proclea emmi*	2.6
Statoil	*Yoldia* spp.	486	*Astarte borealis*	59.8
	Macoma spp.	254	*Macoma calcarea*	57.7
	Ennucula tenuis	212	*Golfingia margaritacea*	43.6
	Cirratulidae	148	*Yoldia hyperborea*	32.0
	Protomedeia spp.	114	*Nuculana pernula*	16.9
	Ostracoda	79	*Maldane sarsi*	16.0
	Praxillella praetermissa	63	*Musculus niger*	14.6
	Paraphoxus spp.	51	*Ennucula tenuis*	11.1
	Capitellidae	41	*Axiothella catenata*	9.5
	Thyasira flexuosa	40	*Macoma moesta*	9.0

Table 2-4. Repeated measures analysis of variance of summary statistics and density (ind. m^{-2}) of major taxonomic groups for 2008 – 2012 CSESP studies in the Klondike and Burger study areas only. Values significant at $\alpha = 0.05$ are in bold type.

Summary Statistics

Density	F-value	p-value
Study Area	14.2	**<0.0001**
Year	18.2	**<0.0001**
Study:Year	1.1	0.37684

Biomass	F-value	p-value
Study Area	72.7	**<0.0001**
Year	3.2	**0.01593**
Study:Year	0.9	0.46942

Taxa	F-value	p-value
Study Area	18.4	**<0.0001**
Year	10.6	**<0.0001**
Study:Year	2.8	**0.02921**

Key Taxa

Amphipoda	F-value	p-value
Study Area	35.2	**<0.0001**
Year	13.1	**<0.0001**
Study:Year	4.3	**0.00284**

Bivalvia	F-value	p-value
Study Area	30.2	**<0.0001**
Year	21.7	**<0.0001**
Study:Year	3.0	**0.02096**

Gastropoda	F-value	p-value
Study Area	9.5	**0.00258**
Year	5.7	**0.00033**
Study:Year	1.6	0.18679

Polychaeta	F-value	p-value
Study Area	28.3	**<0.0001**
Year	1.2	0.32786
Study:Year	0.6	0.66891

Multiple Comparisons		
Density	Year	**08, 10 < 11, 12**
	Study Area	**K < B**
Biomass	Year	**09 < 12**
	Study Area	**K < B**
Taxa	Study:Year	**09 K, 10 B, 10 K < 09 B, 11-12 B, 11-12 K, 10B < 08 K, 09B**
Amphipods	Study:Year	**08-09 K, 10 B & K < 08 B; 08 K < 11-12 B & K; 09 K, 10 B & K < 09 B; 09 K < 11-12 B & K; 10 B < 11-12 B; 10 K < 11-12 B & K**
Bivalves	Study:Year	**08-10 K < 08 B; 08 K < 09 B, 11-12 B & K; 09-10 K <09 B; 09-10 K < 11-12 B &K; 10 B < 12 B & K**
Gastropods	Year	**08, 09, 10 < 11, 12**
	Study Area	**B < K**
Polychaetes	Study Area	**K < B**

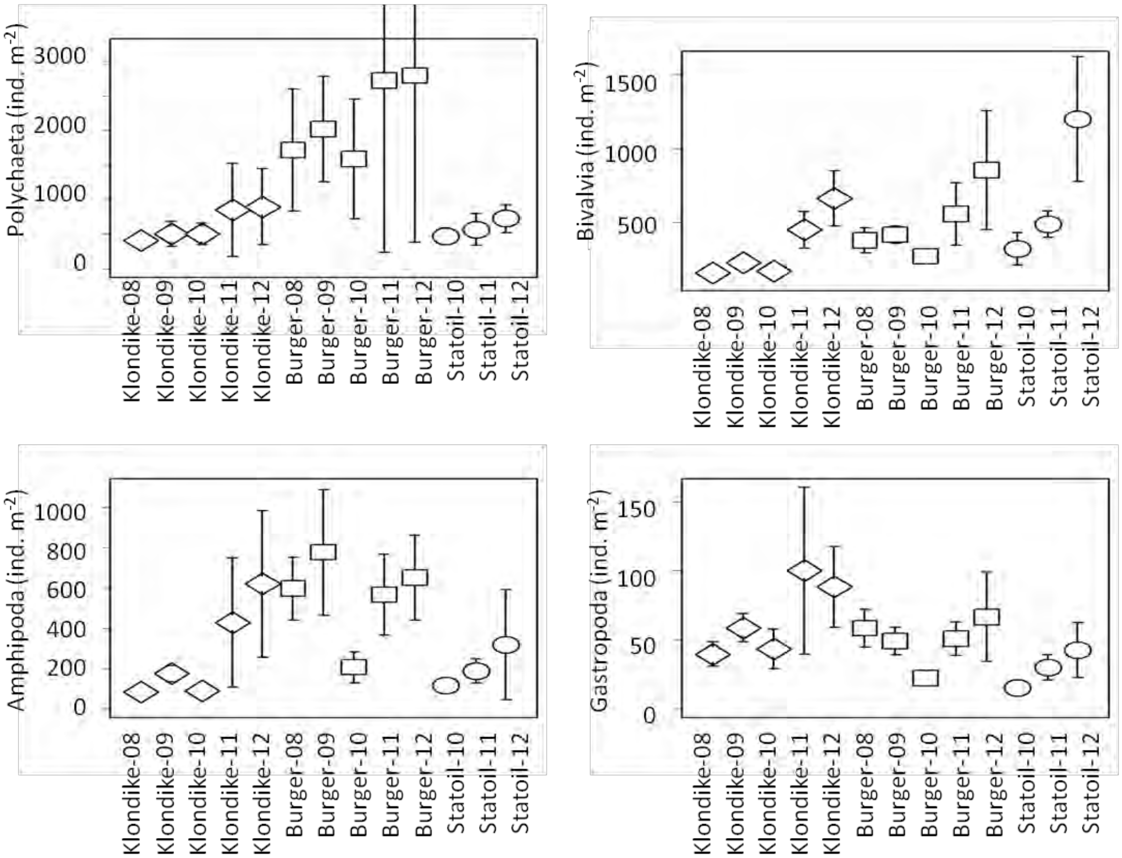


Figure 2-5. Plots of means and 95% confidence intervals based on the raw data of the density of major taxonomic groups in study areas over the 2008 – 2012 CSESP study.

When comparing data for Klondike, Burger, and Statoil from 2010 to 2012, the rm ANOVA indicated significant study area and year effects for density and number of taxa, and significant study area for biomass (Table 2-5 and Fig. 2-4). Multiple comparisons for density and the number of taxa demonstrated that in 2010 both were significantly lower than in 2011 or 2012. Density was lower in Klondike and Statoil than in Burger, biomass was lower in Klondike than in Burger or Statoil, and the number of taxa in Statoil was lower than in Klondike or Burger.

Significant study area and year effects were found for average density of amphipods, bivalves, and gastropods (Table 2-5 and Fig. 2-5). Polychaetes differed only by study area. The densities of amphipods, bivalves, and gastropods were lower in 2010 than 2011 and 2012. The densities of amphipods and gastropods were lower in Statoil than Klondike or Burger, bivalves were lower in Klondike than in Statoil or Burger, and polychaetes were lower in Klondike and Statoil than in Burger.

Table 2-5. Repeated measures analysis of variance of summary statistics for 2010-2012 CSESP studies, including Statoil.

Summary Statistics

Density	F-value	p-value
Study Area	14.2	**<0.0001**
Year	18.2	**<0.0001**
Study:Year	1.1	0.37684

Biomass	F-value	p-value
Study Area	21.4	**<0.0001**
Year	0.9	0.42609
Study:Year	1.0	0.41535

Taxa	F-value	p-value
Study Area	12.6	**<0.0001**
Year	19.8	**<0.0001**
Study:Year	1.1	0.33912

Key Taxa

Amphipoda	F-value	p-value
Study Area	11.9	**<0.0001**
Year	21.4	**<0.0001**
Study:Year	1.1	0.37083

Gastropoda	F-value	p-value
Study Area	21.2	**<0.0001**
Year	7.6	**0.00095**
Study:Year	0.4	0.80124

Bivalvia	F-value	p-value
Study Area	6.1	**0.00337**
Year	48.3	**<0.0001**
Study:Year	1.9	0.11252

Polychaeta	F-value	p-value
Study Area	13.5	**<0.0001**
Year	3.1	0.05130
Study:Year	0.6	0.67900

Multiple Comparisons		
Density	Year	**10 < 11-12**
	Study Area	**K & S < B**
Biomass	Year	**No significant differences**
	Study Area	**K < B & S**
Taxa	Year	**10 < 11, 12**
	Study Area	**S < B & K**
Amphipods	Year	**10 < 11- 12**
	Study Area	**S < B & K**
Bivalves	Year	**10 < 11-12**
	Study Area	**K < B & S**
Gastropods	Year	**10 < 11-12**
	Study Area	**S < B & K**
Polychaetes	Study Area	**K & S < B**

Multivariate analysis of macrofaunal community composition (density) for all CSESP sampling years (2008 – 2012) indicates separations by study area but not by year (Fig. 2-8). Klondike stations cluster to the bottom right, Burger stations cluster above and to the left of the Klondike stations. Statoil stations are positioned above the Klondike stations, to the right of Burger stations and mix with the other study areas. Within a study area, all years overlap suggesting little temporal trend. Thus, the MDS ordination for macrofauna reflects a moderate influence of environmental gradients in the region.

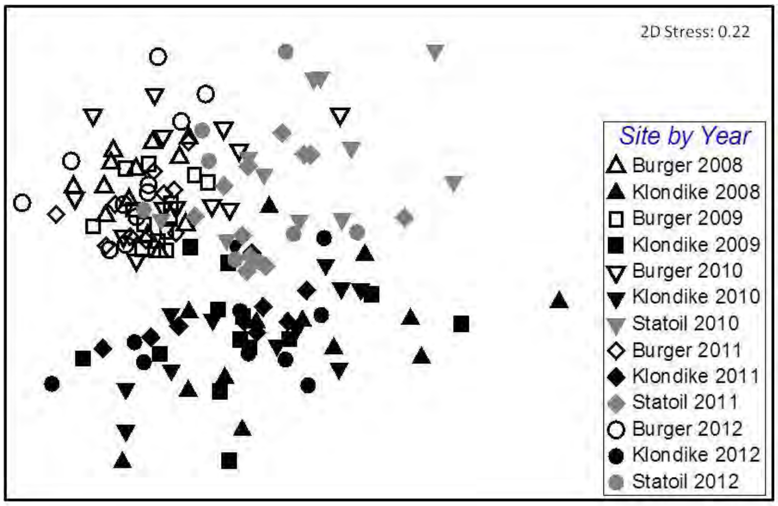


Figure 2-6. Nonmetric multidimensional scaling ordination plot of Bray-Curtis similarities for *ln*(X+1)-transformed benthic density data from 2008 – 2012 CSESP sampling.

To further investigate structure of the benthic community, the SIMPER routine of PRIMER was used to examine the taxa contributing most to the composition of each study area. Taxa (first three, by sampling period) contributing to study area similarity by density at Klondike stations were the bivalve *E. tenuis* (2008 – 2012) and the polychaetes *Barantolla americana* (2008 and 2011), Cirratulidae (2009–2010, 2012), and *M. sarsi* (2008–2010, 2012) (Table 2-6). Animals contributing most to within-study area similarity by density in Burger were the amphipod *Photis* spp. (2009), *E. tenuis* (2010–2012), ostracods (2008–2010, 2012), and the polychaetes *Lumbrineris* spp. (2008) and *M. sarsi* (2008 – 2012). In the Statoil study area, the taxa contributing to study area similarity include the bivalves *E. tenuis* (2010–2012), *Macoma* spp. (2011), *Yoldia hyperborea* (2010), and *Yoldia* spp. (2011), Cirratulidae (2012), and the maldanid polychaete *Praxillella praetermissa* (2010 and 2012).

Table 2-6. The three macrofaunal taxa contributing most to within study area average density. Sim = average similarity.

2008 Klondike
Average similarity = 41.95

Taxon	Density	Sim
Maldane sarsi	70.51	6.22
Ennucula tenuis	67.95	7.96
Barantolla americana	43.97	3.26

2010 Klondike
Average similarity = 43.78

Taxon	Density	Sim
Ennucula tenuis	112.31	10.50
Cirratulidae	59.49	3.66
Maldane sarsi	47.05	3.15

2009 Klondike
Average similarity = 44.46

Taxon	Density	Sim
Ennucula tenuis	112.31	10.50
Cirratulidae	59.49	3.66
Maldane sarsi	47.05	3.15

2011 Klondike
Average similarity = 44.76

Taxon	Density	Sim
Ennucula tenuis	172.22	9.59
Barantolla americana	61.85	3.28
Macoma spp.	65.19	2.90

2008 Burger
Average similarity = 38.27

Taxon	Density	Sim
Maldane sarsi	748.39	2.68
Ostracoda	286.67	3.98
Lumbrineris spp.	188.51	4.34

2010 Burger
Average similarity = 34.14

Taxon	Density	Sim
Maldane sarsi	1084.74	6.15
Ostracoda	135.26	2.59
Ennucula tenuis	130.90	5.41

2009 Burger
Average similarity = 40.30

Taxon	Density	Sim
Maldane sarsi	749.62	2.53
Ostracoda	289.49	3.47
Photis spp.	212.05	0.90

2011 Burger
Average similarity = 36.57

Taxon	Density	Sim
Maldane sarsi	1788.33	5.41
Ennucula tenuis	312.33	4.85
Ostracoda	415.00	3.84

2010 Statoil
Average similarity = 35.06

Taxon	Density	Sim
Ennucula tenuis	87.08	5.93
Yoldia hyperborea	65.97	1.22
Praxillella praetermissa	59.86	3.11

2011 Statoil
Average similarity = 37.72

Taxon	Density	Sim
Ennucula tenuis	159.44	10.38
Yoldia spp.	74.72	2.68
Macoma spp.	39.17	2.39

Table 2-6. Continued.

2012 Klondike
Average similarity = 37.16

Taxon	Density	Sim
Ennucula tenuis	128.66	8.83
Maldane sarsi	66.99	4.42
Cirratulidae	99.67	3.7

2012 Burger
Average similarity = 33.17

Taxon	Density	Sim
Ennucula tenuis	226.11	5.34
Maldane sarsi	1109.03	3.89
Ostracoda	268.25	3.79

2012 Statoil
Average similarity = 35.13

Taxon	Density	Sim
Ennucula tenuis	169.67	9.46
Cirratulidae	70.89	2.51
Praxillella praetermissa	56	2.4

Macrofauna, 2011 – 2012

Average density in the study area 2011–2012 ranged from 1,465 ind. m^{-2} in the North to 3,878 ind. m^{-2} in Central A. Average biomass ranged from 192 g m^{-2} in the North to 370 g m^{-2} in Central B (Table 2-7). Density and biomass varied significantly among the strata. The North stratum had lower density than South, Central A, and Central B and lower biomass than Central A and Central B (Fig. 2-7). The sample number of taxa (based on station averages) declined from south to north, from a high of 51 taxa in South and Central A to a low of 31 in the North stratum. The total number of taxa (total in each stratum) also declined with greater distance north, from 280 taxon categories in South to 182 in North. Diversity and evenness were highest in the South stratum (4.16 and 0.97) and lowest in Central A (2.90 and 0.81). The contour plot of the geostatistical model for density indicate greatest density in Burger with values declining to the south, west, and north of Burger (Fig. 2-8). The geostatistical model for biomass indicates that a peak in biomass occurs just to the east of Burger and extends slightly to the north, with low values in the southern and the northeastern regions (Fig. 2-8). Bivalve biomass peaks just to the east of the Burger study area as well (Fig. 2-9). Polychaete biomass peaks south of Burger and east of Klondike (Fig. 2-9).

Table 2-7. Average and standard deviations of total density and biomass between the four strata (South, Central A, Central B, and North), 2011 – 2012. Ave. = Average, SD = Standard deviation, Sample # Taxa = Average number of Taxonomic categories per stratum, Total # Taxa = Total number of Taxonomic categories per stratum, "--" = not calculated, density was ind. m^{-2}, and biomass was g m^{-2}.

	South		Central A		Central B		North	
Variable	Ave.	SD	Ave.	SD	Ave.	SD	Ave.	SD
Density	2,391	1,170	3,878	3,923	2,958	1,516	1,465	881
Biomass	247	148	301	152	370	162	192	101
Sample # Taxa	51	16	51	13	46	15	31	8
Total # Taxa	280	--	239	--	239	--	182	--
Shannon Diversity	4.16	--	2.90	--	3.73	--	3.83	--
Simpson's Evenness	0.97	--	0.81	--	0.95	--	0.96	--

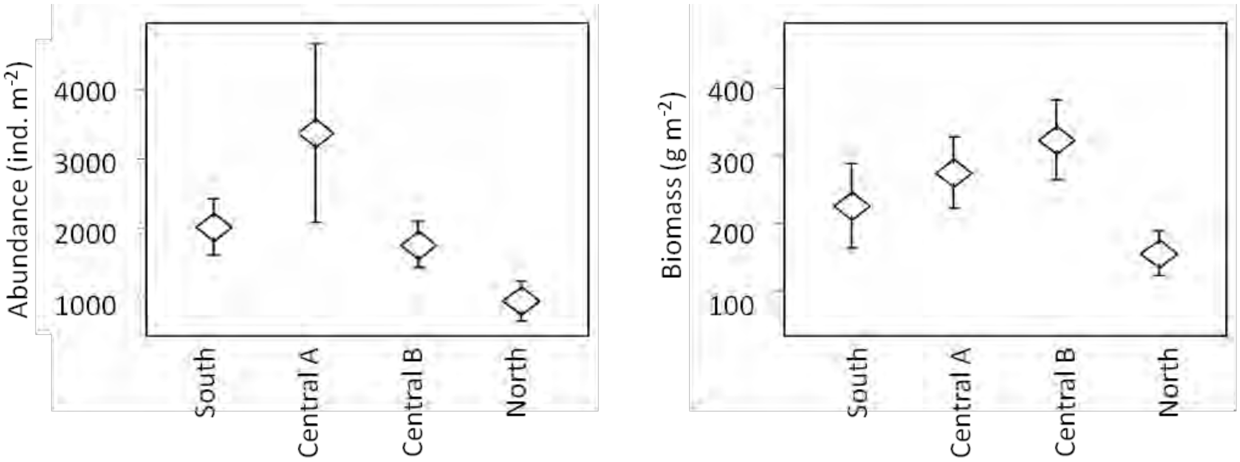


Figure 2-7. Plot of mean density (ind. m^{-2}) and biomass (g m^{-2}) with 95% confidence intervals, 2011 – 2012.

Ranking of the dominant taxon categories by density for each stratum sampled in 2011–2012 indicates an overall predominance of bivalves and polychaetes (Table 2-8). Density in the South stratum was numerically dominated by *E. tenuis*, the amphipod *Protomedeia* spp., and the polychaete family Cirratulidae. Central A was dominated by *E. tenuis*, ostracods, and *M. sarsi*. In Central B, dominants were *E. tenuis, Yoldia* spp., and Cirratulidae. *Ennucula tenuis*, *Macoma* spp. and Cirratulidae were numerical dominants of density in the North stratum.

By biomass, South was dominated by *A. borealis*, *G. margaritacea,* and *M. sarsi* (Table 2-8). Dominants in Central A were *A. borealis, M. calcarea*, and *M. sarsi*. The animals with greatest biomass in Central B were *A. borealis*, *M. calcarea*, and *Y. hyperborea* while North was dominated by *M. calcarea*, *N. pernula*, and *Y. hyperborea*.

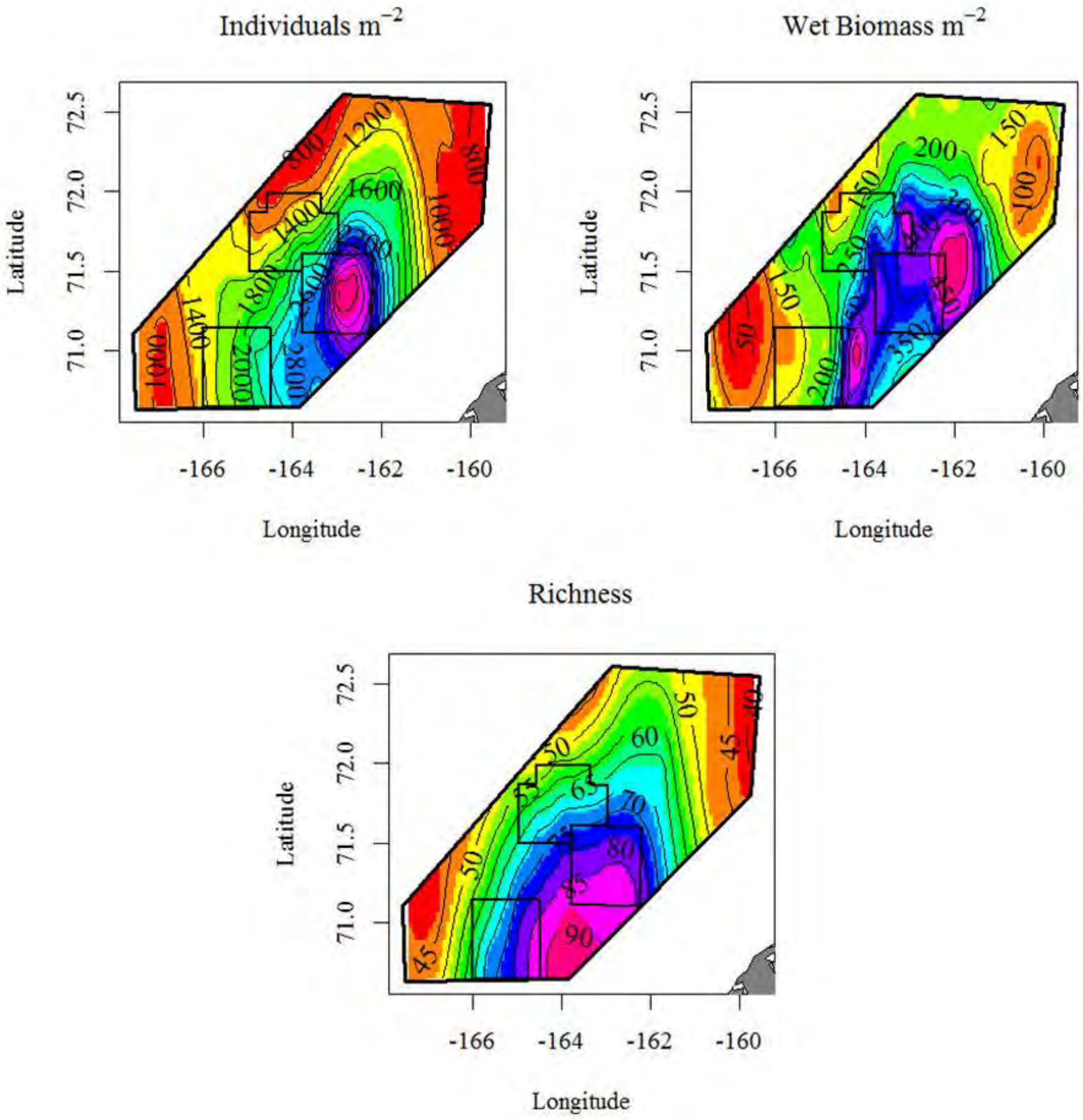


Figure 2-8. Spatial models of density (ind. m^{-2}), biomass (g m^{-2}), and richness (total number of taxa) for the regional study area of the 2011 – 2012 CSESP.

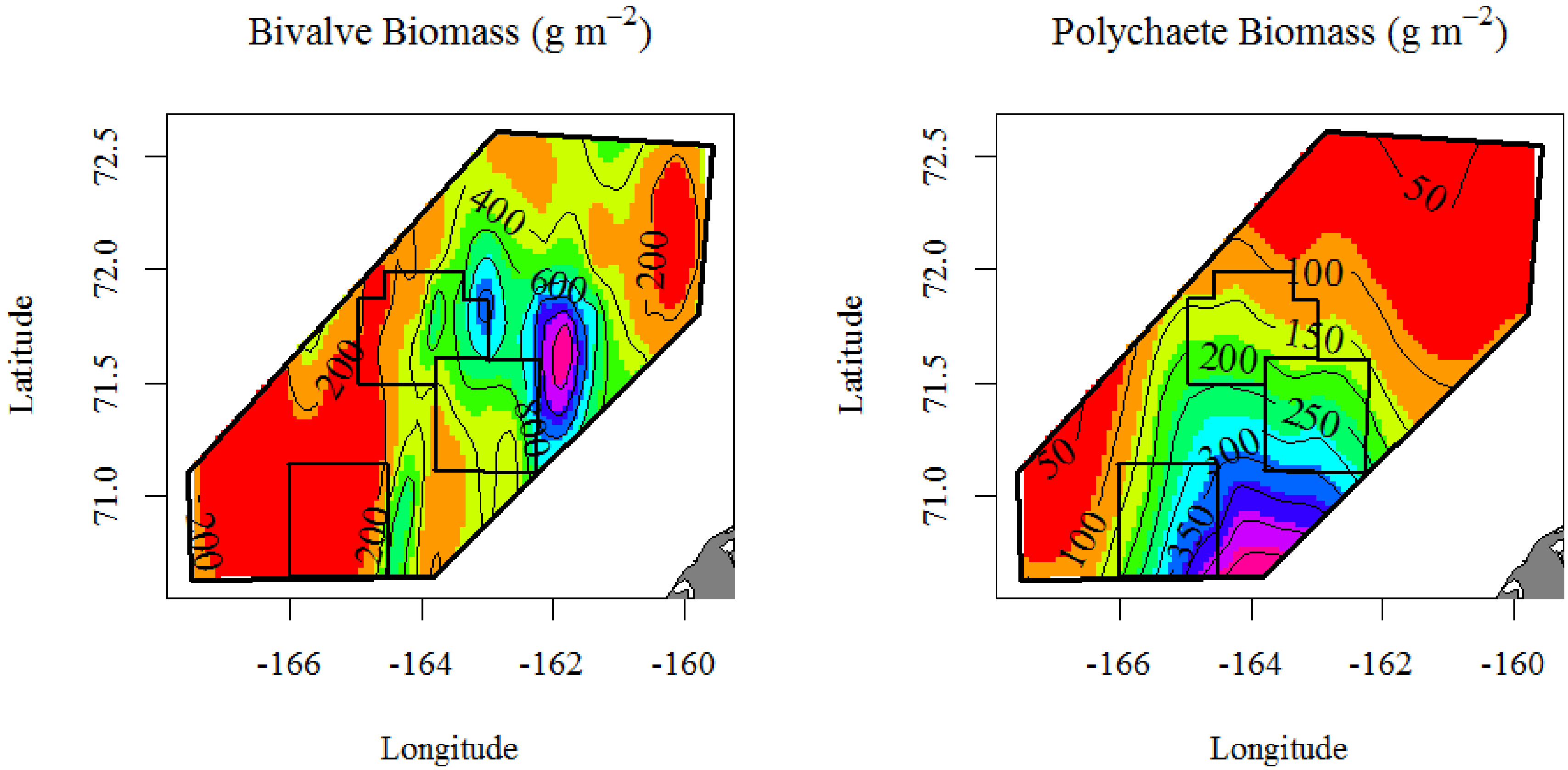
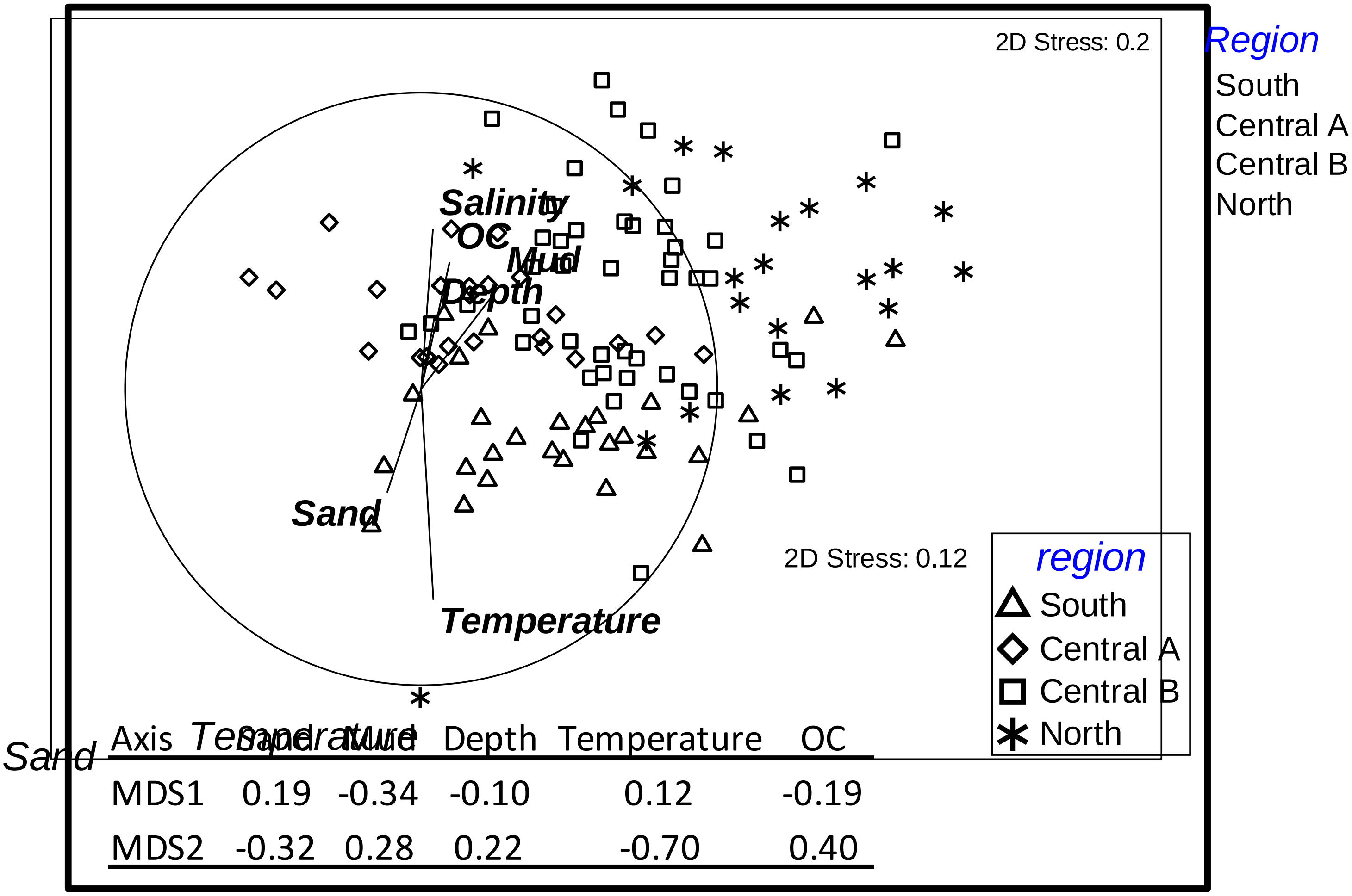


Figure 2-9. Spatial models of bivalve and polychaete density (ind. m^{-2}) and biomass (g m^{-2}) for the regional study area of the 2011 – 2012 CSESP.

Table 2-8. Rankings by density and biomass of dominant animals (top ten) by stratum of the 2011 – 2012 CSESP regional study.

Stratum	Taxon	Density	Taxon	Biomass
South	*Ennucula tenuis*	253	*Astarte borealis*	44.5
	Protomedeia spp.	148	*Maldane sarsi*	35.9
	Cirratulidae	116	*Golfingia margaritacea*	31.2
	Macoma spp.	96	*Macoma calcarea*	14.2
	Maldane sarsi	85	*Axiothella catenata*	13.8
	Capitellidae	67	*Ennucula tenuis*	8.7
	Melita spp.	66	Maldanidae	6.2
	Nuculana spp.	62	*Nuculana pernula*	4.2
	Barantolla americana	58	*Praxillella praetermissa*	3.8
	Praxillella praetermissa	43	*Musculus niger*	3.1
Central A	*Maldane sarsi*	1235	*Golfingia margaritacea*	42.4
	Ostracoda	328	*Maldane sarsi*	40.4
	Ennucula tenuis	309	*Macoma calcarea*	35.5
	Paraphoxus spp.	99	*Astarte borealis*	32.6
	Photis spp.	94	*Ennucula tenuis*	26.3
	Macoma spp.	80	*Axiothella catenata*	11.9
	Nuculana spp.	65	*Yoldia hyperborea*	8.0
	Barantolla americana	58	*Liocyma fluctuosa*	5.8
	Myriochele heeri	57	Maldanidae	5.6
	Capitellidae	51	*Protomedeia* spp.	4.1
Central B	*Ennucula tenuis*	215	*Macoma calcarea*	71.3
	Yoldia spp.	209	*Astarte borealis*	36.9
	Cirratulidae	159	*Yoldia hyperborea*	30.1
	Macoma spp.	142	*Ennucula tenuis*	22.7
	Macoma calcarea	50	*Nuculana pernula*	21.8
	Paraphoxus spp.	46	*Golfingia margaritacea*	21.3
	Protomedeia spp.	42	*Maldane sarsi*	16.9
	Yoldia hyperborea	38	*Macoma moesta*	16.7
	Lumbrineris spp.	32	Hydrozoa	11.9
	Thyasira flexuosa	28	*Musculus niger*	5.6
North	*Macoma* spp.	124	*Macoma calcarea*	48.5
	Ennucula tenuis	116	*Yoldia hyperborea*	18.6
	Cirratulidae	61	*Nuculana pernula*	16.9
	Yoldia spp.	54	*Ennucula tenuis*	13.1
	Sabellidae	37	*Astarte borealis*	8.2
	Macoma calcarea	26	*Maldane sarsi*	4.2
	Nereimyra aphroditoides	22	*Liocyma fluctuosa*	3.5
	Byblis spp.	22	*Nephtys punctata*	3.4
	Nuculana pernula	22	*Macoma moesta*	3.4
	Nuculana spp.	18	*Golfingia margaritacea*	2.8

Multivariate analysis of macrofaunal density indicated a gradient following the latitudinal difference among strata from the middle to the upper right corner of the plot (Fig. 2-12). The South stations cluster in middle of the plot and to the upper right, followed by mixed Central A and Central B stations to the right, and finally stations from the North stratum in the upper right but spreading to the lower portion of the plot. This gradient reflects, to some extent, the influence of known environmental gradients from the southwest of Hanna Shoal to the northeast (Fig. 2-3). The overlay of fitted correlations on the MDS ordination shows stations increasing in bottom-water temperature towards the upper left, increasing in longitude towards the bottom right, and increasing in percent mud and water depth towards the upper right corner of the plot.



Axis	Sand	Mud	Depth	Temperature	OC
MDS1	0.19	-0.34	-0.10	0.12	-0.19
MDS2	-0.32	0.28	0.22	-0.70	0.40

Figure 2-10. Nonmetric multidimensional scaling ordination plot of Bray-Curtis similarities for *ln*(X+1)-transformed macrofaunal density data. Overlays of environmental variables and their correlations (Spearman's ρ) with the MDS axes are presented.

The BIOENV analysis demonstrates moderate spatial structuring of the biological communities in the CSESP study area. The three-variable combination of latitude, longitude, and bottom-water salinity had the highest correlation with the biological similarity matrix (Table 2-9). Water depth, salinity, temperature, and organic carbon had the highest correlation with the biological similarity matrix when the spatial coordinates were excluded, although the correlation was low (ρ= 0.24) (Table 2-9).

The taxa contributing most to regional similarity, by density within the South, Central A, and North strata were the bivalves *E. tenuis* and *Macoma* spp. and the polychaete family Cirratulidae (Table 2-10). The bivalve *Yoldia* spp. contributed to stratum similarity in Central B, as well.

Table 2-9. Best fitting Spearman correlations from BIOENV program listing the variables with the highest correlation (Spearman's ρ) with the density similarity matrix.

Variables	ρ
Latitude, Longitude, Salinity	0.479
Latitude, Longitude	0.476
Longitude, Salinity	0.443
Without spatial coordinates:	
Depth, Salinity, Water temperature, OC	0.244

Table 2-10. The three macrofaunal taxonomic categories contributing most to within-stratum similarity. Sim = average similarity as determined by SIMPER.

South Average similarity: 42.94

Taxon	Ave. Abun	Ave. Sim	% Contr
Ennucula tenuis	239	15.89	37.01
Macoma spp.	78	4.56	10.63
Cirratulidae	61	3.38	7.86

Central A Average similarity: 28.30

Taxon	Ave. Abun	Ave. Sim	% Contr
Ennucula tenuis	271	6.61	23.36
Macoma spp.	90	2.6	9.19
Cirratulidae	130	1.94	6.84

Central B Average similarity: 40.23

Taxon	Ave.	Ave.	%

North Average similarity: 30.73

Taxon	Ave.	Ave.	%

	Abun	Sim	Contr		Abun	Sim	Contr
Ennucula tenuis	257	12.49	31.05	*Ennucula tenuis*	124	6.51	21.18
Yoldia spp.	137	4.5	11.2	*Macoma* spp.	185	5.51	17.93
Macoma spp.	116	4.45	11.07	*Cirratulidae*	135.62	5.32	17.31

Megafauna, 2011 – 2012

Nineteen to thirty-three megafaunal taxon categories were identified from van Veen grab samples collected in the CSESP regional study area, 2011 – 2012, with the highest number of taxa in the South stratum (33) and the lowest in the North stratum (19; Table 2-11; see Appendix II for a list of megafaunal organisms). The South stratum had the highest density (137 ind. m^{-2}) and the Central B strata the lowest (16 ind. m^{-2}), while biomass was highest in Central A (40.9 g m^{-2}) and lowest in the North stratum (19 g m^{-2}). Comparing confidence intervals, density in Central B was significantly less than in the Central A stratum while biomass in the Central B and North strata was significantly less than in Central A.

Table 2-11. Average density and biomass and the total number of taxa for each strata in the CSESP regional study area 2011 – 2012.

	Density			Biomass				
Strata	Ave.	SD	95% CI	Ave.	SD	95% CI	N	Total # Taxa
South	137	254	(10.3, 263.2)	29.1	39.5	(9.4, 48.8)	18	33
Central A	60	44	(39.8, 80.8)	40.9	31.3	(26.2, 55.5)	20	25
Central B	16	18	(9.1, 22.3)	14.7	16.0	(8.8, 20.6)	31	23
North	69	231	(-42.4, 180.5)	6.4	10.2	(1.5, 11.3)	19	19

Dominant megafauna by density across the strata in 2011 – 2012 included barnacles, brittle stars, bryozoans, and Urochordata (sea squirts; Table 2-12). Animals with the highest densities in South included the barnacles *Balanus* spp., class Ophiuroidea (unidentifiable brittle stars), and the limpet *Lepeta caeca*. The most numerous megafauna in Central A were brittle stars, *O. sarsi*, Ophiuroidea, and *Amphiodia craterodmeta*, with the top five animals all being echinoderms. In Central B, the most numerous organisms were the brittle stars Ophiuroidea and *O. sarsi*, as well as class Holothuroidea, the sea cucumbers. The bryozoan *Alcyinidium disciforme* was most numerous in North followed by *Balanus* spp. and Holothuroidea.

Animals with highest biomass in the study area were echinoderms (brittle stars and sea cucumbers), large snails, and sea squirts (Table 2-13). The sea cucumber *Psolus fabricii*, *O. sarsi*, and *Balanus crenatus* were dominant by biomass in the South stratum. *Ophiura sarsi* and the large snails *Neptunea heros* and *Buccinum polaris* were dominant in Central A. Biomass in Central B was dominated by *O. sarsi*, the sea squirt *Pelonaia corrugata*, and the snow crab *Chionoecetes opilio*. North was dominated by *O. sarsi*, *P corrugata* and class Ascidiacea.

Table 2-12. Ranking by density (ind. m^{-2}) of dominant megafauna from the CSESP regional study area 2011 – 2012.

Strata	Taxon	Density	Analysis Group
South	*Balanus* spp.	86	Cirripedia
	Ophiuroidea	30	Echinodermata
	Lepeta caeca	20	Gastropoda
	Amphiodia craterodmeta	12	Echinodermata
	Psolus fabricii	8	Echinodermata
	Ophiura sarsi	7	Echinodermata
	Ascidiacea	7	Urochordata
	Ophiuridae	6	Echinodermata
	Bryozoa	4	Bryozoa
	Ischnochiton albus	4	Polyplacophora
Central A	*Ophiura sarsi*	43	Echinodermata
	Ophiuroidea	16	Echinodermata
	Amphiodia craterodmeta	8	Echinodermata
	Holothuroidea	5	Echinodermata
	Ophiuridae	3	Echinodermata
	Bryozoa	2	Bryozoa
	Balanus spp.	2	Cirripedia
	Gersemia rubiformis	1	Cnidaria
	Pelonaia corrugata	1	Urochordata
	Ascidiacea	1	Urochordata
Central B	Ophiuroidea	7	Echinodermata
	Ophiura sarsi	6	Echinodermata
	Holothuroidea	3	Echinodermata
	Pelonaia corrugata	3	Urochordata
	Ophiuridae	2	Echinodermata
	Bryozoa	2	Bryozoa
	Amphiodia craterodmeta	1	Echinodermata
	Ascidiacea	1	Urochordata
	Amphiophiura pachyplax	1	Echinodermata
	Brachyura	1	Decapoda
North	*Alcyonidium disciforme*	44	Bryozoa
	Balanus spp.	8	Cirripedia
	Holothuroidea	5	Echinodermata
	Ascidiacea	5	Urochordata
	Ophiuroidea	3	Echinodermata

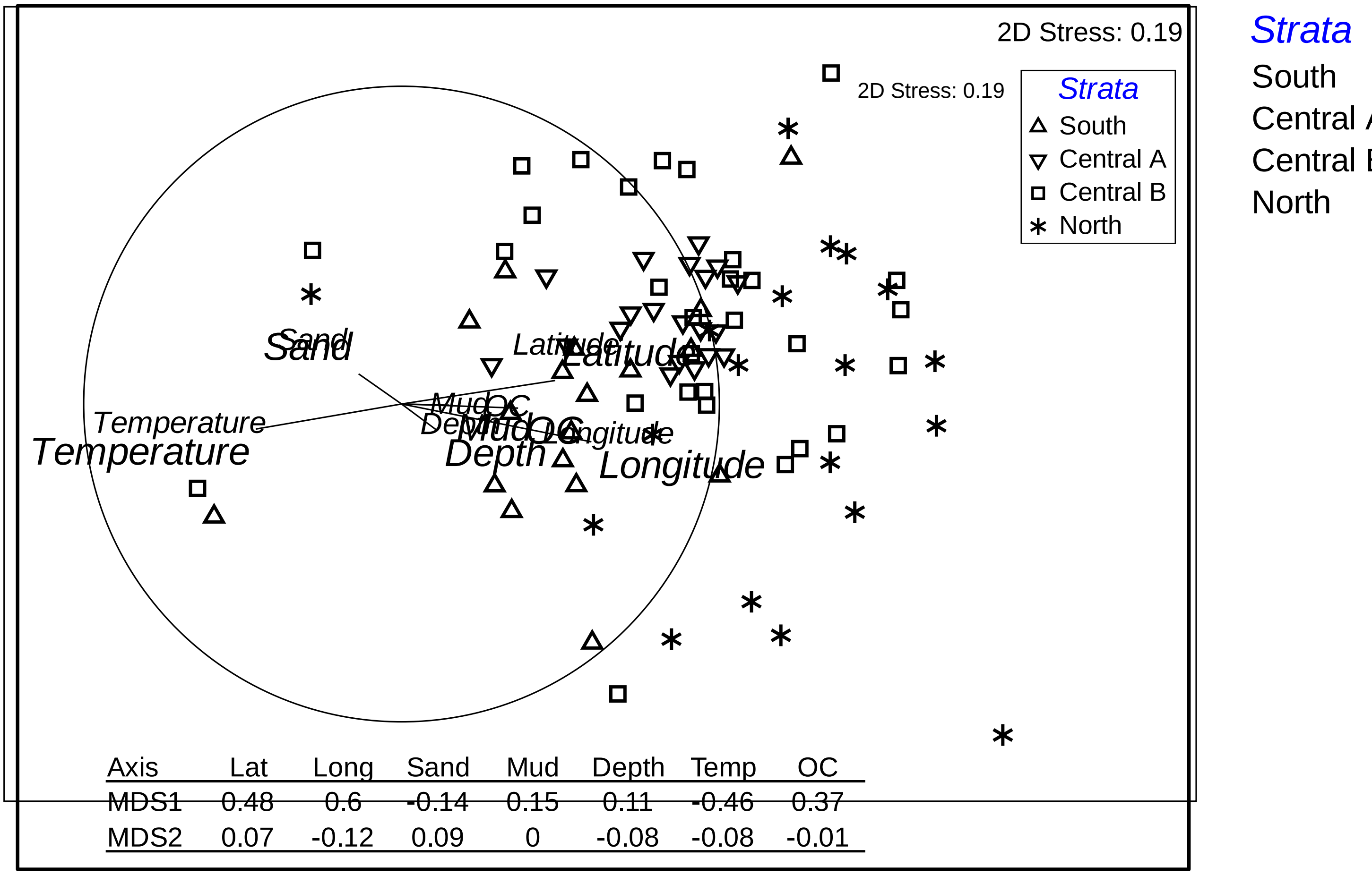
	Bryozoa	1	Bryozoa
	Ophiuridae	1	Echinodermata
	Ophiura sarsi	1	Echinodermata
	Amphiophiura pachyplax	1	Echinodermata
	Myriotrochus rinkii	1	Echinodermata

Table 2-13. Ranking by biomass (g m^{-2}) of dominant megafauna from the CSESP regional study area 2011 – 2012.

Strata	Taxon	Biomass	Analysis Group
South	*Psolus fabricii*	7.84	Echinodermata
	Ophiura sarsi	5.66	Echinodermata
	Balanus crenatus	3.29	Cirripedia
	Neptunea ventricosa	2.21	Gastropoda
	Ascidiacea	2.20	Urochordata
	Bryozoa	1.67	Bryozoa
	Gersemia rubiformis	1.54	Cnidaria
	Neptunea communis	1.30	Gastropoda
	Pagurus spp.	0.99	Decapoda
	Holothuroidea	0.86	Echinodermata
Central A	*Ophiura sarsi*	23.25	Echinodermata
	Neptunea heros	3.35	Gastropoda
	Buccinum polare	3.05	Gastropoda
	Psolus fabricii	1.36	Echinodermata
	Neptunea spp.	1.26	Gastropoda
	Neptunea ventricosa	1.12	Gastropoda
	Leptasterias spp.	1.11	Echinodermata
	Caridea	1.08	Decapoda
	Pelonaia corrugata	0.80	Urochordata
	Amphiodia craterodmeta	0.74	Echinodermata
Central B	*Ophiura sarsi*	6.41	Echinodermata
	Pelonaia corrugata	3.22	Urochordata
	Chionoecetes opilio	1.02	Decapoda
	Bryozoa	0.88	Bryozoa
	Amphiophiura pachyplax	0.34	Echinodermata
	Holothuroidea	0.31	Echinodermata
	Myriotrochus rinkii	0.25	Echinodermata
	Hyas coarctatus	0.24	Decapoda
	Buccinum polare	0.23	Gastropoda
	Gersemia rubiformis	0.20	Cnidaria
North	*Ophiura sarsi*	1.28	Echinodermata
	Ascidiacea	1.16	Urochordata
	Pelonaia corrugata	1.15	Urochordata
	Styelidae	0.93	Urochordata
	Alcyonidium disciforme	0.87	Bryozoa

Chiridota spp.	0.86	Echinodermata
Neptunea communis	0.42	Gastropoda
Myriotrochus rinkii	0.42	Echinodermata
Bryozoa	0.29	Bryozoa
Holothuroidea	0.20	Echinodermata

The MDS ordination of the megafaunal data demonstrated moderate overlap of community structure among the strata (Fig. 2-11). There was some trend in the ordination as stations from the North stratum tended towards the right, South stations were largely to the left, and Central A and B stations were in the center of the ordination. Latitude, longitude, bottom-water temperature, and OC had moderate correlations with the MDS axes. Temperature and latitude were strongly correlated with Axis 1 reflecting warmer water in the southern stations (Fig. 2-3). OC, percent mud, and water depth were positively correlated and all were negatively correlated with percent sand, but only OC had moderate correlation with Axis 1 (Fig. 2-11).



Axis	Lat	Long	Sand	Mud	Depth	Temp	OC
MDS1	0.48	0.6	-0.14	0.15	0.11	-0.46	0.37
MDS2	0.07	-0.12	0.09	0	-0.08	-0.08	-0.01

Figure 2-11. Nonmetric multidimensional scaling of log(X+1)-transformed megafauna density from the CSESP regional sampling area 2011 – 2012. Spearman's correlations between MDS axes and physical variables are presented. Lat = latitude, Long = longitude, Temp = bottom-water temperature.

Population Dynamics of Ennucula tenuis and Macoma *spp.*

Spatial variability in the length-frequency distributions of *E. tenuis* was high (Figs. 2-12 and 2-13). Overall, the bivalve populations were bimodal with peaks at 2–3 mm and around 12–13 mm. Length-frequency distributions in Klondike were generally unimodal with a very small peak at lengths around 12–13 mm and strongly right-skewed with a sharp decline in the number of larger individuals (Fig. 2-12). Burger demonstrated bimodal distributions for all years with peaks at 2–3 mm and 12-14 mm. The length-frequency distribution for *E. tenuis* in Statoil was bimodal in 2010, but there was a much smaller peak at 12 mm in 2011 and all curves were dominated by a peak at about 2–3 mm in 2010 – 2012. The high proportions of smaller bivalves at Klondike and Statoil suggest poorer survival for *E. tenuis*. For the regional study area, the length frequency histograms for *E. tenui*s demonstrated a reduced peak for larger bivalves in the South stratum but bimodal distributions in the other strata (Fig. 2-13).

Average and median lengths of *E. tenuis* in Klondike (median from 2.65 to 4.24 mm) from 2008 and 2010 were smaller than those found in Burger (median from 4.78 to 8.01 mm) and Statoil (2.38 to 7.38 mm) with smallest lengths observed in 2012 for all study areas (Fig. 2-12). Presuming that peaks in lengths at 2–3 mm were cohort 1 bivalves (experiencing their first year's growth after late-winter/early-spring recruitment), the second peak in the histograms may reflect a second year's growth. Maximum lengths were similar, although the maximum length in Klondike from 2008 – 2012 (14.9 mm) was slightly smaller than in Burger (17.9 mm) or Statoil (16.8 mm). There was little difference in length among strata for *E. tenuis* although mean and median lengths were smallest in the South stratum reflecting the patterns observed in Klondike (Fig. 2-13). Overall, annual variations in juvenile bivalve recruitment were the stronger features of the length frequency histograms. The length frequency distributions provide no evidence for significant temporal variations, aside from highly variable recruitment.

Length frequency histograms for *Macoma* spp. were highly right-skewed (Fig. 2-14). There were no meaningful differences among histograms as all strata were dominated by smaller bivalves (median lengths between 2.7 to 5.1 mm), although median lengths were smaller in the northern strata. Maximum lengths varied between 37.8 mm to 46.2 mm, with the largest lengths found in the South stratum.

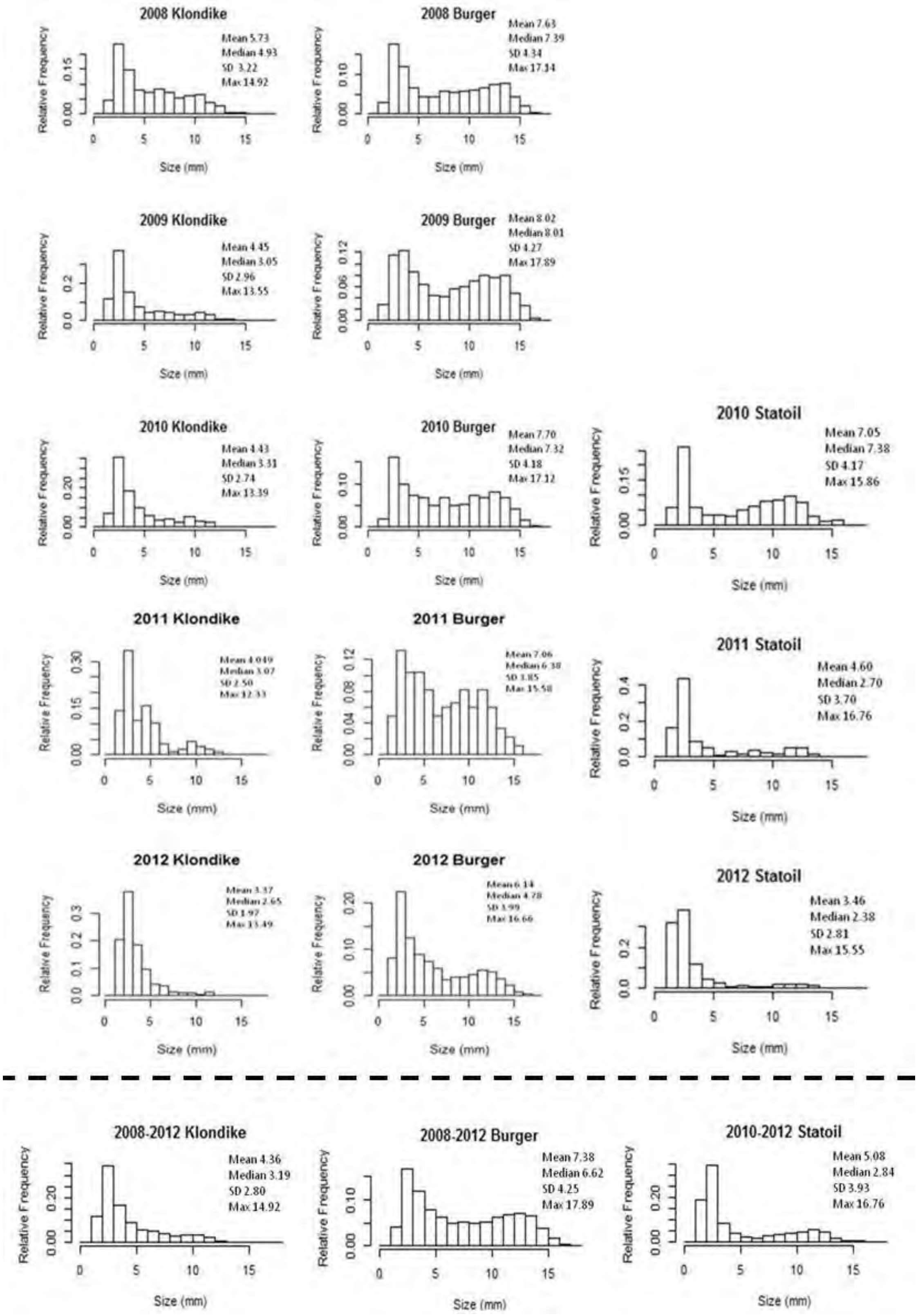
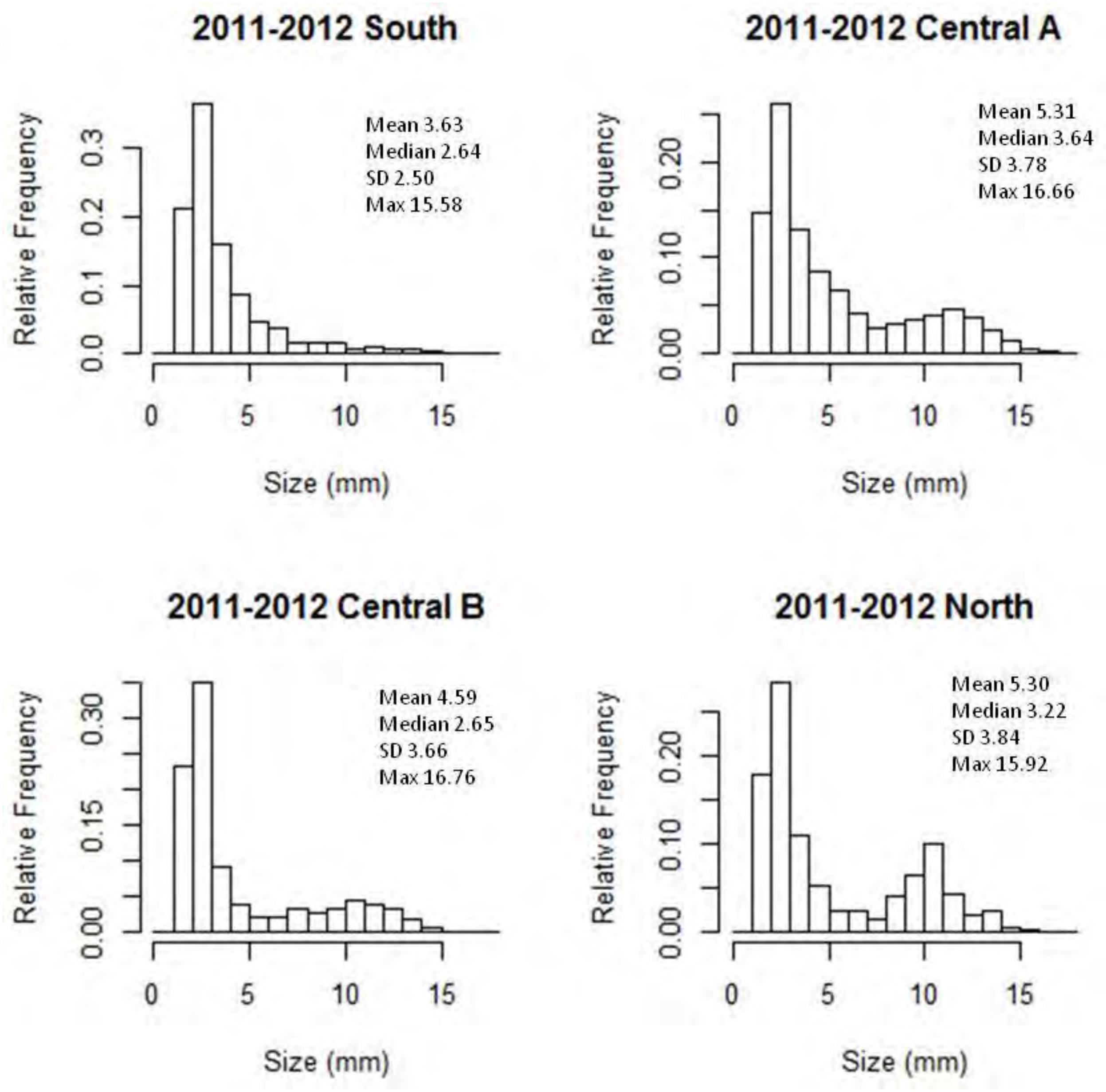


Figure 2-12. Relative length-frequency histograms of *Ennucula tenuis* for the Klondike, Burger, and Statoil study areas, 2008 – 2012.


2011-2012 South

2011-2012 Central A

2011-2012 Central B

2011-2012 North

Figure 2-13. Relative length-frequency histograms of *Ennucula tenuis* for the regional study area, 2011–2012.

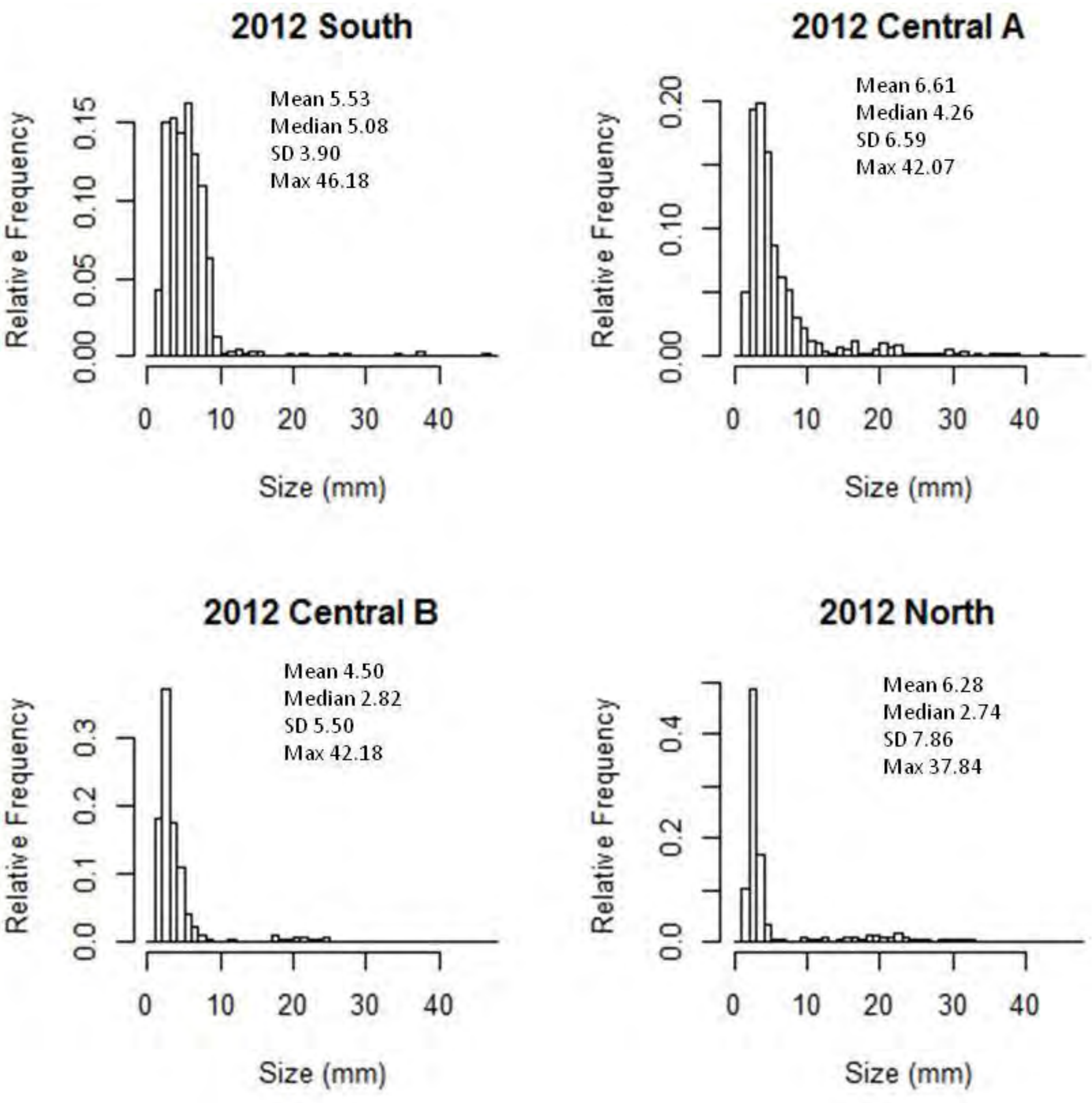


Figure 2-14. Relative length-frequency histograms of *Macoma* spp. for the regional study area, 2012.

The CSESP Distributed Biological Observatory Line

Eleven benthic stations were sampled along the CSESP Distributed Biological Observatory (DBO) line in 2012. They were, from inshore to offshore, stations DF002, DF004, DF006, BF005, BF009, BF013, BF017, BF021, SF009, SF0014, and DF007.

Sediment characteristics of the DBO line change with distance offshore. The most eastern stations (DF002 and DF004; closest to shore) had coarser substrates while stations further from shore had higher proportions of mud (Fig. 2-15). The coarsest sediments were observed at DF002 and the muddiest sediments at BF013. The increased mud follows closely with increased water depth.

Biological trends along the DBO line were weakly apparent from DF002 to DF007. Neither density nor biomass demonstrated a spatial trend as peak values occurred in the middle of the DBO line (Fig. 2-15). Peak density occurred at BF013 and high biomass values occurred at DF004 and BF021. Numerical densities at stations on the DBO line were dominated by amphipods, bivalves, and polychaetes. Amphipod density was proportionally greater inshore, lowest at BF013, but still substantially high at the remaining DBO stations. Polychaete density peaked at BF013 and was highest offshore. Bivalve density was also proportionally higher offshore. Bivalves were proportionally, the most dominant macrofaunal group by biomass ranging from about 20% to nearly 60% of total biomass. Starting with the most eastern stations, those closest inshore, characteristic taxa shifted from the amphipods *Protomedeia* spp. and *Ampelisca macrocephala* to the bivalve *Nuculana pernula* and amphipod *Melita* spp. at station DF007 (Table 2-14). Characteristic taxa at the remaining DBO stations were ostracods, polychaetes of the family Maldanidae including *M. sarsi*, and bivalves, including *Ennucula tenuis*. Biomass was dominated by large bivalves with dominants including *Astarte borealis* and *Macoma calcarea*, large or numerous polychaetes, and the peanut worm *Golfingia margaritacea*. Mean density was very high at station BF013 due to extremely high densities of *Maldane sarsi*.

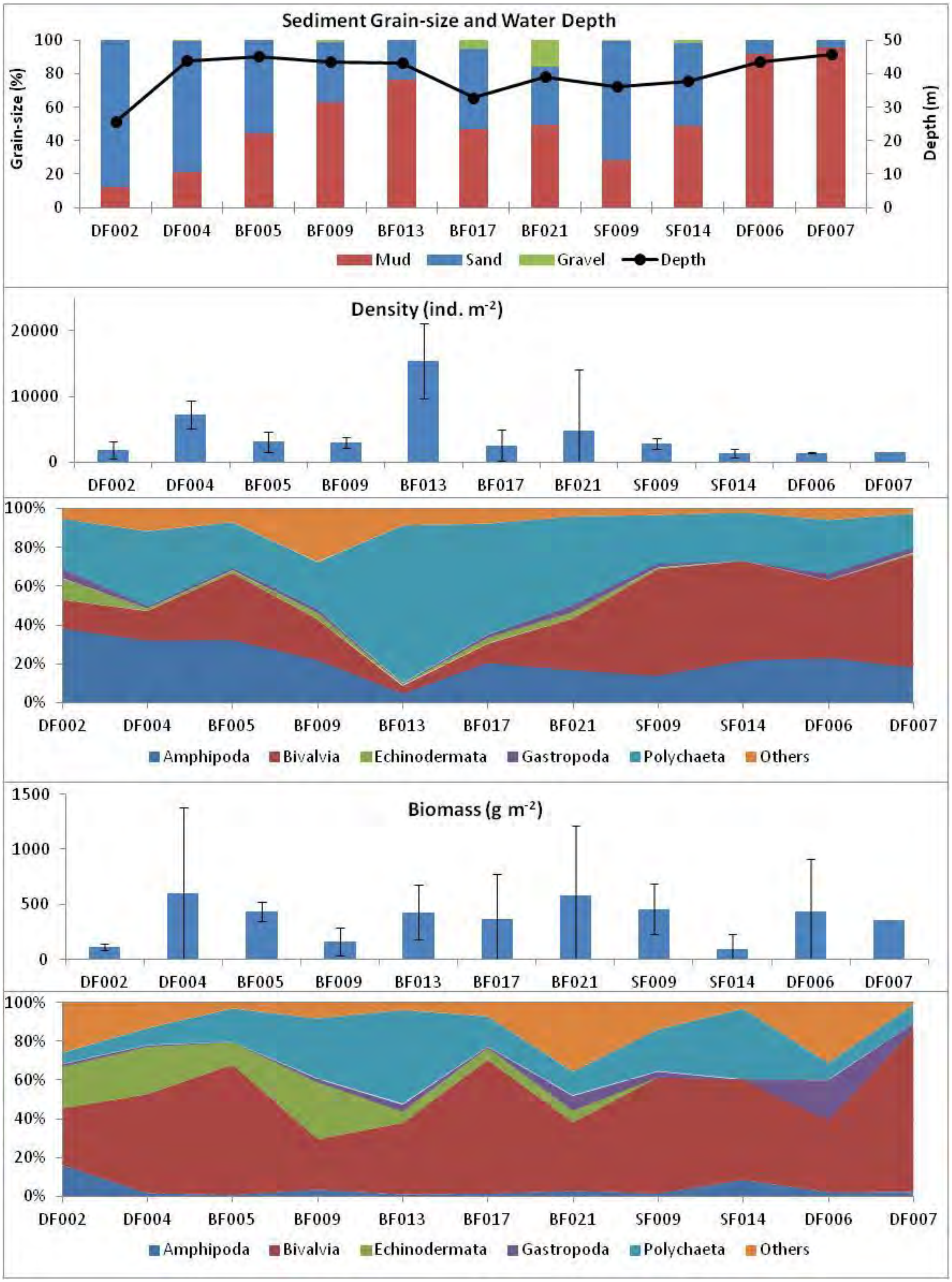


Figure 2-15. Environmental and biological characteristics of stations along the Distributed Biological Observatory line, 2012.

Table 2-14. Ranking of dominant taxa (first three) by density (ind. m^{-2}) and biomass (g m^{-2}) for stations along the Distributed Biological Observatory line, 2012.

Station	Taxon	Density	Taxon	Biomass
DF002	*Protomedeia* spp.	253	*Cyclocardia crebricostata*	18.45
	Ampelisca macrocephala	143	*Ampelisca eschrichti*	14.36
	Galathowenia oculata	143	*Yoldia myalis*	13.77
DF004	*Ennucula tenuis*	663	*Astarte borealis*	346.15
	Protomedeia spp.	530	*Hyas coarctatus*	44.45
	Capitellidae	427	*Nicomache lumbricalis*	18.35
BF005	*Ennucula tenuis*	587	*Astarte borealis*	158.76
	Photis spp.	437	*Liocyma fluctuosa*	74.78
	Haploops laevis	233	*Macoma calcarea*	32.70
BF009	Ostracoda	540	*Flabelligera mastigophora*	32.18
	Ennucula tenuis	433	*Ennucula tenuis*	29.47
	Photis spp.	293	*Axiothella catenata*	16.40
BF013	*Maldane sarsi*	10420	*Maldane sarsi*	202.33
	Ostracoda	733	*Ennucula tenuis*	57.93
	Ennucula tenuis	453	*Astarte borealis*	45.33
BF017	*Paraphoxus* spp.	323	*Astarte borealis*	148.34
	Orbiniidae	163	*Axiothella catenata*	33.73
	Sabellidae	157	*Ennucula tenuis*	33.38
BF021	*Paraphoxus* spp.	573	*Golfingia margaritacea*	95.19
	Yoldia spp.	437	*Macoma moesta*	79.20
	Ennucula tenuis	287	*Macoma calcarea*	63.69
SF009	*Macoma* spp.	557	*Astarte borealis*	181.26
	Yoldia spp.	483	*Golfingia margaritacea*	56.60
	Ennucula tenuis	300	*Macoma calcarea*	44.50
SF014	*Yoldia* spp.	303	*Astarte borealis*	30.86
	Melita spp.	217	*Macoma calcarea*	9.51
	Macoma spp.	177	*Praxillella praetermissa*	7.83
DF006	*Ennucula tenuis*	227	*Golfingia margaritacea*	143.20
	Macoma s spp.	170	*Yoldia hyperborea*	127.61
	Protomedeia spp.	123	*Astarte borealis*	35.08
DF007	*Nuculana pernula*	547	*Macoma calcarea*	115.63
	Melita spp.	193	*Serripes groenlandicus*	87.72
	Macoma spp.	90	*Yoldia hyperborea*	33.21

DISCUSSION

Benthic Ecology of the Northeastern Chukchi Sea

Benthic fauna of Klondike, Burger, and Statoil are diverse, very 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, 2013 a and 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, in press). The high density and biomass of the communities in the study area indicate that a large amount of seasonal production is reaching the benthos. The benthic macrofaunal community in Burger has higher density and biomass, deeper water depths, and a longer persistence of cold winter water (indicating environmental and biological differences resulting from a change in oceanographic conditions relative to Klondike) (Faulkner et al., 1994; Weingartner et al., 2005, 2013; Blanchard et al., 2011, 2013). Feder et al. (1994) also demonstrated higher biomass at stations closest to the Burger study area and related broad-scale biological patterns to landscape-level environmental gradients. The high density and biomass values in Burger (adjacent to a documented biological hot spot) presumably reflect the high availability of food resources within the sediments due to interactions of the bottom topography with water currents, as reflected in its greater depth Blanchard et al., 2013 a).

Associations of Fauna with Environmental Characteristics

Animal-sediment interactions are a complex mosaic of biologically-mediated relationships of fauna with their physical environment and there are many factors influencing community development of macrofauna. These factors include water currents and current speeds, frequency of disturbance, flux of carbon to the benthos, adsorption of organics to sediment particles, deposition of organics, percent total organic carbon in sediments (TOC), and bioturbation (Weston, 1990; Hall, 1994; Snelgrove and Butman, 1994; Lenihan and Micheli, 2001; Bluhm and Gradinger, 2008). Feeding and burrowing activities of macrofauna can substantially modify habitat and sediment column characteristics as well (Romero-Wetzel, 1987; Levin et al., 1997; Shields and Kędra, 2009); macrofauna are noted to burrow to depths of 20 – 30 cm in soft sediments of the northeastern Chukchi Sea (Nelson et al., 1994). Community structure commonly correlates with sediment grain-size as a proxy for the range of physical processes covarying with grain-size and driving biodiversity, biomass, and community structure. The covariance between biological and environmental characteristics is reflected in the dominance of deposit-feeding organisms in muddy sediments as finer particle sizes indicate lower physical dynamics and disturbances. Higher proportions of particulate organic carbon are associated with greater percent mud (organics bind to mud), which then leads to increased deposit-feeding. Thus, the actual determinants of community structure can be difficult to clearly identify. Bluhm and Gradinger (2008) and others suggest food resources, seawater salinity and temperature, disturbance, and sediment factors are major determinants of arctic benthic community structure (Cusson et al., 2007). The underlying environmental features driving gradients in food availability, oceanographic and geochemical characteristics, and physical dynamics are driven in part, by interactions between seafloor geomorphology and water movements in the present study area. Distance from shore, increasing water depth, and disturbance from storms and ice gouging also contribute to measurable environmental and biological gradients, as well as to variations in water circulation that can affect carbon deposition. Topographic control over water current flow and divergences may be a large-scale source of change that can result in increased food availability through altered current patterns in the Chukchi Sea.

Factors associated with the structure and densities of macrofaunal communities in the northeastern Chukchi Sea include sediment grain-size, sediment organic carbon concentrations, and characteristics of water masses (Feder et al., 1994; Grebmeier et al., 2006; Blanchard and Feder, in press). A portion of the Burger study area lays in a trough (a submerged watershed draining towards Barrow canyon) to the south of Hanna Shoal with Klondike stations to the southwest. Weingartner et al. (2013) demonstrated higher water temperature and salinity values in Klondike, as compared to Burger, reflecting divergent current flows transporting winter water into Burger from the north. The Statoil and Transitional stations complete the environmental and biological gradient between Klondike and Burger, falling in between the two areas in most physical characteristics. Expanding to the larger region of the 2011 and 2012 study, macrofaunal community structure is spatially structured and most highly correlated with depth, bottom-water temperature and salinity, and organic carbon. Megafaunal community structure also indicates moderate correlations with the same variables. In general, water depth is greater, bottom water temperatures colder, salinity highest, and sediments muddier where density and biomass are highest (Figs. 2-3, 2-8, and 2-9). Oceanographic studies will continue to provide insights as to how interactions between geomorphology and currents affect differences in available organic carbon (food) sources and local deposition.

Achieving a detailed understanding of the environmental gradients associated with the large spatial variations in dominant biological characteristics such as polychaete density and bivalve biomass has been challenging. The raw data and contour plots of overall density demonstrate extremely high densities of animals in Burger, largely driven by the extremely high numbers of *Maldane sarsi*. There is also high biomass in the Central stratum just to the east of Burger that extends northward towards Hanna Shoal and southward down to the Transitional stations (Fig. 2-8). The high biomass values across the central portion of the study area are due to the bivalves *Astarte borealis*, *Macoma calcarea*, and *Yoldia hyperborea* and the sipunculid worm *Golfingia margaritacea*. The MDS analysis for the regional study indicated that bottom water temperature is the variable most closely associated with benthic community structure, followed by percent mud and water depth. Water depths do not vary greatly over the study area but the areas of highest density and biomass are in the areas with greatest depth, greatest proportion of mud, and lowest bottom-water temperatures (Figs. 2-1 and 2-8).

Feeding by Higher Trophic Level Organisms

In the Chukchi Sea, 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, crabs) (Lovvorn et al., 2003; Feder et al., 2005; Grebmeier et al., 2006; Feder et al., 2007). Benthic organisms in the northern Bering and Chukchi seas are important food resources for higher trophic level organisms such as demersal fishes, various seals, walrus, and gray whales (e.g. Fay, 1982; Oliver et al., 1983; Feder et al., 1994, 2005, and 2007; Barber et al., 1997; Coyle et al., 1997; Green and Mitchell, 1997; Moore et al., 2003; Highsmith et al., 2006; Bluhm et al., 2007; Bluhm and Gradinger, 2008, Norcross et al., 2013). Primary production supports rich benthic communities that in turn support benthic-feeding fishes and marine mammals, serving as a vital link between the high levels of primary production and upper trophic organisms (Fay 1982; Lowry et al., 1980; Sheffield et al., 2001; Bluhm and Gradinger, 2008). This trophic link extends to coastal residents that hunt marine mammals.

Barber et al. (1997) documented 66 species of fishes in the Chukchi Sea, many of which are likely to utilize the benthos for food. The diets of a few benthic-feeding fishes, including those of Arctic cod *Boreogadus saida*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, Bering flounder *Hippoglossoides robustus*, saffron cod *Eleginus gracilis,* and the fish doctor *Gymnelus viridis* (an eelpout), in the northeast Chukchi Sea have been reported (Jewett and Feder, 1980, 1981; Coyle et al., 1997; Green and Mitchell, 1997; Feder et al., 2005). Prey of fishes ranged from planktonic (water column) and epibenthic (living on the sediment surface) crustaceans to polychaetes and other fishes. Arctic staghorn sculpin consumed macrofaunal prey (those living within sediments including bivalves and gastropods) and all species consumed epibenthic crustaceans (those organisms living on the sediment surface but closely associated with sediment processes). 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). Five fish species were analyzed for diet composition and macrofaunal organisms, primarily polychaete worms, were found in gut contents of all species. Polychaetes, however, were a major dietary component for only the Arctic staghorn sculpin. Areas of highest concentrations of benthic fishes during the summer do not, however, overlap with areas of high benthic biomass, possibly due to fish habitat preferences (Day et al., 2013; Norcross et al., 2013).

Gray whales feed primarily in the northern Bering and south-central 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 amphipods (Highsmith and Coyle, 1992; Nelson et al., 1994; Bluhm and Gradinger, 2008). In addition to feeding areas along the northern coastline, in 1989 Moore and Clark (1990) observed gray whales presumably feeding to the northeast of Hanna Shoal where very abundant ampeliscid amphipods were found during sampling by Nelson et al. (1994). While amphipods are an important component of the macrofaunal community within the present study area, their numbers were lower in the Burger and Klondike areas than in the known, preferred feeding areas (the Mammal Feeding stations), indicating suboptimal gray whale feeding habitat, as noted above (Nelson et al., 1994; Highsmith and Coyle, 1992). The ampeliscid beds noted north of Hanna Shoal by Nelson et al. (1994) with densities > 1,500 ind. m^{-2} were not found in this study.

Walrus feed by rooting in the sediments as they dig for clams and other benthic organisms (Fay 1982; Ray et al., 2006). Collectively they may consume up to ~3 million tons of benthic biomass and disturb sediments over thousands of km^2 yr^{-1} (Ray et al., 2006; Krupnik and Ray, 2007). It is an accepted opinion that walrus primarily favor large bivalves. Fay (1982) and Sheffield et al. (2001), however, found that walrus in the Bering and Chukchi seas also feed on many other organisms including small and large soft-bodied benthic worms. Softer animals are digested quickly in walrus stomachs leaving little trace of their presence. They are, therefore, underrepresented in walrus feeding studies based on gut analyses (Sheffield et al., 2001). Fay (1982) found a broad array of walrus prey that were observed in macrofaunal samples from 2008 – 2012 and by Nelson et al. (1994). In addition to walrus, 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; Bluhm and Gradinger, 2008).

The areas of high overall benthic biomass and, more specifically, bivalve biomass in the present study coincide with areas of high walrus feeding activities in summer (Aerts et al., 2013; Hannay et al., 2013). Gray whales feed largely to the east, closer to the coastline where ampeliscid amphipods are numerous (Blanchard et al., 2013a).

Bioturbation by marine mammals through feeding activities mixes sediments, creates space for macrofauna to occupy, transfers buried nutrients to the surface, and contributes to increasing and maintaining diversity (via maintaining patches in various stages of recolonization and recovery; Boesch and Rosenberg, 1981). A positive feedback may therefore, exist between foraging by these higher trophic level predators and benthic communities as nutrient flux (and thus productivity) tends to increase as a result of the extensive disturbance caused by foraging activities (Ray et al., 2006). Consequently, predation by benthic-feeding organisms in the Chukchi Sea is likely a substantial and ecologically important cause of heterogeneity for macrofaunal communities.

Temporal Variability

The seasonal ice cover and influx of water from the North Pacific Ocean and Bering Sea through Bering Strait are major influences on productivity patterns in the Chukchi Sea. The short growing season and seasonal ice cover limits primary production within the region to the late spring and summer months. Melting sea ice stratifies the water column, creating the necessary conditions for primary production, resulting in a summer phytoplankton bloom with the timing dependent on ice cover (e.g., Questel et al., 2013). The mismatch of zooplankton community development with the phytoplankton bloom and the lower numbers of zooplankton in the Chukchi Sea result in a large flux of unconsumed, primary production to the benthos, enhancing benthic community growth (Grebmeier et al., 1988; Grebmeier et al., 2006). In contrast, zooplankton in pelagic systems such as Port Valdez, Alaska, can consume much of the primary production and very little may reach the seafloor (Blanchard et al., 2010). Patterns of seasonal production and zooplankton community development in the present study area are dependent on the seasonal development and environmental characteristics of the water column. Large, interannual differences of zooplankton density can result from environmental variations, as observed by Questel et al. (2013) over the study period 2008-2010. Zooplankton community composition and lower production in 2009 reflected both the early warming of the Chukchi and melting of ice due to winds from the south. Water temperatures were lowest in 2008 and highest in 2009 while salinity was highest in 2008 and lowest in 2009 reflecting annual differences in melt patterns (Weingartner et al., 2013).

Water temperature changes influence benthic communities through altered survival of pelagic larvae and juvenile stages, as well as variations in food resources. For example, some bivalve larvae are sensitive to water temperature and temperature variations have been suggested as a key factor in the varying distribution of *Macoma calcarea* in the Chukchi Sea (Pearson and Barnett, 1987; Sirenko and Gagaev, 2007). Interannual variations in the volumes of production falling to the seafloor are probably the greatest source of temporal variability in benthic systems. The declines in density and diversity (number of taxon) of macrofaunal animals in the study area in 2010 and increases in 2011–2012 reflect change in oceanographic conditions, suggesting responses of benthic animals to large-scale environmental variability. The large change in density and number of taxa and the absence of such a strong response in biomass in Burger in 2010 suggest a loss of smaller, less competitive species rather than the larger, multi-year animals dominating biomass. In 2011 and 2012, the communities exceeded prior density levels, although the total number of taxa at each site remained low. The length-frequency histograms of the bivalve *Ennucula tenuis* do not show major shifts from 2008 to 2010, but do demonstrate greater proportions of juveniles in 2011, suggesting favorable conditions for bivalve reproduction and recruitment in 2011. Blanchard et al. (2010) found a tight relationship between the Pacific

Decadal Index (an index of climatic variability in the North Pacific Ocean) and macrofauna density in Port Valdez, Alaska. Grebmeier et al. (2010) also documented benthic responses to climatic variability, as was also observed in the CSESP. A longer data record is necessary to understand covariances of benthic communities with oceanographic changes as the sample size is very small (n = 4 with a one year lag in seasonal production and next year's benthic biomass reflecting overwintering survival). Nevertheless, the evidence to date (though limited) suggests that benthic communities in the northeastern Chukchi Sea are very responsive to oceanographic variability.

Population Dynamics of Ennucula tenuis *and* Macoma *spp.*

The length-frequency histograms of *E. tenuis* in this study suggest distinct length categories presumed to be different length/age cohorts, although the lengths of older bivalves often overlap (Fig. 2-13). The first cohort is centered on the 2-3 mm length category with much larger numbers of new recruits (less than 1.0 mm) in the meiofauna samples. The lengths of the first cohort match lengths found for other bivalve populations in Alaska. Average cohort length of newly settled mussels in mid-summer of the first year was 2-3 mm in Port Valdez (Blanchard and Feder, 2000) and 2.4 mm for *E. tenuis* from the Bering Sea (McDonald et al., 1981), similar to lengths measured in the present study. The meiofaunal sampling correlates well with the *E. tenuis* histograms as very small juveniles would have passed through the 1.0-mm mesh sieves used for macrofaunal sampling, but were retained in the 64-µm sieves. The meiofaunal data suggest that small *E. tenuis* occur in densities up to 6,000 ind. m^{-2}. These numbers are similar to results from investigations of the blue mussel *Mytilus trossulus* in Port Valdez, Alaska, where newly settled recruits could number into the thousands per square meter (~2,000 ind. m^{-2}, A. L. Blanchard, unpublished observations).

Mean, median, and maximum lengths of *E. tenuis* varied by study area with the Klondike study area having smaller lengths than Burger and Statoil (Fig. 2-13). The lower medians reflect dominance of smaller bivalves (new cohorts) in Klondike while the very small peaks at larger lengths in Klondike suggest lower survival than in Burger or Statoil. Burger and Statoil had more balanced distributions with strong peaks around 12-13.0-mm lengths (the second-year cohort). Differences in bivalve shell growth related to environmental conditions are common, as also found to occur in blue mussels in Port Valdez, (Blanchard and Feder, 2000).

Growth studies of *E. tenuis* in the Bering Sea suggest that these bivalves may live up to nine years (McDonald et al., 1981). Age determinations of the Bering Sea samples were based on counting variations in shells that appeared to be age annuli. The distributions of age classes in the Bering Sea study were skewed to the right with a peak at Age 1 and counts decreasing regularly to a minimum at Age 9. There was no peak for older age classes. Bering Sea *E. tenuis* were found to grow 1.5 mm per year in the first 5 years and 1 mm after that (McDonald et al., 1981). A difficulty with the Bering Sea study is that no confirmation was provided that the annuli were truly age marks, as was done with mussels in Port Valdez. This step of determining that annuli represent age marks is necessary. Therefore, ages reported by McDonald et al. (1981) cannot be applied or assumed for the current study. A review of a small sample of *E. tenuis* shells by a researcher experienced in aging bivalves (A. L. Blanchard) found few marks suggesting age annuli and limited erosion of bivalve shells as would be evident in older specimens. The few possible age annuli observed suggested a maximum age of five years for *E. tenuis* in the Chukchi Sea.

Shell growth of bivalves is highly dependent on environmental conditions such as food availability and water temperature. Where food is not limited, bivalve shell growth can be extremely rapid, as was found in the southeastern Chukchi Sea where first year cohort mussels from buoys near Kivalina grew extremely quickly approaching lengths of age 2 mussels (up to 15 mm and more) from Port Valdez (S. C. Jewett and A. L. Blanchard, personal observations). An increase in *E. tenuis* length of 10 mm from one length cohort to the next is possible in environments with unrestricted food resources, as may be the case in the present study area, although winter food resources are not known. Maximum lengths of 17 mm in the Chukchi Sea are 5 mm longer than the maximum found in the Bering Sea, suggesting better conditions for this bivalve in the Chukchi Sea than in the Bering.

Maximum age is difficult to determine without in-depth verification of age annuli. Larger *E. tenuis* shells were moderately scarred (possibly by non-mammal predators) in the present study whereas the Bering Sea study indicated that little predation occurred. Assuming that the first cohort is newly settled individuals and that there are only two cohorts represented, the histograms suggest that *E. tenuis* commonly lives for a minimum of 1.5 to two years (the second peak in the histograms) and at most 3 years (the largest specimens). In the presence of plentiful food resources and substantial predation in the Chukchi Sea, ages of 3–5 years seem reasonable, whereas limited predation in the Bering Sea may allow survival to nine years (McDonald et al., 1981). Determination of age annuli via an acetate-peel method could be a direction for further research.

The CSESP 2012 Distributed Biological Observatory

The Distributed Biological Observatory (DBO) line established in the CSESP regional study area in 2012, included 11 benthic stations. Biological and environmental relationships along the DBO line were not clear. The eastern most stations, DF002 and DF004, had coarser substrates, more amphipods, and were overall, similar to the nearby Burger station, BF005. Burger station BF013 was the muddiest site and as expected, was the site with numerous *Maldane sarsi* and highest density. A strong association of the faunal gradient from inshore to offshore with sediment grain-size and water depth was expected, but the observed trends were less clear than anticipated. Amphipods, bivalves, and polychaetes were dominant by density at all stations with the exception of BF013, proportions were generally similar; there was a slight decline in the proportions of amphipods offshore. Bivalves dominated biomass at most stations with large peanut worms and large and numerous polychaetes contributing to some stations. Trends should become clearer following sampling of the full DBO line in 2013 and with repeated sampling of the transect over time.

CONCLUSIONS

Benthic communities in the Klondike, Burger, and Statoil study areas reflect the high volume of seasonal production reaching the benthos in the shallow water of the Chukchi Sea (Grebmeier et al., 2006). The macrofaunal assemblages of 2008 – 2012 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 average density of macrofauna was higher in Burger than in Klondike and Statoil, the assemblages at all study areas were generally similar (containing most of the same species) and trends weakly reflect local environmental gradients co-varying with bottom-water temperature, sediment grain-size characteristics, and water depth. Short-term temporal differences in community structure from 2008 – 2012 were associated with climatic variations influencing the Chukchi Sea, which likely altered larval survival and recruitment.

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CHAPTER 3

BENTHIC ECOLOGY 2012:
Meiofaunal Community Structure

By Marissa M. Hajduk and Arny L. Blanchard

INTRODUCTION

Marine meiofauna fill a variety of ecological roles from predators to species integral in organic matter turnover, and play a vital role in the functioning of marine ecosystems (Heip et al., 1985; Giere, 2009). The typical meiofaunal community is comprised of "transitory" or "temporary" species, such as juveniles which only spend part of their life cycle as meiofauna, and "permanent" species, the organisms which spend their entire life cycle as meiofauna (Newell, 1979; Giere, 2009). With small body size (~500 µm as upper size limits, and ~63 µm as lower size limits) and relatively short life spans (for some taxa life spans are on the order of days), meiofauna experience high community and generational turnover rates. With high density (in some cases outnumbering macrofaunal taxa 25:1), meiofauna are crucial components in nutrient cycling and turn over within the benthos (Newell, 1979; Heip et al., 1985; Kennedy and Jacoby, 1999). The contribution of meiofauna to benthic ecological processes in arctic shelf ecosystems is relatively understudied, despite their documented importance to benthic communities. They also provide a large carbon pool for use by macrofauna (Warwick et al., 1979; Armonies and Reise, 2000; McLachlan and Brown, 2006).

Coupling of seasonal primary production and benthic production in the Arctic supports rich macrofaunal benthic communities, and presumably, meiofaunal communities are also substantial. Meiofauna contribute to biological processes as habitat modifiers, have functional roles ranging from consumers to scavengers, and are partly responsible for recycling nutrients (Renaud et al., 2006; Fonseca and Soltwedel, 2007; Giere, 2009). Recent work in the northeastern Chukchi Sea has examined temporal and spatial trends in macrofaunal benthic communities and their response to environmental variations (Blanchard et al. 2013). The high diversity and abundance of Chukchi benthos has been documented through various studies which describe the tight benthic-pelagic coupling in the Chukchi (Feder et al., 1994, 2005, 2007;

Grebmeier and Cooper, 1994; Grebmeier et al., 2006). We still know very little, however, about the community, distribution, and density of meiofauna in the northeastern Chukchi Sea region.

The objectives of this study are to quantify the density of the meiofauna community in the northeastern Chukchi Sea, and to determine associations between the meiofaunal community and environmental characteristics such as depth, organic carbon, sediment grain size, and bottom-water temperature.

METHODS

Benthic Meiofauna Sampling Methods

Meiofauna samples were collected as part of the Chukchi Sea Environmental Studies Program (CSESP), a multi-year, multi-disciplinary study in northeastern Chukchi Sea (Figure 3-1). A double van Veen grab was used to collect samples at 31 stations during August to October 2012, following a combination of sampling methods described by Bessière et al. (2007) and Piepenburg et al. (1995). Surface sediment samples were collected from one side of each successful grab by inserting a 7-cm diameter corer to 1-cm depth in the sediments, with three replicate samples taken per station. Samples were stored in whirlpacks with 10% buffered formalin for transport. They were rinsed of the formalin in the lab using a 64-µm mesh sieve. Following silica solution separation methods outlined in Burgess (2001), the samples were placed in a 50-mL centrifuge tube with Ludox HS-40, mixed using a variable speed vortex mixer, and run through a centrifuge. Once the majority of meiofauna was separated out, each sample was placed in a plastic jar with ethanol and rose Bengal stain. The remaining sediment pellets were sorted to remove missed meiofaunal organisms. Recovered organisms were recombined with their corresponding samples. After the separation process, samples were rinsed a second time through a 500-µm mesh sieve to remove the larger non-meiofaunal organisms. Permanent meiofauna were identified to order or higher and transitory meiofauna were identified to family or lower where possible.

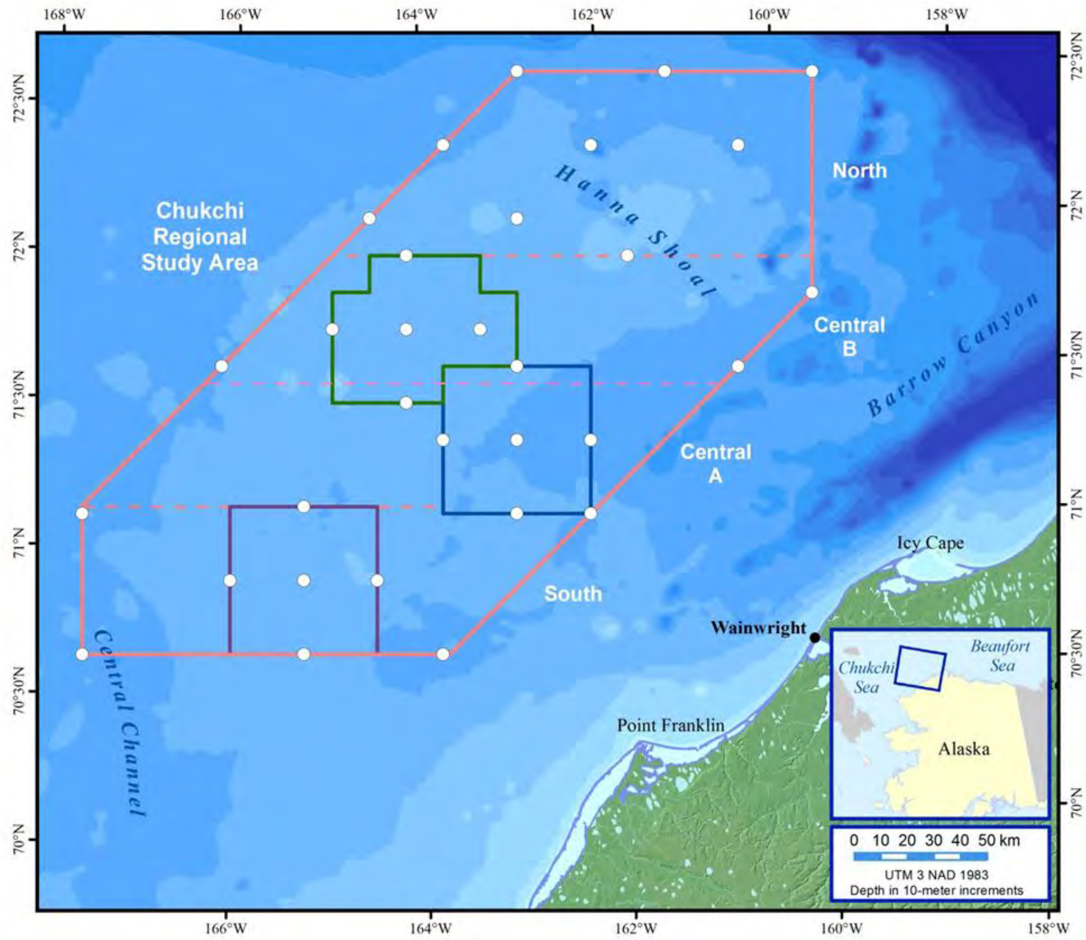

Figure 3-1. Map of meiofaunal stations sampled and processed during the 2012 CSESP benthic surveys. White circles indicate station locations.

Analysis

Meiofaunal community composition was evaluated to provide insights into regional variability and associations with environmental characteristics. Biological data were the density (individuals cm^{-2}) of permanent and temporary meiofaunal taxa. Environmental variables included sediment grain-size, organic carbon content of sediments (OC), water depth, and bottom-water temperature, with the additional variable of total macrofaunal polychaete biomass. The sediment and macrofaunal polychaete biomass data were from the macrofaunal ecology component of the 2012 CSESP (Chapter 2) and hydrographic data were from oceanographic sampling (Weingartner et al., 2013). Non-metric multidimensional scaling (MDS) was applied to determine meiofaunal community structure followed by permutational multivariate analysis of variance (PERMANOVA) to compare differences among strata using PRIMER (www.primer-e.com). The Bray-Curtis similarity coefficient was used for MDS and PERMANOVA. The similarity of percentages (SIMPER) routine was used to evaluate the main taxonomic groups contributing to each stratum. Associations of meiofaunal community structure were evaluated by correlating the environmental variables using the BIOENV routine with the MDS ordination.

RESULTS

Meiofauna of the Regional Study Area

A total of 44 taxonomic categories of meiofaunal organisms were identified from the 2012 CSESP regional study (Appendix III). The total number of taxonomic categories identified ranged from 27 for the South stratum to 31 for Central B (Table 3-1). Central A and North had the second highest numbers of taxa with 30, whereas the South stratum had the lowest number of taxa at 27. Average density and average number of taxa per sample were highest in Central B (9.87 ind. cm^{-2} and 30 taxa). The North stratum had the second highest average density (10.22 ind. cm^{-2}) but also had the lowest average number of taxa per sample (11.08 taxa). South and Central A were very similar in density (9.87 and 9.54, respectively) and number of taxa per sample (12.06 and 11.79).

PERMANOVA tests demonstrated significant differences ($p < 0.05$) in density across all taxonomic categories among the strata (Table 3-2). The South stratum was significantly different than both Central B and North. Density in Central A was significantly lower in Central B. Central B was also significantly different than the North stratum. No significant differences were detected between the Central A, South, and North strata (Tables 3-1, 3-2).

Table 3-1. Summaries of biotic variables for regional strata sampled for meiofauna during the 2012 CSESP. Ave. = average, SD = standard deviation, Sample # Taxon = average number of taxonomic categories, Total # Taxon = number of taxonomic categories found in each stratum, -- = not calculated and density was ind. cm^{-2}.

	South		Central A		Central B		North	
Variable	Ave.	SD	Ave.	SD	Ave.	SD	Ave.	SD
Density	9.54	3.54	9.87	2.46	12.89	3.35	10.22	4.77
Sample # Taxa	11.79	2.25	12.06	0.77	12.70	2.93	11.08	2.07
Total # Taxa	27	--	30	--	31	--	30	--

Table 3-2. Permutational multivariate analysis of variance (PERMANOVA) pair-wise testing of summary statistics for the 2012 CSESP meiofauna study. Significant terms are in bold.

Summary Statistics

Groups	t	p-value
South, Central A	1.2519	0.127
South, Central B	1.8817	**0.011**
South, North	1.9392	**0.010**
Central A, Central B	1.8650	**0.022**
Central A, North	1.1038	0.322
Central B, North	1.8231	**0.043**

The meiofaunal taxa in the 2012 regional study area included permanent and temporary taxa with nematodes dominating community characteristics (Table 3-3). The three taxonomic groups contributing most to within-stratum similarity in the South stratum were nematodes, ostracods, and protozoans of the order Foraminifera. Groups contributing most to within-stratum similarity in Central A and Central B were nematodes, copepods, and polychaetes. In the North stratum, the taxa contributing most to within-stratum similarity included nematodes, polychaetes, and copepods.

Nematodes, a permanent meiofaunal group, had the highest density across all four strata, ranging from approximately 7 to 10 ind. cm^{-2}, with higher densities reported in Central B than the other three strata (Table 3-1 and Fig. 3-2). Additional permanent taxonomic groups Harpacticoida, Ostracoda, Tanaidacea, Kinorhyncha, and the protozoan order Foraminifera had similar densities (<1 ind. cm^{-2}). Ostracods and protozoans had similar density distributions, with greater number of individuals in Central B, followed by Central A, and lowest density in the North stratum. Copepods exhibited highest density in the South stratum, followed by Central B and North, with lowest density in Central A. For the group Kinorhyncha, lowest densities occurred in South and Central A (<0.1 ind. cm^{-2}), and highest densities were found in Central B. Density for Tanaidacea, on the other hand, was highest in South and Central A, and lowest in Central B and North (<0.05 ind. cm^{-2}).

Temporary meiofaunal taxa (juvenile macrofauna) that were present in the study area included bivalves (e.g. *Ennucula tenuis*), and polychaetes (including *Cossura* spp., *Nephtys* spp.). These taxa occurred with densities less than 1.0 ind. cm^{-2} (Fig. 3-2). Density for bivalves was highest in Central B, followed by the North and South strata. Central A had the lowest density of bivalves. Juvenile polychaetes exhibited increasing density from South to Central B, followed by a slight drop in density in the North stratum.

Bubble plots of density aid in illustrating the distributions of meiofauna throughout the study area, and depict variable concentrations of meiofauna. Bivalves, ostracods, copepods, and Protozoa exhibit a greater density in the Central A and B strata, and to some extent the South stratum, and appear at lower densities in the North (Figs. 3-2, 3-3). Polychaetes have a more even spread, with slightly higher numbers occurring in the Central A and Central B strata (Fig. 3-2). The taxonomic group Nematoda had higher density in Central A and Central B but also had a few spots of higher density in the North and South strata (Fig. 3-3). The meiofaunal groups Kinorhyncha and Tanaidacea displayed contrasting trends in density as kinorhynchs were found in higher density in the north-west portion of the study area, whereas tanaids tended to concentrate in the southeast (Fig. 3-3).

Table 3-3. The three meiofaunal groups contributing most to within–stratum similarity. Density = ind. cm^{-2}; Sim = average similarity.

South
Average similarity = 77.38

Taxon	Density	Sim
Nematoda	2.09	50.42
Copepoda	0.53	11.38
Protozoa	0.18	3.53

Central A
Average similarity = 84.61

Taxon	Density	Sim
Nematoda	2.24	62.70
Copepoda	0.29	6.31
Polychaeta	0.24	6.04

Central B
Average similarity = 79.21

Taxon	Density	Sim
Nematoda	2.42	53.71
Copepoda	0.45	6.82
Polychaeta	0.30	5.15

North
Average similarity = 78.74

Taxon	Density	Sim
Nematoda	2.23	62.14
Polychaeta	0.29	7.63
Copepoda	0.03	4.13

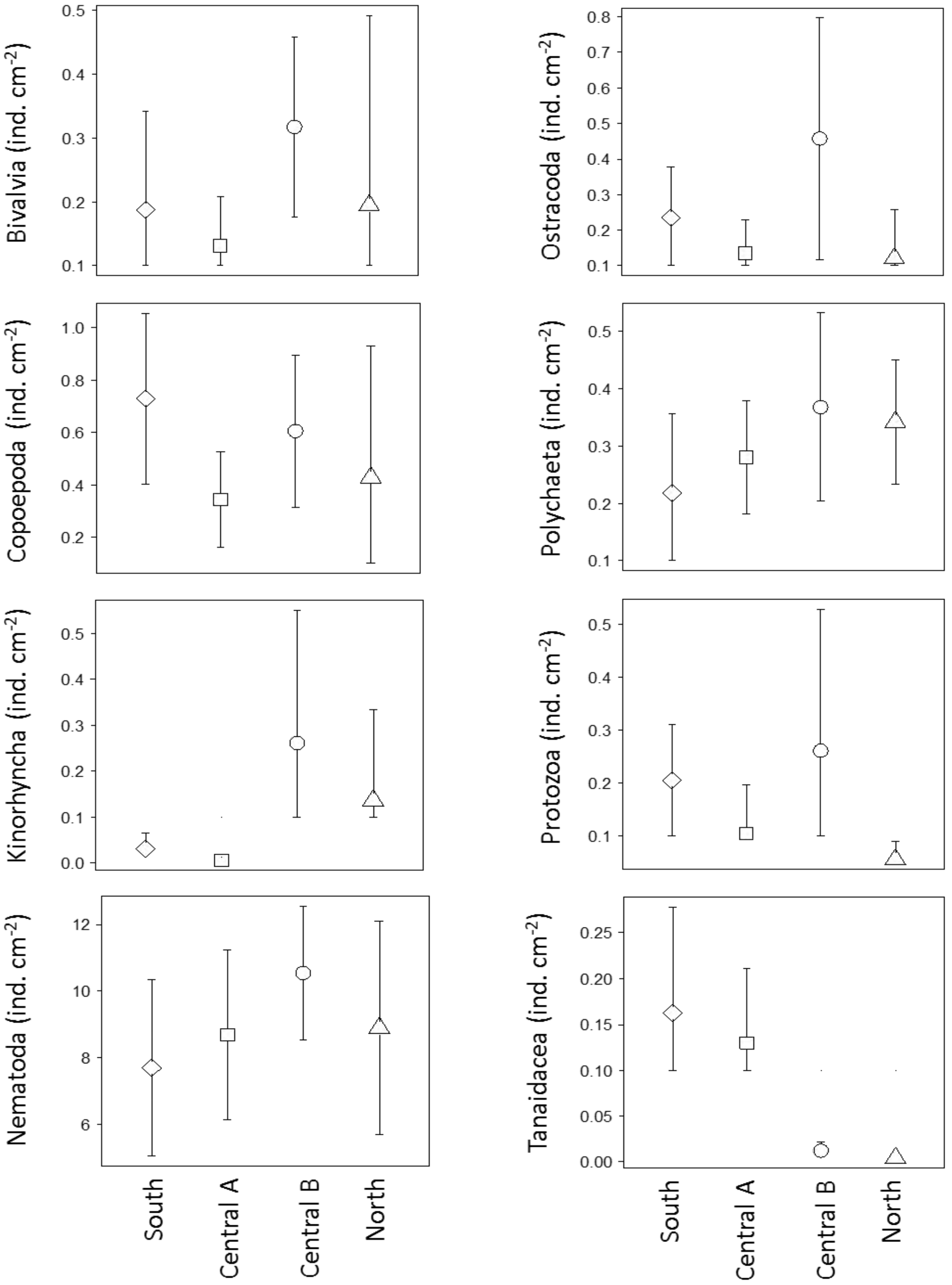

Figure 3-2. Plots of means and 95% confidence intervals by strata based on density of major meiofaunal taxonomic groups from the 2012 CSESP study.

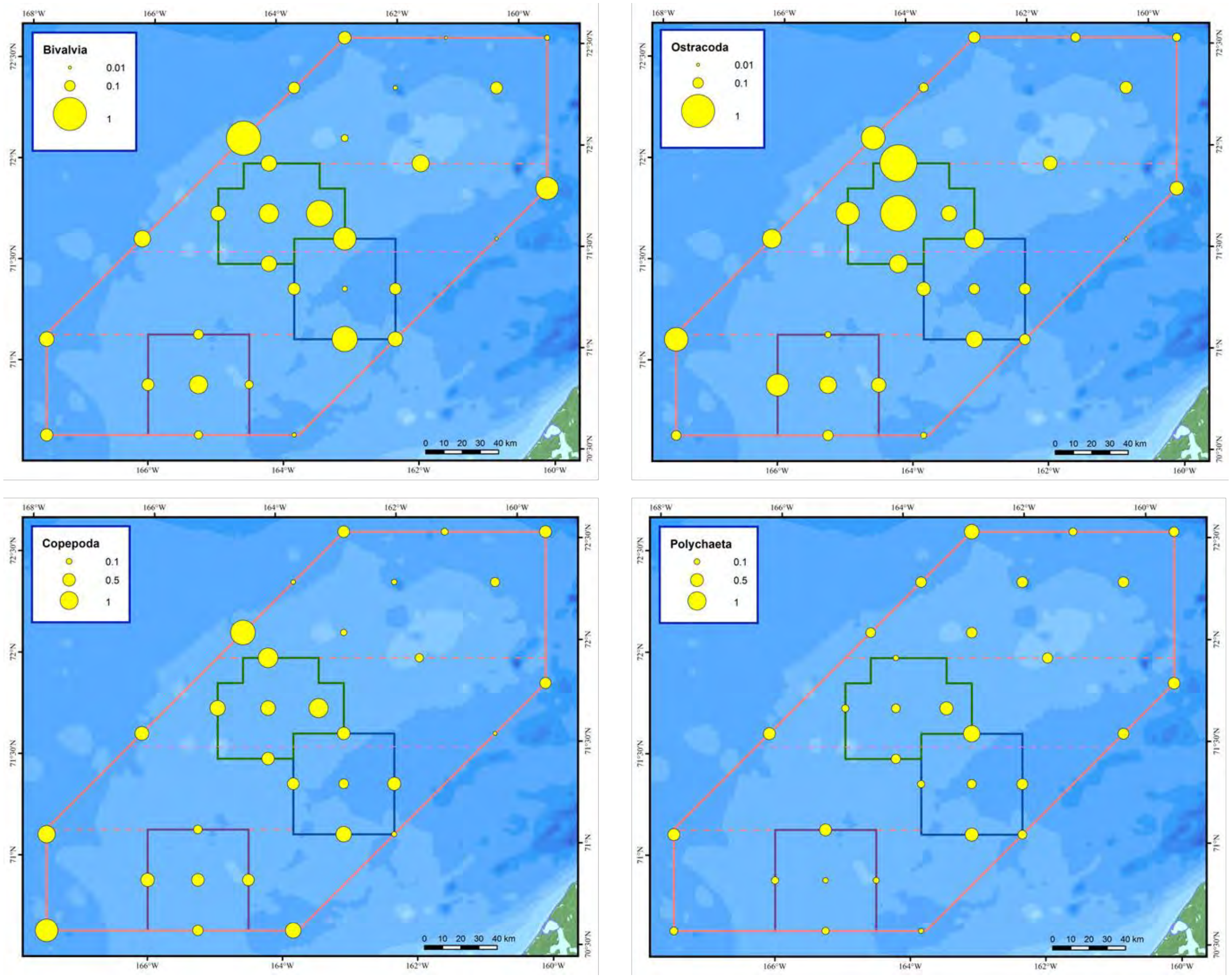

Figure 3-3. Bubble plots of meiofaunal density (ind. cm^{-2}) for Bivalvia, Ostracoda, Copepoda, and Polychaeta in the CSESP regional study area.

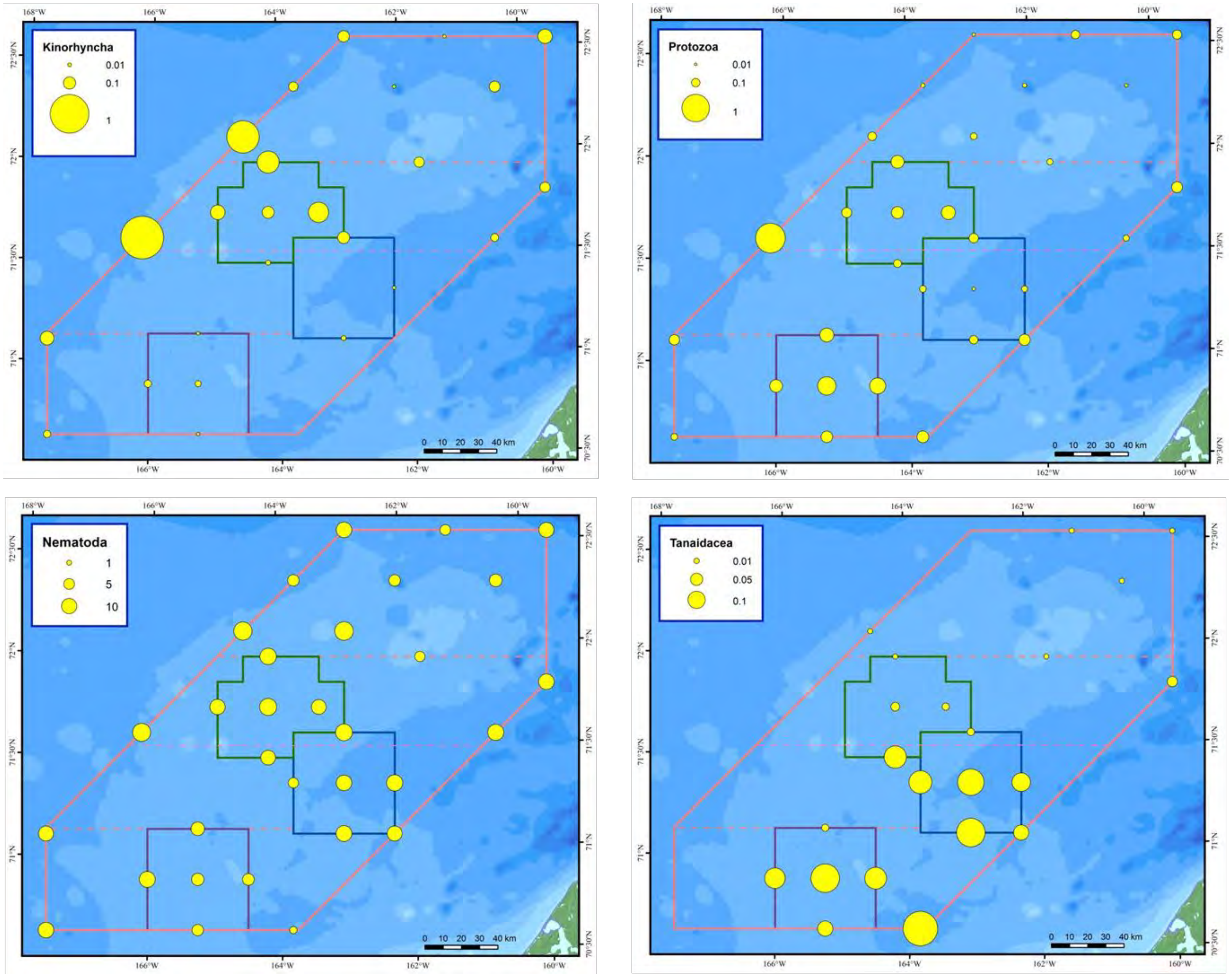

Figure 3-4. Bubble plots of meiofaunal density (ind. cm^{-2}) for Kinorhyncha, Protozoa, Nematoda, and Tanaidacea in the CSESP regional study area.

Multivariate analysis of meiofaunal community data indicates no clear separation of strata (Fig. 3-5). Although it appears some North and South stations may cluster together, stations from all four strata exhibit mixing. The overlay of physical variables on the MDS ordination shows weak associations among community structure and environmental characteristics. Percent mud and bottom temperature had weak correlations with meiofauna community structure (ρ= 0.198) (Table 3-4).

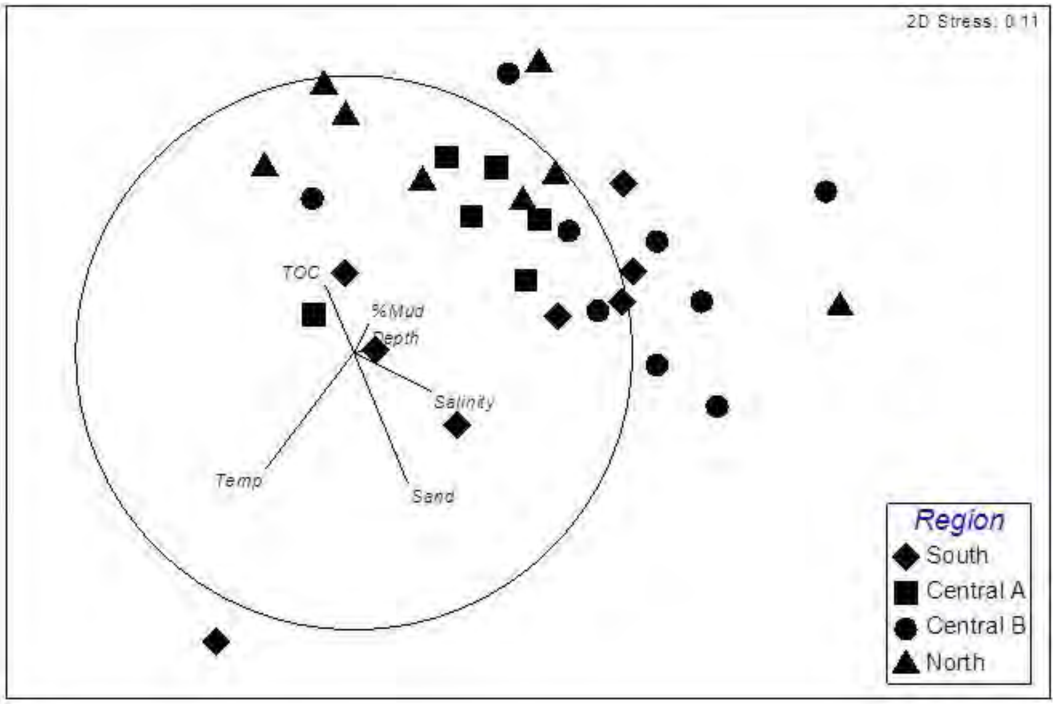

Figure 3-5. Nonmetric multidimensional scaling ordination plot of Bray-Curtis similarities for *ln*(X+1)-transformed meiofauna density by region from the 2012 CSESP study. Overlays of environmental variables are presented.

Table 3-4. Best fitting Spearman correlations from BIOENV program listing the variables with the highest correlation (Spearman's ρ) with the density similarity matrix.

Variables	ρ
% Mud, Bottom-water Temperature	0.198
% Sand, Bottom-water Temperature	0.195
% Mud, Salinity, Bottom-water Temperature	0.190
% Sand, Salinity, Bottom-water Temperature	0.190

DISCUSSION

Densities of dominant meiofaunal taxa vary among the four strata in the present study, although the strata appear to support roughly similar numbers of taxa. Total density values were very similar throughout the four strata but densities of major permanent and temporary groups demonstrated some differences. For example, the permanent groups Kinorhyncha and Tanaidacea have contrasting density distributions with kinorhynchs having higher density in Central B and North, and tanaids having higher density in the South and Central A. Nematodes and polychaetes demonstrated similar density patterns. Meiofauna, and in particular nematodes, are food sources for polychaetes (Fauchald and Jumars 1979) so a covariance between nematodes and polychaete densities may reflect a biological interaction, as a greater density of nematodes will supply a larger food source to a greater density of polychaetes.

Little is known about Alaskan meiofauna or how they may respond to environmental variations in the Chukchi Sea. Studies from Southeast Alaska (Port Valdez) in the late 1970s and early 1980s indicated high temporal and spatial variability within meiofauna communities, in particular harpacticoid copepods, resulting from naturally changing environmental conditions (Jewett and Feder, 1977; Feder and Paul, 1980). Long-term studies in Port Valdez provided evidence of benthic community disturbance and alteration coinciding with natural and anthropogenic environmental stressors (Blanchard et al., 2002, 2003, and 2010; Blanchard and Feder, 2003). Similar findings have also been shown in the Barents Sea (Olsen et al., 2007) and in the Gulf of Mexico, where strong responses in benthic communities affected by oil products (petroleum compounds), drilling, and general sediment disturbance were observed (Green and Montagna, 1996; Peterson et al., 1996). In the Gulf of Mexico, overall density of meiofauna also decreased like the macrofauna did with increased disturbance. With short turnover/generation times, meiofaunal organisms have been known to respond to environmental changes and disturbances more quickly than other organisms.

There is an expectation that meiofauna densities would correlate with environmental variables measured in the Chukchi Sea, and any associations may well pass upward through the food web to macrofauna, and possibly to higher level tropic organisms (Herman and Heip, 1988; Kennedy and Jacoby, 1999; Renaud et al., 2006). Since meiofauna represent a large percent of the carbon pool in marine sediment, their responses to environmental fluctuations may have large influences extending throughout benthic food webs (Renaud et al., 2007). Without a general baseline analysis and knowledge of distribution and density it will be difficult to assess changes and detect or describe future effects of anthropogenic or environmental stressors within the meiofauna community. Current analyses indicate lack of evidence for significant effects of environmental factors on meiofauna density suggesting more complex analyses (e.g., regression interactions models) are needed to discern patterns.

The communities of the CSESP study area include permanent and temporary taxa, as expected. The permanent meiofauna are dominated by nematodes, harpacticoid copepods, and protozoans of the order Foraminifera, similar to the dominants in Port Valdez (Feder and Paul, 1980). Permanent meiofauna in the study area occurred in very high densities compared to the macrofauna (1-10 ind. cm^{-2} translating to 10,000-100,000 ind. m^{-2} compared to 500-10,000 ind. m^{-2} for macrofauna; Chapter 2). Temporary taxa (juvenile organisms) included common macrofaunal species. This group occurred at lower densities than the permanent taxa (generally less than 1.0 ind. cm^{-2} translating to 10,000 ind. m^{-2} or less). Temporary taxa included juvenile *Ennucula tenuis* and polychaetes (e.g., Cirratulidae, *Cossura* spp., and *Nephtys* spp.). A lack of diversity in the temporary meiofauna (juvenile macrofauna; see Appendix III) was unexpected but may reflect sampling error, timing of reproduction and life history events, growth rates, and timing of recruitment into the macrofauna.

ACKNOWLEDGMENTS

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CHAPTER 4

BENTHIC ECOLOGY 2012:

Caloric Content of Macrobenthic Communities in the Northeast Chukchi Sea

By Steven S. Savard and Arny L. Blanchard

INTRODUCTION

The Chukchi Sea continental shelf is a highly productive region that supports high benthic biomass. Low zooplankton grazing allows higher proportions of organic carbon to settle to the seafloor, resulting in strong pelagic-benthic coupling (Grebmeier et al., 2006; Questel et al., 2013). As a result, benthic communities in this arctic shelf ecosystem play a large role in the food web (Iken et al., 2010). There are several higher-trophic level predators that feed on benthic fauna in the Pacific arctic shelf areas, including walruses (*Odobenus rosmarus divergens*), gray whales (*Eschrichtius robustus*), and bearded seals (*Erignathus barbatu*) (Lowry et al., 1980; Highsmith and Coyle, 1992; Ray et al., 2006; Grebmeier et al., 2006; Bluhm et al., 2007; Aerts et al., 2013; Hannay et al., 2013). Previous studies have examined community differences in macrobenthic density and biomass within the northeastern Chukchi Sea, and their relationships to environmental variables, such as food, water mass properties, and sediment characteristics (Feder et al., 1994; Grebmeier et al., 2006; Bluhm et al., 2009; Blanchard et al., 2013 a and b). Relatively little work, however, has gone into examining spatial variations in caloric content.

Energy gained from the consumption and digestion of organic matter is incorporated into biological and ecological functions such as reproduction, nutrition, and growth (Lucas, 1996). How much energy is appropriated into each function varies by species. For example, egg-bearing females of the shrimp *Argis dentata* were found to have higher caloric content than other adult shrimp (Brawn et al., 1968). Caloric content can also vary with life history stage, sex, age, and season. Most seasonal variation in caloric content is correlated with variation in body size (Griffiths, 1977). Food quality and quantity contribute to variations in caloric content of organisms (Villanueva et al., 2004), and the relationship becomes unpredictable with increasing latitude due to the greater variations in seasonality of food availability. As a result of environmental unpredictability, organisms at higher latitudes will tend to store more energy and consequently have higher caloric values (Griffiths, 1977). Trophic level can also affect caloric content of communities; populations of herbivorous organisms would have a greater amount of energy in the lower trophic level (be more numerous) than those at higher levels (Bagatini, 2010). Studies have also found that caloric content of organisms covaries with sediment grain size, although the relationship is indirect as variables that control sediment grain size, such as water flow, also drive differences in biomass and caloric content of organisms (Brawn et al., 1968).

Many studies evaluating energy flow and production values use weight to energy conversions (Brey et al., 1988) to determine total caloric content of organisms (Villanueva et al., 2004; Brey and Gerdes, 1998). Those studies assumed that the caloric content per gram of tissue for organisms was spatially constant. This might not necessarily be true as caloric content can covary with environmental characteristics (Brawn et al., 1968). The overall goal of this project is to determine if caloric content per gram of key macrofauna varies among benthic habitats in the northeastern Chukchi Sea, and if so, to determine associations between caloric content and environmental variables. A significant predictive relationship between the caloric content of a species and environmental variables will indicate a violation of the assumption of constant energy content. The environmental variables that will be used for this study are percent mud, bottom water temperature, salinity, total chlorophyll, and water depth.

METHODS

General Sampling Methods

The present study was conducted during the 2012 open water season as part of the Chukchi Sea Environmental Studies Program (CSESP) in the northeastern Chukchi Sea (Figure 4-1). The CSESP project included three main study areas of interest to the sponsors, Klondike, Burger, and Statoil, which are located where successful lease bids were made in the February 2008 Chukchi Sea Lease Sale 193. The study also included a larger study area of the CSESP encompassing an area extending from the southern latitude of Klondike to the northern part of Hanna Shoal (Fig 4-1).

Caloric content samples were collected from a total of 36 fixed stations in 2012 (Figure 4-1). Three replicate double van Veen grabs were taken at each station. One side of the van Veen grab was sieved to collect macrofaunal specimens for analysis of caloric values. Sediments were washed on a 1.0-mm stainless steel screen. Biological material was then placed into plastic jars and frozen for transport to the lab. In the laboratory, samples were thawed and biological material sorted into selected categories. Sampling coordinates and water depths were recorded for each replicate taken. Environmental characteristics were determined as part of the 2012 CSESP benthic ecology component (Chapter 2). Bottom-water salinity and temperature measurements were obtained from oceanographic sampling (Weingartner et al., 2013).

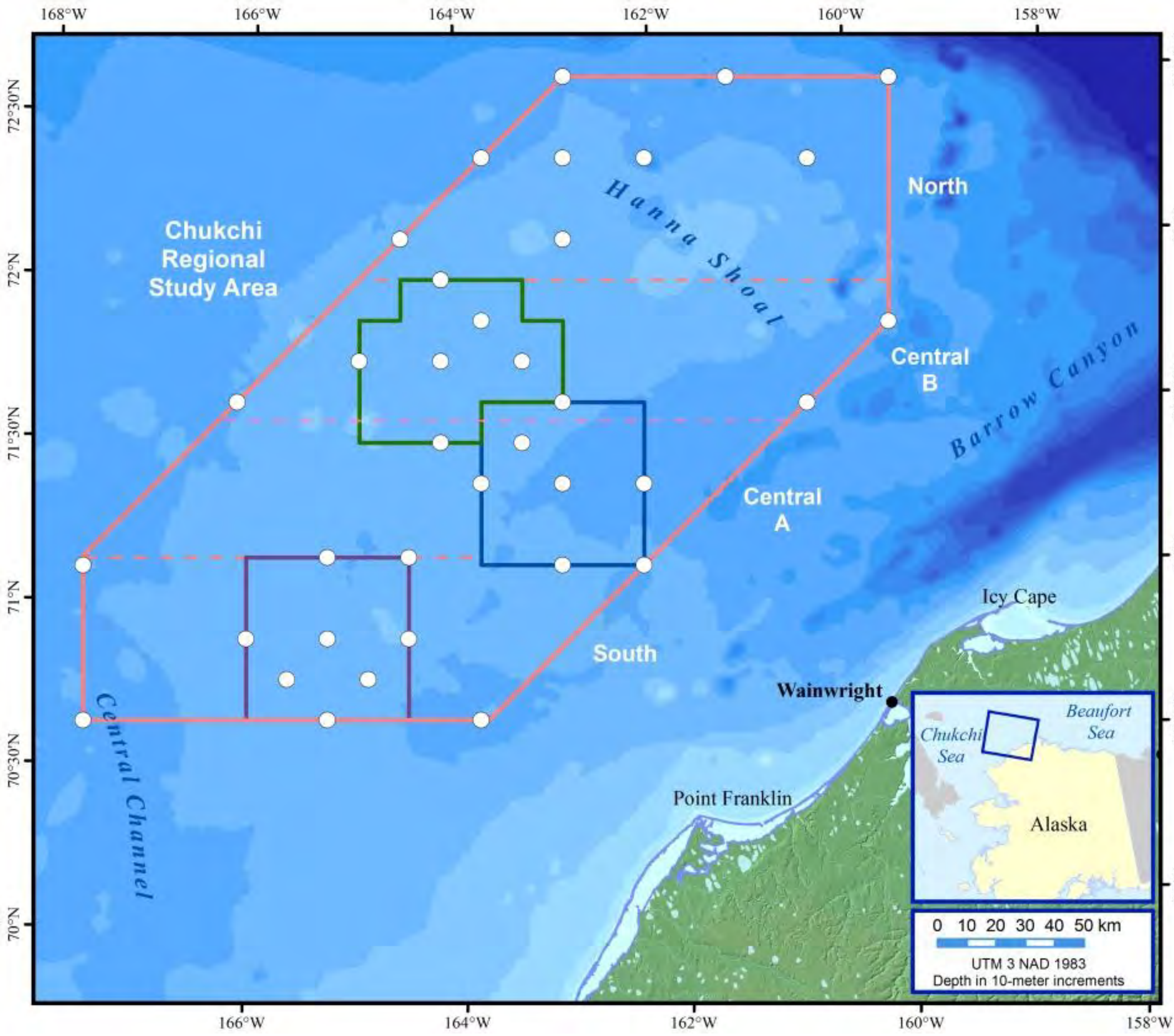

Figure 4-1. Sampling stations in the northeastern Chukchi Sea, 2012. The large polygon represents the regional study area, while the smaller boxes represent, from South to North, Klondike, Burger, and Statoil.

Laboratory Analysis

In the laboratory, caloric samples were thawed and organisms were sorted into the categories Ampeliscidae, *Ennucula tenuis, Golfingia margaritacea*, *Macoma* spp., Maldanidae, *Nephtys* spp., and all remaining organisms ("Others"). Ampeliscidae, *Ennucula tenuis, Golfingia margaritacea*, *Macoma* spp., Maldanidae, and *Nephtys* spp. are dominant species by biomass in the study area (Blanchard et al., 2013a). They are common prey items for walrus and bearded seals, except for ampeliscid amphipods which are prey for grey whales (Fay, 1982; Blanchard et al., 2013a). Aggregating samples into these categories allowed for comparisons of major taxa in the study area while not excluding non-dominant species ("Others"). Shells from gastropods and bivalves were removed. Wet weights of aggregated organisms were measured then dried to a constant weight by freeze-drying for 48 hours (Lucas, 1996). Dry weights were then recorded, followed by a homogenization of aggregated samples from each station using a mortar and pestle.

Calcium carbonate was removed from organisms that have a calcium carbonate exoskeleton, such as ophiuroids, by the slow addition of 10% HCl solution until bubbling ceased. Although the addition of HCl may cause a slight overestimation in caloric content (~1%) (Wacasey and Atkinson, 1987), this overestimation is less than the error created from the heat loss caused by carbonate breakdown if carbonate is not removed (Beukema, 1997; Hondolero et al., 2012). A t-test was performed to determine whether the slight overestimation caused by acidification would make a significant difference in caloric content and was found to be not significant ($p = 0.59$). Samples were then freeze dried for another 48 hours.

Homogenized dried samples were then either made into pellets, or packed into gelatin capsules, and their weights were recorded. Determination of whether a sample was to be pelletized or packed into a capsule was based on sample volume, where samples with small volumes were packed into capsules. Pellets and capsules were then analyzed in a Parr oxygen bomb calorimeter (model 6300). Subsamples were taken if there was enough material available to form multiple pellets. The number of subsamples of composited tissue was dependent on how much of the sample was available for replication, up to a maximum of three subsamples. Energy density of pellets was determined after combustion and expressed as kilocalories per gram dry weight (kcal g^{-1} DW). To determine the relative contribution of the gelatin capsules, five empty capsules were weighed and then analyzed to determine their average weight and added caloric content, which was 4.5 kcal g^{-1}. As a result, the energy density of samples measured via gelatin capsules was calculated using formula (1):

$$Cal_{Sample} = ((Wt_{Total} \times Cal_{Total}) - (Wt_{Capsule} \times Cal_{Capsule})) / Wt_{Sample} \qquad (1)$$

where $Wt_{Capsule}$ is the weight of the empty gelatin capsule (grams), $Cal_{Capsule}$ is the average caloric content of an empty gelatin capsule in (kcal g^{-1} DW), Wt_{Sample} is the weight of the sample contained within the capsule, Cal_{Sample} is the unknown caloric value of that sample, Wt_{Total} is the combined weight of the capsule and the sample, and Cal_{Total} is the gross heat generated by the entire sample determined via combustion in the bomb calorimeter.

Statistical Analysis

Caloric content of the dominant taxa and community data was compared between strata (South, Central A, Central B, and North) to determine the spatial distribution of caloric content within these regional separations. Energy (kcal g^{-1}) of each taxa was compared among regions using ANOVA followed by Tukey multiple comparisons using R (www.r-project.org). Geospatial models were used to visually demonstrate differences in caloric content of the dominant taxa over the entire CSESP study area. Geospatial models were also used to create contour plots of environmental variables. The energy values of the dominant taxa were then compared to the environmental variables using multiple linear regression to determine which of these variables predictors of caloric content were significant. Pearson's correlation statistic was used to determine the correlations between energy content and environmental variables.

RESULTS

General Results of Energy Content for Dominant Taxa and Community

Energy contents of dominant taxa were highly variable and had a wide range of values, from 0.6 kcal g^{-1} (*Nephtys* spp.) to 7.7 kcal g^{-1} (*Ennucula tenuis*) (Table 4-1). Ampeliscidae ranged from 2.8 to 7.2 kcal g^{-1} with an average of 4.4 kcal g^{-1}. *Ennucula tenuis* ranged from 1.9 to 7.7 kcal g^{-1} with an average of 4.2 kcal g^{-1}. Caloric content of *Golfingia margaritacea* was on average, lower in comparison to the other taxa with values ranging from 1.8 to 3.8 kcal g^{-1},

Table 4-1. Energy content (kcal g^{-1}) of dominant taxa by station. An “na” represents values that are missing either by loss of the sample or because the station did not have that taxa.

Station	Ampeliscidae	*E. tenuis*	*Golfingia*	*Macoma*	Maldanidae	*Nephtys*	Other
BF003	4.5	4.5	na	na	3.4	na	3.0
BF005	3.9	2.3	na	4.9	3.0	na	3.8
BF011	5.5	4.3	na	4.8	6.8	na	3.9
BF013	na	4.3	na	4.7	3.7	na	3.6
BF015	3.5	4.2	na	4.6	3.8	na	2.2
BF017	na	3.8	na	3.6	3.7	na	3.9
BF023	3.8	4.6	na	5.0	na	na	3.4
HC010	na	6.4	na	4.5	4.1	na	3.7
HC020	na	4.9	3.8	na	na	na	na
HC028	na	na	na	4.6	na	3.5	4.1
HN001	4.9	4.4	2.9	4.7	3.5	6.2	3.5
HN003	na	na	na	4.9	na	na	3.8
HN014	na	na	na	5.0	na	na	na
HN015	4.1	4.2	na	4.1	na	na	4.1
HN016	3.9	na	2.7	4.8	na	na	3.8
HN018	4.6	na	na	na	na	na	3.5
HN025	4.2	4.7	na	na	4.0	na	4.6
HN027	4.2	3.5	na	4.5	na	na	3.6
HN029	na	na	na	5.0	na	na	3.2
HS001	na	4.8	na	na	3.4	4.0	3.5
HS009	na	4.1	na	na	3.2	0.6	3.5
HS011	3.8	4.6	2.2	4.2	3.5	na	3.4
KF003	6.9	na	na	na	2.9	3.6	na
KF007	2.8	3.8	na	3.5	3.2	3.1	3.4
KF009	3.0	4.2	na	4.3	2.5	2.5	3.4
KF011	5.2	7.7	na	na	3.0	na	4.0
KF013	7.2	3.8	1.8	4.0	3.1	5.0	3.6
KF015	5.4	na	na	4.6	2.7	3.9	3.2
KF023	4.1	4.0	na	3.4	3.7	na	3.9
KF025	3.1	3.9	na	3.2	3.6	2.0	3.4
SF003	4.1	4.5	2.8	5.1	3.6	na	3.3
SF007	na	3.4	na	5.5	3.5	3.7	3.9
SF009	4.1	3.1	na	4.6	2.9	3.2	4.0
SF011	3.8	1.9	2.3	4.6	3.6	4.2	4.4
SF016	na	na	na	4.2	3.4	na	4.4
SF020	5.3	na	na	na	3.0	3.4	3.5
min	2.8	1.9	1.8	3.2	2.5	0.6	2.2
max	7.2	7.7	3.8	5.5	6.8	6.2	4.6
average	4.4	4.2	2.6	4.5	3.5	3.5	3.6
SD	1.1	1.1	0.7	0.6	0.8	1.3	0.5

with an average of 2.6 kcal g^{-1}. Energy values for *Macoma* spp. ranged from 3.2 to 5.5 kcal g^{-1}. Maldanidae had energy values ranging from 2.5 to 6.8 kcal g^{-1}. *Nephtys* spp. had the largest range in values, with a minimum of 0.5 kcal g^{-1} and maximum of 6.3 kcal g^{-1}. The energy values for Others ranged from 2.2 to 4.6 kcal g^{-1}.

Regional and Geospatial Differences in Energy Values

The variability in energy values for each taxa among regions was moderate (Table 4-2). Ampeliscidae and *Ennucula tenuis* had maximum values in the South with a value of 7.2 and 7.7 kcal g^{-1}, respectively. The maximum value in the Central A region was for Maldanidae (6.8 kcal g^{-1}), while in Central B and South it was for *Ennucula tenuis* (6.4 and 7.7 kcal g^{-1}, respectively). In the North, the highest energy values belonged to the polychaete *Nephtys* spp. with a value of 6.2 kcal g^{-1}. *Golfingia margaritacea* had a maximum value in the Central B region with a value of 3.8 kcal g^{-1}, along with *Macoma* spp. (5.5 kcal g^{-1}). The maximum energy value of Others was in the North (4.6 kcal g^{-1}). The only taxa that demonstrated a significant difference in energy content among strata was Maldanidae (Table 4-3). Tukey multiple comparisons demonstrated that the average caloric content of Maldanidae was significantly greater in the Central A stratum than in the South stratum.

The geospatial models varied greatly among taxa (Figure 4-3). The bivalves *Ennucula tenuis* and *Macoma* spp., as well as *Nephtys* spp., have peak energy values centered on individual stations reflecting high small-scale variability with no spatial trend. *Golfingia margaritacea* had higher energy values in the northeast section of the region, and lower values in the southwest but the sample size was low so the model must be considered with caution. Energy values for Maldanidae were highest on the western side of Burger, and had low values in the other lease sale sites (Klondike and Statoil). Energy values for *Ampeliscidae* appear to have highest energy values in the southern section, and lowest in the northern portion of the study area. The geospatial model for Others depicts low energy on the eastern side of Burger, and high energy in the northwestern section.

Table 4-2. Averages, standard deviations (SD), and sample counts (n) of energy content (kcal g^{-1}) for dominant taxa by strata (Central A, Central B, North, South). NA = not applicable. *Ampeliscidae*

Taxon	Region	Ave.	SD	n
Ampeliscidae	Central A	4.0	0.8	6
	Central B	4.2	0.7	4
	North	4.3	0.4	6
	South	4.9	1.6	8
Ennucula tenuis	Central A	3.9	0.7	8
	Central B	4.0	1.6	6
	North	4.2	0.5	4
	South	4.7	1.3	8
Golfingia margaritacea	Central A	2.8	NA	1
	Central B	3.1	1.1	2
	North	2.8	0.2	2
	South	2.0	0.3	2
Macoma spp.	Central A	4.3	0.8	8
	Central B	4.7	0.4	7
	North	4.7	0.3	7
	South	4.1	0.4	5
Maldanidae	Central A	4.0	1.2	8
	Central B	3.4	0.4	6
	North	3.7	0.3	2
	South	3.1	0.3	10
Nephtys spp.	Central A	2.0	NA	1
	Central B	3.6	0.4	5
	North	6.2	NA	1
	South	3.2	1.4	7
Other	Central A	3.5	0.6	8
	Central B	3.9	0.4	8
	North	3.8	0.4	8
	South	3.4	0.3	9

Table 4-3. ANOVA of log-transformed energy content for the dominant taxa data among the four strata. Bold values are significant at $\alpha = 0.05$.

Taxon	F-value	P-value
Ampeliscidae	0.45	0.722
Ennucula tenuis	0.78	0.519
Golfingia margaritacea	1.33	0.411
Macoma spp.	2.05	0.135
Maldanidae	3.23	0.040
Nephtys spp.	0.97	0.446
Other	2.02	0.133

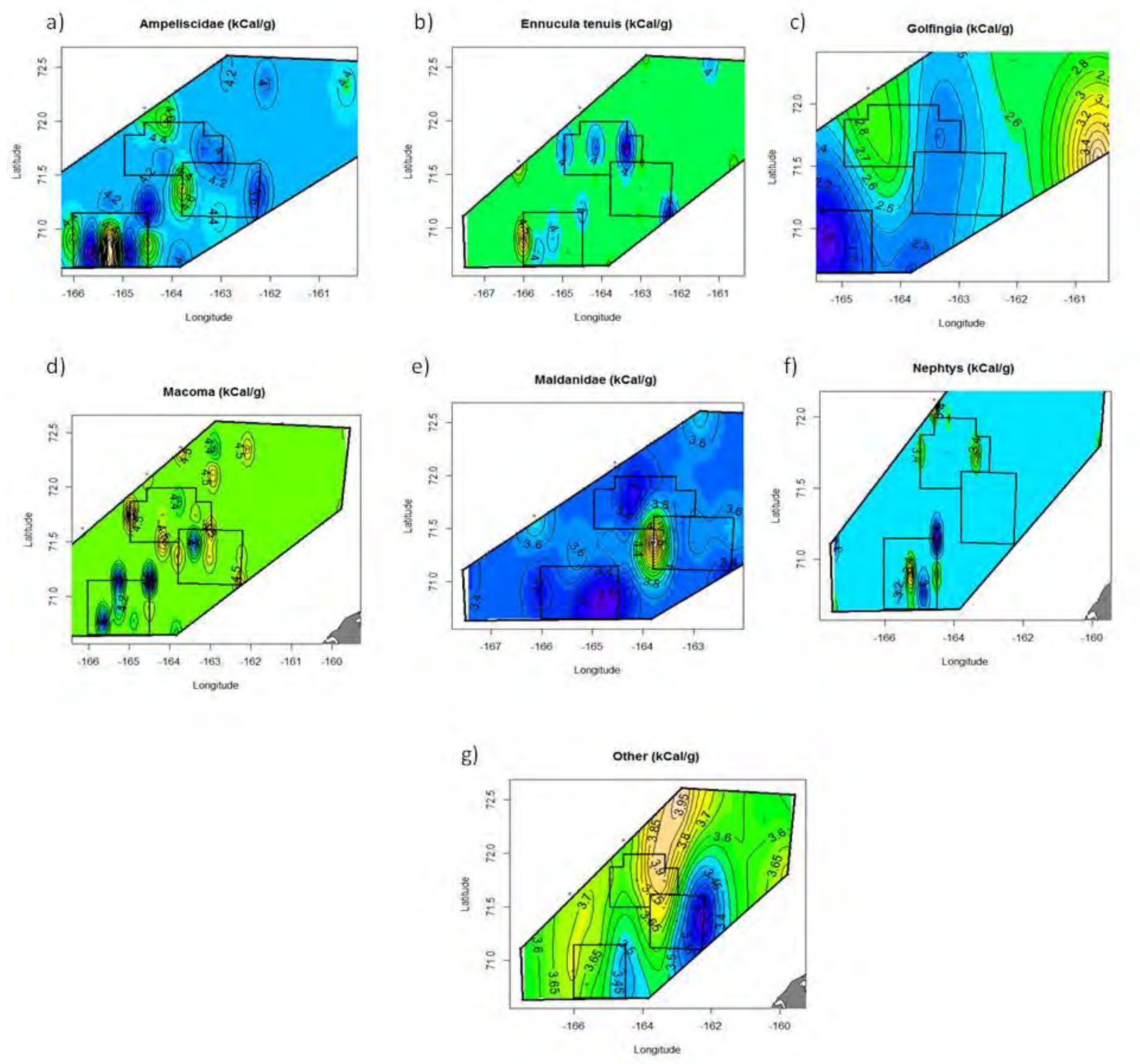

Figure 4-2. Spatial models of energy content (kcal g^{-1}) of dominant taxa for the CSESP study area. Plots are for a) Ampeliscidae, b) *Ennucula tenuis*, c) *Golfingia margaritacea*, d) *Macoma* spp., e) Maldanidae, f) *Nephtys* spp., and g) Other. A blue/violet coloration represents low values, while yellow/white represents values of high caloric content.

The geostatistical model of percent mud reflects high variability around individual stations (Figure 4-4, a; see Chapter 2 for a more complete map). Depth is greatest in the southwest and northeast, and shallowest in the middle section towards the north. Salinity is greatest in the northeast, with decreasing values towards the south. Bottom temperature was lowest in the north and highest in the south, reflecting the influx of warm Pacific water from the Bering Sea. Total Chlorophyll was highest on the eastern side of Burger. The models for Maldanidae and Others showed patterns generally similar to water depth while the model for Ampeliscidae was similar to that for temperature (Figs. 4-2 and 4-3).

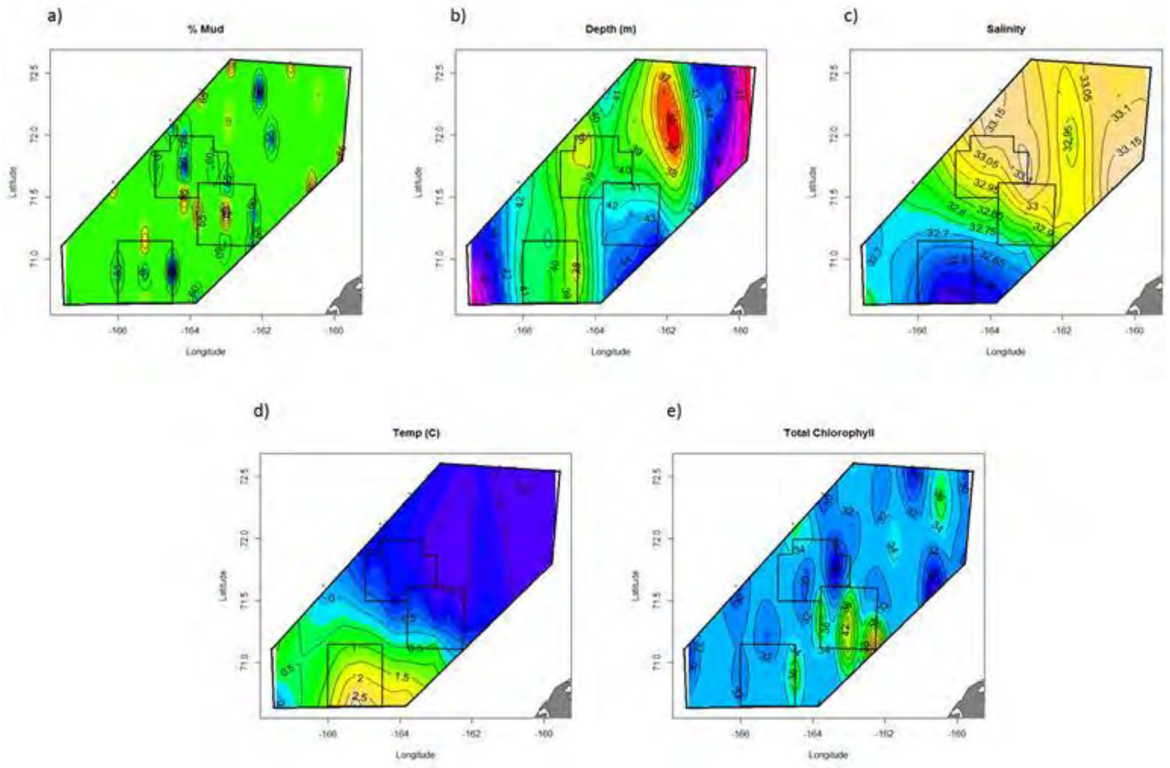

Figure 4-3. Spatial models of environmental variables for the CSESP study area. Plots are for a) percent mud, b) depth, c) salinity, d) temperature, and e) total chlorophyll. A blue/violet coloration represents high values and red represents low values for water depth, whereas blue/violet represents low values and yellow/white represents high values for the other variables.

Regression of Caloric Content with Environmental Variables

Multiple linear regressions demonstrated significant relationships between environmental variables and energy values of some taxa (Table 4-4). Mud was a significant predictor of caloric content of Maldanidae with a high positive correlation (p = 0.021, Pearson's correlation r = 0.599), and a weak predictor for "Others" (p = 0.01, r = 0.344). Depth was a significant, but very weak predictor for the caloric content of "Others" as well (p = 0.019, r = -0.181). Bottom water temperature was a significant predictor of the caloric content *Macoma* spp. with a high negative correlation (p = 0.018, r = -0.487). Predictors of caloric content of *Ennucula tenuis* were significant at a higher significance level ($\alpha = 0.10$; p = 0.064 for percent mud and p = 0.070 for total Chlorophyll a). There were no significant environmental predictors of energy content for *Nephtys* spp. and Ampeliscidae.

Table 4-4. Multiple Linear Regressions (MLR) of environmental variables with log-transformed caloric content for dominant taxa. P-values in bold are significant at $\alpha = 0.05$. Data for *Golfingia margaritacea* were not included in this analysis due to the small sample size.

Variable	*E. tenuis*	*Macoma*	Maldanidae	*Nephtys*	Ampeliscidae	Others
% Mud	0.139	0.355	**0.021**	0.364	0.256	**0.010**
Depth	0.750	0.611	0.340	0.895	0.420	**0.019**
Bottom-water Temperature	0.064	**0.018**	0.153	0.358	0.561	0.803
Total Chlorophyll	0.070	0.987	0.798	0.956	0.683	0.603

DISCUSSION

The present study demonstrates that spatial variations in caloric content are related to environmental characteristics for a few taxa. Caloric content of *Macoma* spp., Maldanidae, and "Others" demonstrated significant regression relationships with environmental variables suggesting that caloric content of these groups is not constant (Table 4-4). Caloric content of *Ennucula tenuis* was significantly associated with environmental variables as well, but reflected weak associations. Spatial models of caloric content indicate spatial trends for Ampeliscidae, *Golfingia margaritacea*, Maldanidae, and "Others", suggesting variable energy contents for animals throughout the study area (Fig. 4-3). Caloric values measured in this study were comparable to those found in previous studies (Brawn et al., 1968; Wacasey and Atkinson, 1987; Hondolero et al., 2012). Caloric content of benthic invertebrates depends on numerous factors. For example, Lawson et al. (1998) found that northern shrimp (*Pandalus borealis*) exhibits sex linked differences when it came to energy content, with males having higher caloric value than females. Animal size and reproductive condition were also shown to influence the volume of tissue (and thus energy) in the gastropod *Hexaplex trunculus* (Vasconcelos et al., 2009). None of these factors were taken into account in this study as many samples were composites and therefore consisted of a mixture of size classes, sex, and body conditions.

Spatial associations were apparent between taxon categories and environmental characteristics, even if the regression was not significant. The highest energy values for Ampeliscidae were found in the south and decreasing northwards (Fig. 4-3). Similar north-south trends were found for the environmental variables bottom-water temperature and salinity, with high temperatures and low salinities in the south, and low temperatures and high salinities in the north (Figure 4-4). This warmer, fresher water results from the influx of Pacific water through the Bering Strait, seasonally heating the area. There were, however, no significant differences in energy content of Ampeliscidae between regions, similar to *Ennucula tenuis*, indicating the need for interaction regression models (Table 3). The energy content of Maldanidae was highest on the western side of Burger (Figure 4-3, d) and was predicted by percent mud (Table 4-4). Sediment grain-size covaries with many physical processes and sediments with a higher percentage of mud exist under lower physical dynamics and are usually found at greater depth. Muddier sediments also have higher proportions of particulate organic carbon as organics can more easily bind to mud. Thus, the higher energy content of Maldanidae would more likely be the result of decreased water column dynamics and increased particulate organic carbon, as noted for an area at and just to the northeast of Burger (Chapter 2). The increased percent mud and organics are due to a convergence of water flows over the eastern side of Burger, resulting in decreased water movement. This decrease in water movement allows for greater deposition of particulate organic matter, resulting in greater macrofaunal density and biomass (Blanchard et al., 2013a; Chapter 2).

Variability in energy content among species can help explain energy flow within the northeastern Chukchi Sea. Results from the present study showed that the taxonomic group with the lowest energy content is *Golfingia margaritacea*, while the greatest caloric content was found in the bivalve *Ennucula tenuis* (Table 4-1). This is most likely due to the large amount of tissue found in bivalves in comparison to *Golfingia margaritacea*, which contain more water (the dry weight of *Golfingia margaritacea* is only a fraction of its wet weight). Thus, areas that have high abundances of bivalves, such as *Ennucula tenuis* and *Macoma* spp., would have higher total energy content than other areas. Previous studies have shown that the highest densities of bivalves are in the South, the Central B region, and the North (Chapter 2), meaning that these regions might have greater total caloric content than other regions. An area of high benthic production adjacent to and slightly northeast of the Burger study area is known to have high bivalve biomass and be a feeding area for walrus, reflecting the higher energy content in prey.

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CHAPTER 5

BENTHIC ECOLOGY IN THE NORTHEASTERN CHUKCHI SEA, 2008-2012:
A Summary of Investigations in the Hanna Shoal Study Area

The Hanna Shoal Study Area

The Chukchi Sea Environmental Studies Program (CSESP) provides insights into the ecology and functioning of the northeastern Chukchi Sea. Recent publications provide a general summary of results from the 2008 – 2010 CSESP benthic surveys focused on the three study areas Klondike, Burger, and Statoil (Blanchard et al., 2013 a and b; Blanchard and Feder, in press). Expansion of the CSESP to a larger study area in 2011 – 2012 provides an invaluable opportunity to expand the more focused study to a larger and ecologically-complex region. We have learned much from the expanded CSESP program including deeper insights into the spatial and temporal variability of benthic fauna, food webs and energy flow through the system, and population dynamics. It was expected that Hanna Shoal would have coarser sediments due to its shallower depths, stronger currents, and persistent ice-gouging, and that the fauna would reflect those environmental differences. That expectation was met as faunal composition of the Hanna Shoal area was different with sandy sediments, fewer organisms overall and particularly fewer upright megafauna, more suspension feeders, and fewer deposit feeders (Blanchard and Knowlton, 2013; Chapter 2). Moving beyond the first demonstration of differences, we desire to understand the environmental conditions framing the composition and structure of the benthic assemblages in the area and compare trends in environmental variables with biological data.

The expanded study area provided the opportunity to test the conclusions of the more focused 2008 – 2010 study. In particular, benthic community characteristics appear to be strongly related to deviations in water circulation patterns (Blanchard et al., 2013 a and b), but that conclusion is not reached from broad-scale studies; Blanchard and Feder (in press) found that the scale of study led to differing conclusions. Determining how patterns might change with an increase in scale in the CSESP has implications for reducing sampling designs and for demonstrating what designs would be appropriate for future studies.

Integrating analyses can be a difficult and daunting task. Methods are often multivariate, correlative approaches that may not always provide clear results. Multivariate methods are often overused and recently, multidimensional scaling ordination has been proven to be inconsistent in some situations (Warton et al., 2012). Nevertheless, such methods are often the only approaches applicable for integrating variables from differing sources (e.g., biological and environmental data). Used with caution, MDS and other multivariate approaches can be valuable tools as they can demonstrate general trends and deviations of individual items from overall patterns. Other useful multivariate tools include principal components analysis (PCA), canonical correspondence analysis (CCA), and canonical correlation analysis (CCOR). The latter technique, CCOR, focuses on correlation analyses whereas PCA emphasizes patterns based on maximizing variances, and CCA is a multivariate regression technique. Here, in addition to the other methods applied throughout the report, we present an analysis based on CCOR as a method for integrating the various types of data.

The CSESP has supported an extensive benthic ecology component. In addition to investigating the community ecology of benthic macro- and megafauna, we have studied environmental characteristics, meiofauna, food webs, and energy content of benthic organisms. Here, we seek to summarize and integrate the results of the 2011 – 2012 study and to draw a final picture of the environmental and biological processes of the area. The chapter also demonstrates methods for integrating disparate data sets.

Associations of Fauna with Environmental Characteristics

The prior CSESP investigations in 2008 – 2010 demonstrated that spatial variability of benthic communities was linked to water circulation. Deviations in water flow patterns caused by circulation around Hanna Shoal resulted in stagnant water circulation at and near Burger where water masses converge (Blanchard et al., 2013 a and b). The stagnant water circulation allows finer sediments and organic carbon to settle in that area. Greater stratification caused by a persistent cold water pool in Burger would favor increased seasonal production in the area as well. The 2008 – 2010 data suggested high benthic biomass extending from Burger to the northwest. Geostatistical modeling of the 2011 – 2012 data support the general trend in biomass observed in the earlier study (Fig. 5-1). High density (ind. m^{-2}), biomass, and bivalve biomass occur in an area of deeper water, muddier sediments, higher organic carbon, and colder water temperatures (Figs. 1-1 and 5-1). Although effects of individual variables on biotic parameters were not always strong (Table 5-1), the interactions among these variables are likely to be very strong. Correlations were strong between percent mud and density, biomass and bivalve biomass, and between bivalve biomass and organic carbon and bottom-water temperature

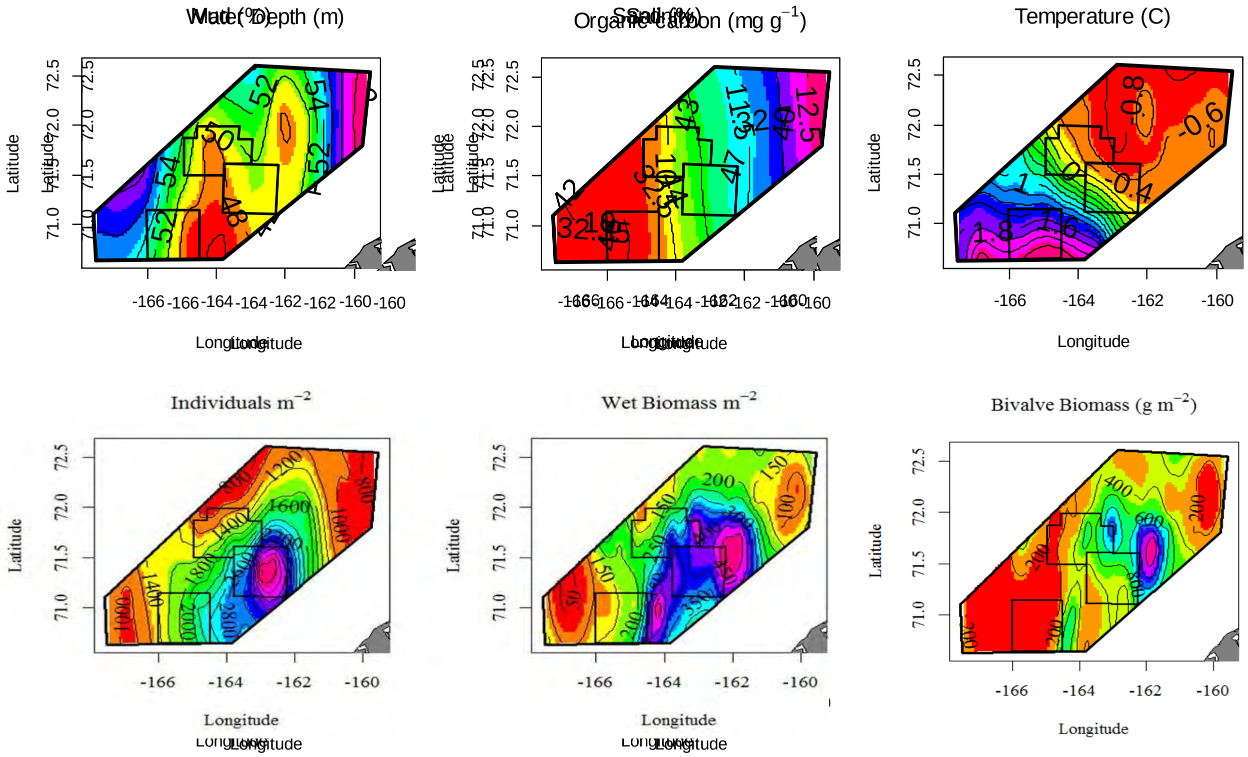
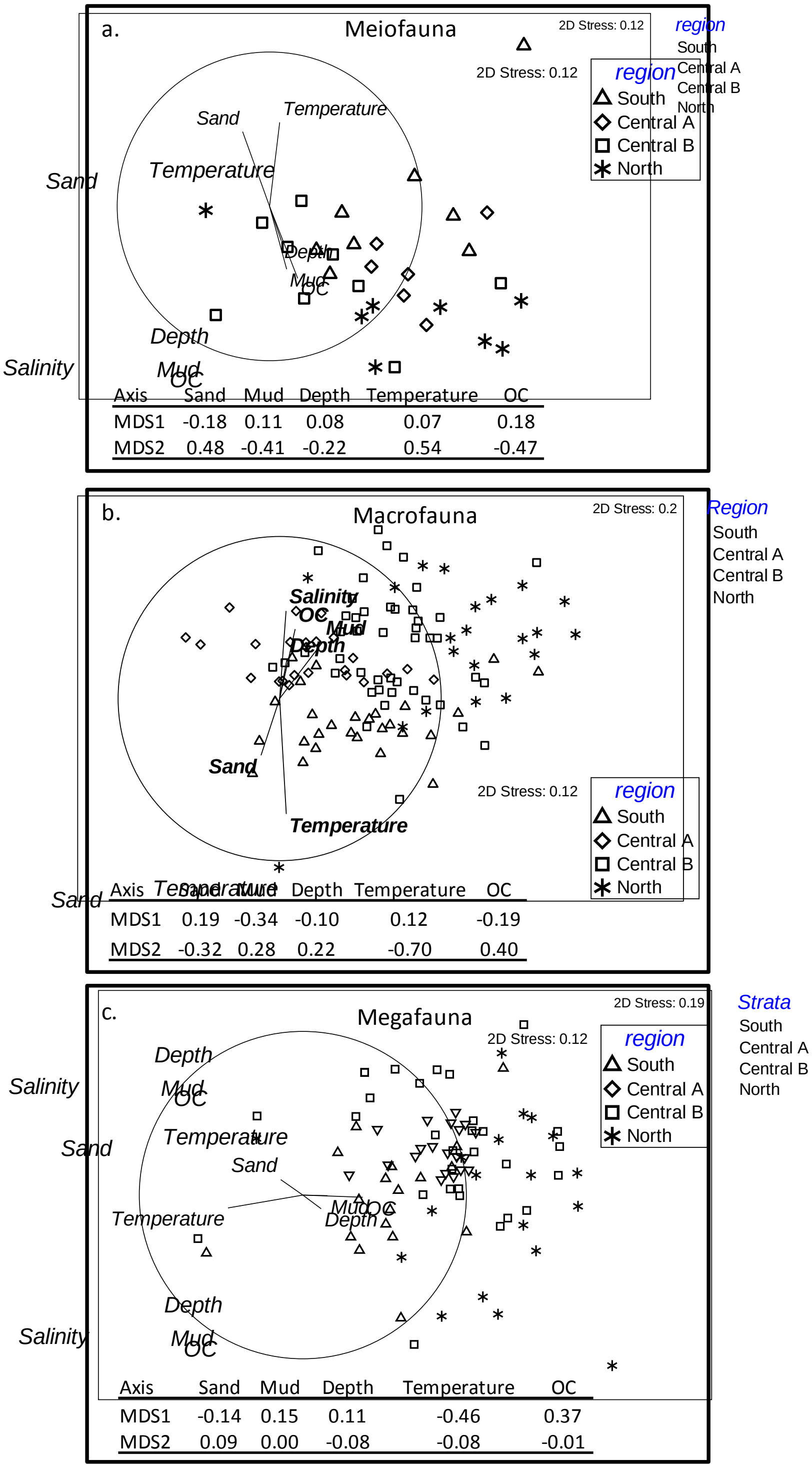


Figure 5-1. Spatial models of environmental and biological variables from the northeastern Chukchi Sea, 2011 – 2012.

Table 5-1. Correlations of modeled values from biological and environmental spatial models.

Variables	Depth	% Mud	Organic Carbon	Temperature
Density	0.01	**-0.49**	-0.09	0.04
Biomass	-0.13	**-0.57**	0.11	-0.22
Bivalve Biomass	-0.27	**-0.31**	**0.51**	**-0.65**

The meio-, macro-, and megafaunal MDS ordinations consistently point to sediment and water mass characteristics as covariates of community characteristics (Fig. 5-2). Although stations from the South and North strata were generally separated in the MDS ordinations, segregation of stations into their strata was not strong and many stations were mixed with other strata. Percent sand and mud were moderate correlates with the MDS ordination axes for meio- and macrofauna but not for megafauna, which may be mobile and large enough to escape the limitations of the smaller organisms. Bottom-water temperature and sediment organic carbon content (OC) were moderate to strong correlates with MDS axes for all three groups of organisms.



Axis	Sand	Mud	Depth	Temperature	OC
MDS1	-0.18	0.11	0.08	0.07	0.18
MDS2	0.48	-0.41	-0.22	0.54	-0.47

Axis	Sand	Mud	Depth	Temperature	OC
MDS1	0.19	-0.34	-0.10	0.12	-0.19
MDS2	-0.32	0.28	0.22	-0.70	0.40

Axis	Sand	Mud	Depth	Temperature	OC
MDS1	-0.14	0.15	0.11	-0.46	0.37
MDS2	0.09	0.00	-0.08	-0.08	-0.01

Figure 5-2. Nonmetric multidimensional scaling ordinations of *ln*(X + 1)-transformed density data for a) meiofauna, b) macrofauna, and c) megafauna from the northeastern Chukchi Sea, 2011 – 2012.

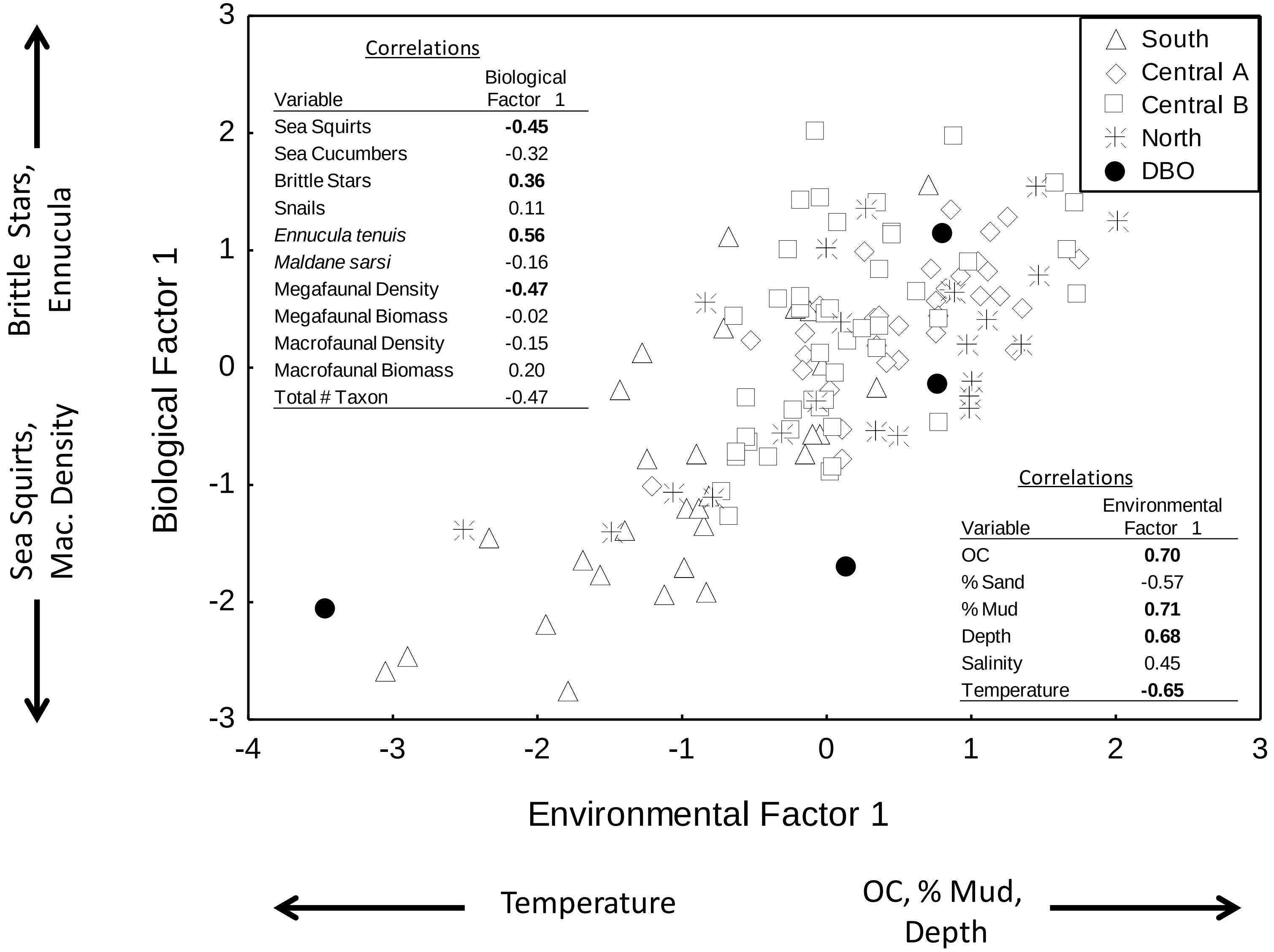
Canonical correlation analysis (CCOR) was applied to determine associations of key biological variables (summary measures and biomass of dominant macro- and megafauna) with environmental variables. To perform CCOR, we start with two data sets of different kinds; biological and environmental data in the present study. The CCOR then simultaneously reduces the two data sets to two variables called the canonical variates, which we refer to here as the derived variables (one variable derived for each data set). The new variables were calculated with the restriction that the derived variables have maximum correlation with each other. The calculation of the initial set of derived variables is the first step, and this can be repeated with the restriction that there is no correlation ($r = 0$) between all prior and subsequent derived pairs of variables (set 1 is uncorrelated with set 2, set 3, or set 4, etc.), and the number of steps possible is limited by the number of variables included in the data set. The first derived variables for the biological and environmental variables will be the maximum possible correlation given the data (biological factor 1 and environmental factor 1).

The CCOR analysis here is based on selected summary variables for macro- and megafauna, biomass of key faunal groups or species, and sediment and physical variables. As an ordination technique, CCOR provides a plot that can be interpreted like an MDS plot plus it provides additional information on correlation structures of the data sets. The method allows for direct inferences about the strengths of associations between data sets. The CCOR method of calculating the derived variables will result in a strong linear pattern in the ordination plot. The ordination can be interpreted by evaluating the position of stations from *a priori* groups in the ordination (the strata), correlations of the original data with the derived variables, and correlations among the derived variables.

The CCOR analysis of the 2011 – 2012 data demonstrates a strong linear trend in the ordination and strong correlation structures. The overall correlation among the data sets was high (canonical $R = 0.76$, canonical $R^2 = 0.54$, $p < 0.0001$) with the derived variables accounting for 58% of total variance in the biological data set and 100% in the environmental data set. The ordination plot of individual stations demonstrates a high correlation between Biological Factor 1 and Environmental Factor 1 ($r = 0.74$), but has no meaningful separation of stations by regional strata; all strata overlap (Fig. 5-3). Looking at the environmental variables, high correlations of OC, % mud, depth, and temperature indicate increasing OC, mud, and depth with increasing values of Environmental Factor 1; temperatures decrease with increasing values of

Environmental Factor 1. Biomass of *Ennucula tenuis* and brittle stars increases with Biological Factor 1 while biomass of sea squirts and megafaunal density decline. The correlations indicate that *E. tenuis* and brittle stars have higher biomass in areas with greater OC, % mud, and greater depth whereas sea squirts have lower biomass in those areas and lower megafaunal density as well (Fig. 5-3), as demonstrated by the bubble plot overlays (Fig. 5-4). These results support prior conclusions that water currents play a major role in structure communities. Suspension feeding megafaunal sea squirts (an upright organism feeding in the water column) will have higher biomass in areas with greater currents and thus, less mud, while the alternate is true of the bivalve *E. tenuis* and deposit-feeding brittle stars that bury themselves into muddy sediments. The negative association of megafaunal density with Biological Factor 1 also suggests declining densities with increasing OC, mud, and water depth.

The geostatistical analyses and the multivariate methods suggest strong covariances between various biological characteristics of the benthic assemblage and environmental conditions. The driving forces underlying the strong covariance are not as easily measured but appear to be linked to the topographic control of water circulation by Hanna Shoal. Alternative hypotheses are not yet clear. Nevertheless, the patterns apparent in the 2008 – 2010 investigation do extend to the greater Hanna Shoal region.



Correlations

Variable	Biological Factor 1
Sea Squirts	**-0.45**
Sea Cucumbers	-0.32
Brittle Stars	**0.36**
Snails	0.11
Ennucula tenuis	**0.56**
Maldane sarsi	-0.16
Megafaunal Density	**-0.47**
Megafaunal Biomass	-0.02
Macrofaunal Density	-0.15
Macrofaunal Biomass	0.20
Total # Taxon	-0.47

Correlations

Variable	Environmental Factor 1
OC	**0.70**
% Sand	-0.57
% Mud	**0.71**
Depth	**0.68**
Salinity	0.45
Temperature	**-0.65**

Figure 5-3. Canonical correlation analysis of selected variables from the northeastern Chukchi Sea, 2011 – 2012.

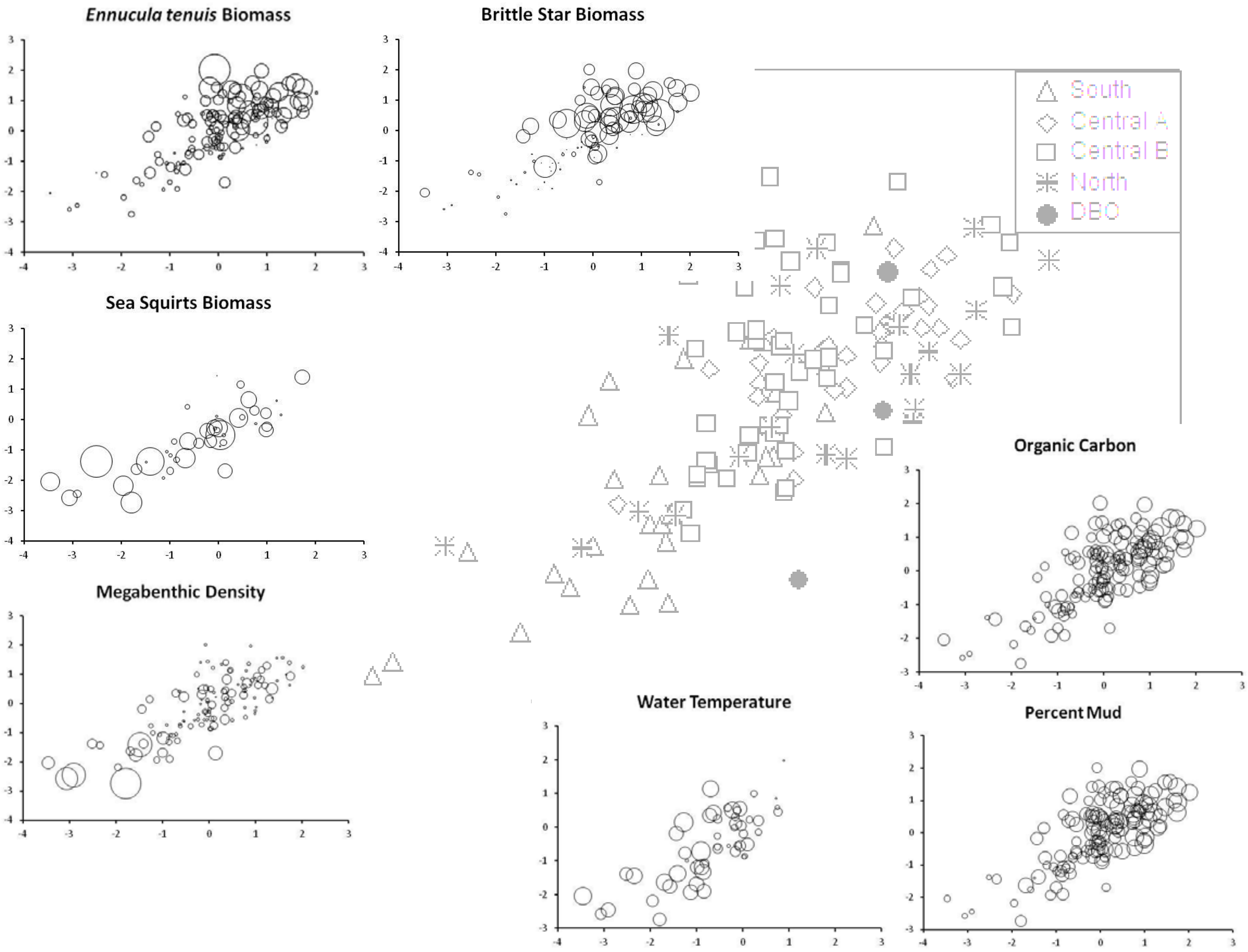


Figure 5-4. Overlays of variables with high correlations on the canonical correlation analysis plot from the northeastern Chukchi Sea, 2011 – 2012.

Energy Flow

The benthic food webs of the Klondike, Burger, and Statoil study areas demonstrated some differences related to water circulation (Tu, 2013). Klondike and Burger had higher proportions of deposit feeders contributing to trophic level 2 and benthic omnivores contributing to trophic level 3 whereas suspension feeders (bivalves) contributed to a high proportion of biomass in trophic level 2 in Statoil (Fig. 5-5). Deposit-feeding animals (the polychaete *Maldane sarsi*) contribute to a high proportion of density in trophic level 3 in Burger whereas Klondike and Statoil were more balanced among trophic levels. Differences among feeding modes and contributions in biomass and density to trophic level composition appears to be related to oceanographic characteristics and water circulation (Fig. 5-6). The convergence of currents over the region with high biomass indicates a strong covariance between currents and faunal characteristics (Figs. 5-1 and 5-6).

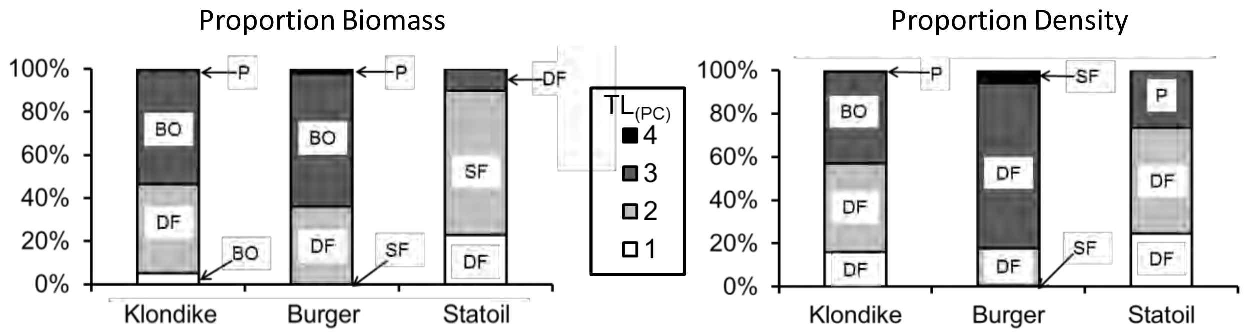


Figure 5-5. Proportional contributions of benthic density (abundance) and biomass of feeding modes to each trophic level at Klondike, Burger, and Statoil. Trophic level (TL) is based on the primary consumer *Ampelisca eschrichti* ($TL_{(PC)}$=2, see Tu, 2013 for details). The feeding mode of the taxa with the highest biomass/abundance contributing to each trophic level is noted within each bar. Feeding modes: BO benthic omnivore, DF deposit feeder (includes surface and subsurface), SF suspension feeder, P predator. Redrawn from Tu (2013).

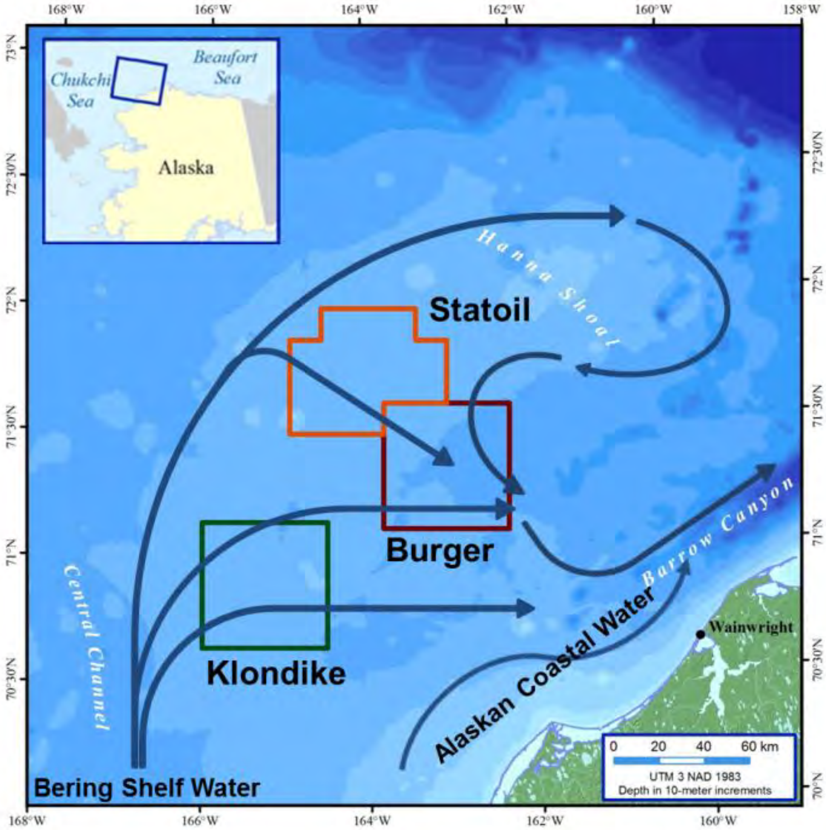


Figure 5-6. The Klondike, Burger, and Statoil study areas and conceptual oceanographic circulation (indicated by arrows) based on Winsor and Chapman (2004), Spall (2007), and Weingartner et al. (2013).

Differences in feeding habits among study areas were also apparent with suspension-feeding amphipods of the family Ampeliscidae feeding on a different food source in Klondike than in Burger or Statoil (the $\delta^{13}C$ signature of Ampeliscidae was shifted to the right in Klondike; Fig. 5-7). The differences in ampeliscid $\delta^{13}C$ reflect differences in the isotopic signature of particulate organic matter (POM; primary production) with Klondike having a more enriched isotopic signature than Burger or Statoil (highlighted in red in Fig. 5-7). The shifts in POM and ampeliscid isotopic signatures in Klondike are presumably due to seasonal progression in primary producer composition and food quality with the changes delayed in Burger and Statoil due to slower water mass flushing (Tu, 2013; Weingartner et al., 2013). The convergence of water currents again plays a role as slow circulation combined with the persistence of the cold pool, and thus greater stratification would favor increased seasonal production. The stagnant water flow would favor carbon deposition in Burger while at the same time, potentially delaying later-summer primary producers (associated with warmer water and lower nutrient concentrations) from establishing themselves over Burger (Questel et al., 2013).

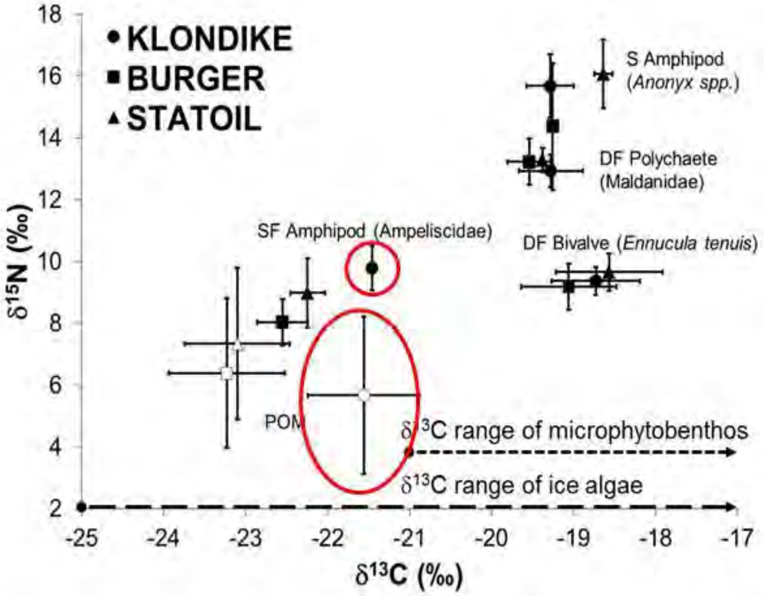
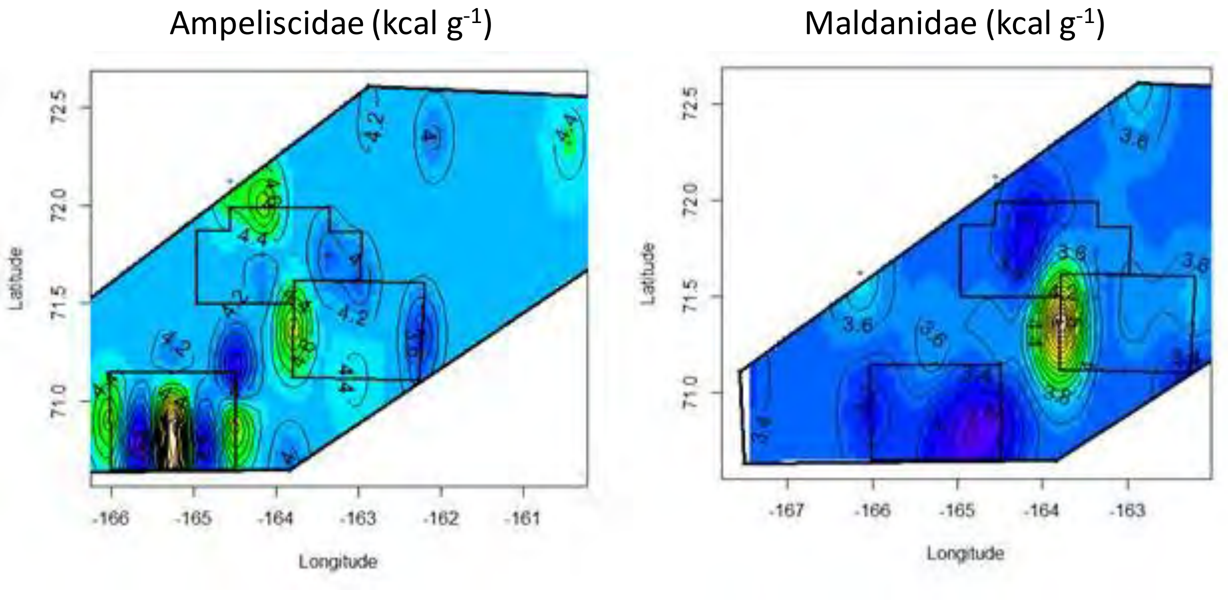


Figure 5-7. Stable nitrogen vs. carbon isotope ratios of four benthic invertebrate taxa at Klondike, Burger, and Statoil (Tu, 2013). Each point represents the mean with standard deviation (SD) bars. Feeding modes: DF: Deposit feeder (includes surface and subsurface), S: Scavenger, SF: Suspension feeder. Ice algal and microphytobenthos δ^{13}C range values from Tremblay et al. (2006) and Gradinger (2009) for comparison of organism stable isotope ratios with those of potential food sources.

In addition to spatial variations in the food web, preliminary analyses suggest that the energy content of some organisms varies with environmental factors as well (Chapter 4; Fig. 5-8). Deposit-feeding polychaetes of the family Maldanidae have higher energy per gram tissue in the Burger study area than elsewhere while the suspension-feeding amphipod Ampeliscidae have higher energy content to the south where food resources may be suspended, rather than deposited (i.e., OC lower; Fig. 5-1). This pattern indicates that not only are maldanid polychaetes more numerous in Burger, but the energy content of their tissues is greater as well. Thus, the preliminary analyses suggest that the energy content of animals appears to be greater per gram of tissue where POM (food) delivery matches preferred feeding methods. The investigation of the interactions of energy content and the environment is ongoing.


Ampeliscidae (kcal g^{-1})

Maldanidae (kcal g^{-1})

Figure 5-8. Geostatistical models of energy content (kcal g^{-1}) for Ampeliscidae and Maldanidae from the northeastern Chukchi Sea, 2011 – 2012.

Temporal Variability

The temporal variations of benthic parameters suggest an assemblage responding quickly to interannual oceanographic variations. The time series is too short to draw strong inferences concerning temporal trends. Nevertheless, some preliminary inferences can be made. First, there are spatial and temporal interactions as temporal patterns among study areas are not consistent (Fig. 5-9). Shifts in density, biomass, and the number of taxa are exaggerated in Burger, suggesting interactions with food deposition, water circulation, life history and biodiversity. Second, temporal changes in benthic parameters roughly follow changes observed in the water column (Questel et al., 2013). Unfortunately, fully supporting the latter conclusion requires a much longer data record than the 5 years currently at hand. The apparent benthic responses to large-scale, oceanographic variations do, however, fall in line with those observed elsewhere in Alaska (Fig. 5-10; Blanchard et al., 2010).

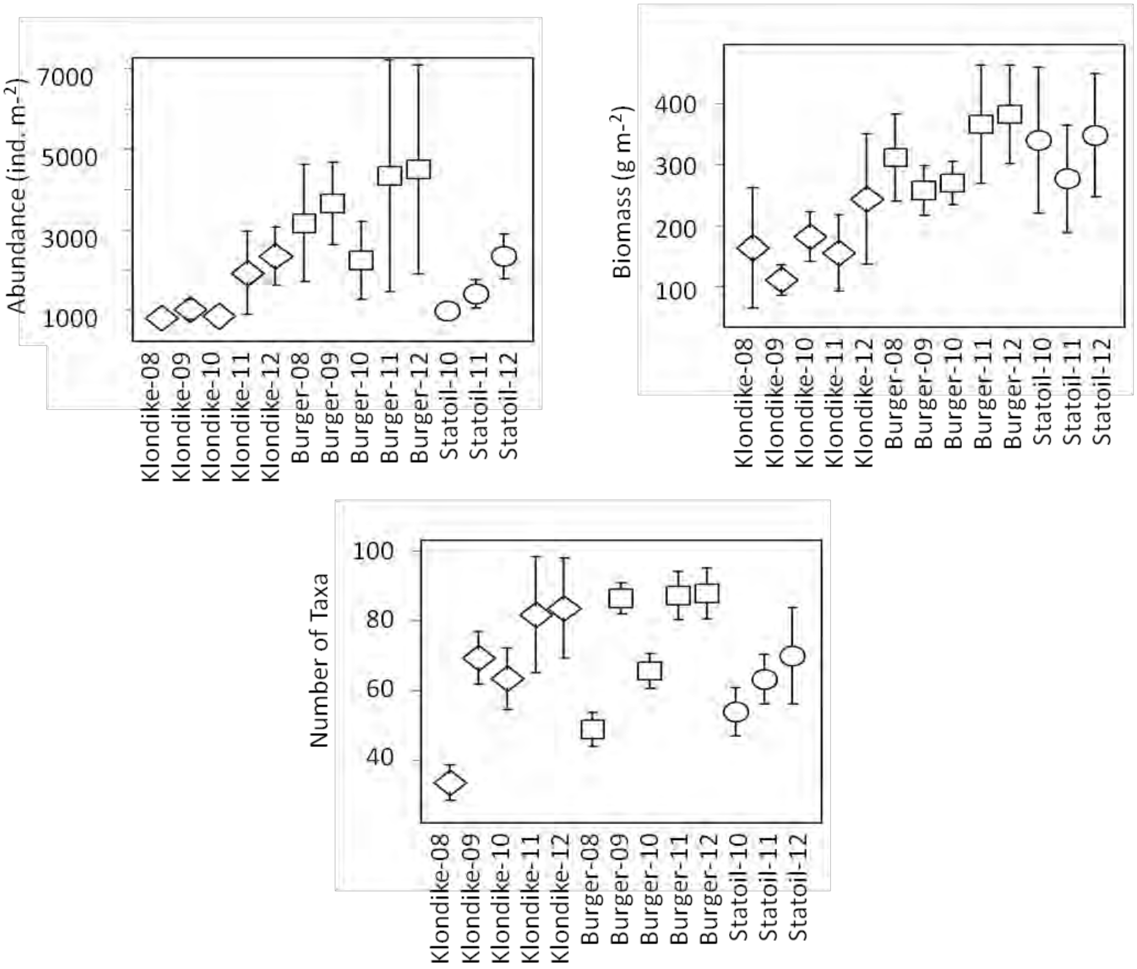


Figure 5-9. Plots of means and 95% confidence intervals based on the raw data for biological summary measures in study areas over the 2008 – 2012 CSESP study.

CONCLUDING COMMENTS

The evolution of the CSESP mirrors that of the environmental studies in Port Valdez, Alaska. Early studies in Port Valdez were comprehensive and continued for a number of years slowly adjusting over time and focusing on collecting data that provided an environmental background for monitoring. Three books resulted from the early investigations (Hood et al., 1973; Colonell, 1980; Shaw and Hameedi, 1988) followed by numerous manuscripts. Ultimately, the program was reduced to endpoints of concern for environmental damage from discharges at the marine oil terminal (Blanchard et al., 2011). The long-term database for Port

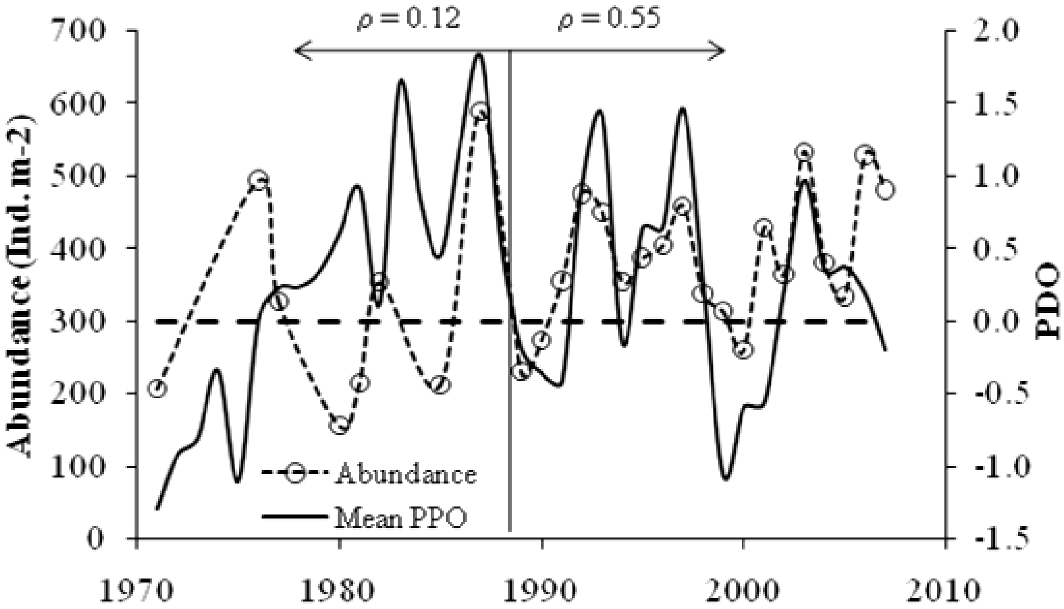


Figure 5-10. Plot of infaunal abundance from Port Valdez and the annual average Pacific decadal oscillation (PDO) index from 1971 to 2007. Spearman's correlation (ρ) are calculated for the period 1971 to 1987 and 1989 to 2007. The high correlation over the period 1989-2007 suggests tight coupling of faunal changes to long-term climatic trends whereas the lack of correlation in earlier years reflects recovery from the 1964 earthquake (Blanchard et al., 2010).

Valdez also includes sampling at sites outside of the immediate area of concern, and those sites provide insights into natural variability and long-term trends (Blanchard et al., 2010). The importance of sampling of natural environmental conditions, rather than only at sites of potential disturbance (e.g., the area at a point-source discharge), cannot be understated. The broader sampling effort prevents conclusions of change due to anthropogenic stressors of concern when extreme natural variations or other influences are drivers. Like the early studies in Port Valdez, the CSESP studies from 2008 – 2012 provide insights into scales of and boundaries for spatial and temporal variability and the factors driving characteristics of the benthic fauna. The expanded 2011 – 2012 CSESP study area provides an even greater opportunity to evaluate variability at multiple scales and gain a deeper understanding of ecosystem processes.

Integration of multiple data sets is challenging for environmental studies. The collection of data from passive acoustics, shipboard observations, CTD casts, pelagic tows, benthic sampling, and more in the CSESP involves multiple sampling scales and methods. Methods for integrating these various data range for simple to complex. Blanchard et al. (2010 and 2011) used spatial modeling and multivariate methods to integrate biological, chemical, and environmental data from Port Valdez, similar to approaches taken in this chapter. The Port Valdez papers demonstrate influences and scales of natural variability and broad-scale stressors separately from biological responses to point-source discharges. Recent advances (e.g., Dunstan et al., 2013) may provide further avenues for integrating results across disciplines.

Spatial variability of benthic communities in the CSESP Hanna Shoal study area is largely driven by water circulation patterns delivering water column production to the fauna in different ways. Starting with food web characteristics, it appears that suspension-feeding organisms in the Klondike study area are exposed earlier to seasonal changes in food characteristics, than Burger or Statoil, as indicated by shifts in stable isotope signatures. As primary producers in later summer may have a different energy content (smaller organisms with less energy in warmer, lower nutrient water), the stagnant water flow could thus be a contributor to the higher energy content of deposit feeders in soft sediments in Burger. The stagnant water circulation may be interacting and influencing spatial and temporal variations in seasonal primary production. The greater contribution of deposit-feeding animals to the food web in Burger and of suspension-feeding animals in Statoil than in Klondike, suggest that organic carbon is being delivered differently to the three study areas. The energy content of some benthic animals also reflect the delivery of POC with deposit-feeding maldanids having more energy per gram of tissue in Burger (where deposit feeding appears to be favored) and suspension-feeding amphipods having more energy per gram tissue adjacent to Klondike (where suspension feeding appears favored). Although not discussed in this chapter, the growth dynamics of *Ennucla tenuis* are also influenced by the environmental characteristics defining Klondike, Burger, and Statoil. Sampling of the whole DBO line in 2013 may contribute to a better understanding the environmental/biological interactions by sampling across points of change in the ecosystem encompassing inshore to offshore environmental gradients.

Benthic communities as a whole were moderately associated with environmental variables, although more complex models are needed to fully assess relationships. From the multivariate methods applied, organic carbon content of sediments, percent mud, water depth, and bottom-water temperature all appear to be covariates with fauna and community structure. Interactions among the environmental variables were not fully evaluated here, but preliminary analyses suggest that the complex landscape and associated interactions in oceanographic, physical, and environmental characteristics are key drivers of benthic assemblages, their densities and biomass, and food webs (Blanchard and Feder, in press; Tu, 2013).

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APPENDIX I:

LIST OF MACROFAUNAL TAXA COLLECTED DURING THE 2008 – 2012 CSESP

- PORIFERA
- CNIDARIA
  - Hydrozoa
  - Anthozoa
    - Actiniidae
    - Edwardsiidae
      - *Edwardsia* spp.
    - Halcampoididae
    - Haloclavidae
    - Halcampidae
      - *Halcampa crypta*
- NEMERTEA
- ANNELIDA
  - POLYCHAETA
    - Polynoidae
      - *Bylgides sarsi*
      - *Bylgides promamme*
      - *Arcteobia anticostiensis*
      - *Enipo canadensis*
      - *Enipo chuckchi*
      - *Enipo gracilis*
      - *Enipo torelli*
      - *Eunoe* spp.
      - *Eunoe nodosa*
      - *Eunoe oerstedi*
      - *Eunoe clarki*
      - *Gattyana* spp.
      - *Gattyana amondseni*
      - *Gattyana ciliata*
      - *Gattyana cirrhosa*
      - *Harmothoe* spp.
      - *Harmothoe beringiana*
      - *Harmothoe extenuata*
      - *Harmothoe imbricata*
      - *Hesperonoe adventor*
    - Pholoidae/Sigalionidae
      - *Pholoe minuta*
    - Phyllodocidae
      - *Phyllodoce groenlandica*
      - *Eteone* spp.
      - *Eteone flava*
      - *Eteone longa*
      - *Eteone spetsbergensis*
    - Hesionidae
    - Syllidae
      - *Proceraea cornuta*

- *Syllis* spp.
- *Typosyllis* spp.
- *Typosyllis alternata*
- *Typosyllis pigmentata*
- *Exogone* spp.

Nephtyidae
- *Nephtys* spp.
- *Nephtys ciliata*
- *Nephtys caeca*
- *Nephtys punctata*
- *Nephtys longosetosa*
- *Nephtys paradoxa*

Sphaerodoridae
- *Sphaerodorum papillifer*
- *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*
    - *Ophelina groenlandica*
    - *Ophelina acuminata*
- Sternaspidae
    - *Sternaspis scutata*
- Capitellidae
    - *Capitella capitata*
    - *Heteromastus filiformis*
    - *Notomastus* spp.
    - *Mediomastus* spp.
    - *Decamastus gracilis*
    - *Barantolla americana*
- Maldanidae
    - *Maldane sarsi*
    - *Nicomache* spp.
    - *Nicomache lumbricalis*
    - *Petaloproctus* spp.
    - *Petaloproctus borealis*
    - *Petaloproctus tenuis*
    - *Axiothella catenata*
    - *Praxillella gracilis*

- *Praxillella praetermissa*
- *Rhodine bitorquata*
- *Rhodine loveni*

Oweniidae
- *Owenia fusiformis*
- *Myriochele heeri*
- *Galathowenia oculata*

Sabellariidae
- *Idanthyrsus saxicavus*

Pectinariidae
- *Pectinaria granulata*
- *Pectinaria hyperborea*

Ampharetidae
- *Amage* spp.
- *Ampharete* spp.
- *Ampharete goesi goesi*
- *Ampharete acutifrons*
- *Ampharete crassiseta*
- *Ampharete finmarchica*
- *Lysippe labiata*
- *Asabellides sibirica*

Terebellidae
- *Neoamphitrite groenlandica*
- *Nicolea zostericola*
- *Thelepus* spp.
- *Thelepus cincinnatus*
- *Thelepus setosus*
- *Artacama proboscidea*
- *Lanassa nordenskioldi*
- *Lanassa venusta venusta*
- *Axionice maculata*
- *Laphania boecki*
- *Proclea* spp.
- *Proclea emmi*
- *Proclea graffii*

Trichobranchidae
- *Terebellides kobei*
- *Terebellides reishi*
- *Terebellides stroemi*
- *Trichobranchus glacialis*

Sabellidae
- *Chone* spp.
- *Chone infundibuliformes*
- *Chone duneri*
- *Chone mollis*
- *Euchone* spp.

- *Euchone analis*
- *Euchone incolor*
- *Bispira crassicornis*
- *Laonome kroeyeri*

Serpulidae

- *Spirorbis* spp.

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.
- *Cingula* spp.

Turritellidae

- *Tachyrhynchus* spp.
- *Tachyrhynchus erosus*
- *Tachyrhynchus reticulatis*

Trichotropidae

- *Trichotropis* spp.
- *Trichotropis borealis*
- *Trichotropis kroyeri*
- *Iphinoe coronata*

Velutinidae

- *Limneria undata*

Naticidae

- *Cryptonatica affinis*
- *Lunatia pallida*

Muricidae

- *Boreotrophon* spp.
- *Boreotrophon clathratus*
- *Boreotrophon truncatus*
- *Nodulotrophan coronatus*

Buccinidae

- *Aulacofusus brevicauda*
- *Buccinum* spp.
- *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
        - *Oenopota* spp.
        - *Oenopota elegans*
        - *Oenopota excurvatas*
        - *Oenopota impressa*
        - *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*
  - 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*
    - *Rochefortia tumida*
  - Carditidae
    - *Cyclocardia* spp.
    - *Cyclocardia crebricostata*
    - *Cyclocardia crassidens*
    - *Cyclocardia ovata*
  - Astartidae
    - *Astarte* spp.
    - *Astarte montagui*
    - *Astarte borealis*
  - Cardiidae
    - *Clinocardium* spp.
    - *Clinocardium ciliatum*
    - *Serripes* spp.
    - *Serripes groenlandicus*
    - *Serripes laperousii*

- Tellinidae
    - *Macoma* spp.
    - *Macoma calcarea*
    - *Macoma brota*
    - *Macoma moesta*
- Veneridae
    - *Liocyma fluctuosa*
    - *Nutricola lordi*
- Myidae
    - *Mya* spp.
    - *Mya arenaria*
- Hiatellidae
    - *Hiatella arctica*
- Pandoridae
    - *Pandora glacialis*
- Lyonsiidae
    - *Lyonsia arenosa*
- Periplomatidae
    - *Periploma aleuticum*
- Thraciidae
    - *Thracia* spp.
    - *Lampeia adamsi*

PYCNOGONIDA
CRUSTACEA

- OSTRACODA
- CUMACEA
    - Lampropidae
        - *Lamprops krasheninnikovi*
    - 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
  - *Pleuroprion murdochi*
- Idoteidae
  - *Synidotea* spp.
  - *Synidotea bicuspida*
  - *Synidotea muricata*
- Munnidae
  - *Munna* spp.

AMPHIPODA
- Odiidae
  - *Odius* spp.
- 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
  - *Crassicorophium* spp.
- Ischyroceridae
  - *Ericthonius* spp.
- Dexaminidae
  - *Guernea nordenskioldi*
- Eusiridae
  - *Eusirus cuspidatus*
  - *Pontogeneia* spp.
  - *Rhachotropis* spp.
- Gammaridae
  - *Maera loveni*
  - *Melita* spp.
  - *Melita dentata*
- Haustoriidae
  - *Eohaustorius eous*
- Pontoporeiidae
  - *Pontoporeia affinis*
  - *Pontoporeia femorata*
  - *Priscillina armata*

- Isaeidae
    - *Photis* spp.
    - *Photis vinogradovi*
    - *Protomedeia* spp.
- Ischyroceridae
    - *Ischyrocerus* spp.
- Lysianassidae
    - *Anonyx* spp.
    - *Hippomedon* spp.
    - *Guernea nordenskioldi*
    - *Orchomene* spp.
- Uristidae
    - *Centromedon* spp.
- Melphidippidae
- Oedicerotidae
    - *Aceroides latipes*
    - *Bathymedon* spp.
    - *Monoculodes* spp.
    - *Westwoodilla caecula*
- Epimeriidae
    - *Paramphithoe polyacantha*
- Phoxocephalidae
    - *Harpiniopsis* spp.
    - *Harpiniopsis kobjakovae*
    - *Harpiniopsis gurjanovae*
    - *Paraphoxus oculatus*
    - *Grandifoxus* spp.
    - *Grandifoxus acanthinus*
    - *Grandifoxus vulpinus*
    - *Grandifoxus nasuta*
- Pleustidae
    - *Pleustes panoplus*
- Podoceridae
    - *Dyopedos arcticus*
- Stenothoidae
- Synopiidae
    - *Syrrhoe longifrons*
    - *Tiron biocellata*
- Caprellidae

BRACHYURA

- Pinnotheridae
    - *Pinnixa* spp.

SIPUNCULA

SIPUNCULIDAE

- Golfingiidae
    - *Golfingia margaritacea*

Phascoliidae
Phascolion strombus
ECHIURA
Echiuridae
Echiurus echiurus alaskanus
CEPHALORHYNCHA
PRIAPULIDAE
Priapulus caudatus
BRACHIOPODA

APPENDIX II:

LIST OF MEGAFAUNAL TAXA COLLECTED DURING THE 2012 CSESP

- CNIDARIA
  - Anthozoa
    - Nephtheidae
      - *Gersemia rubiformis*

      - *Metridium* spp.
- MOLLUSCA
  - GASTOPODA
    - Lepetidae
      - *Lepeta caeca*
    - Buccinidae
      - *Buccinum* spp.
      - *Buccinum scalariforme*
      - *Buccinum polare*
      - *Buccinum plectrum*
    - Neptuneidae
      - *Amicula vestita*
      - *Colus* spp.
      - *Liomesus* spp.
      - *Neptunea* spp.
      - *Neptunea ventricosa*
      - *Neptunea communis*
      - *Neptunea borealis*
      - *Neptunea heros*
      - *Plicifusus kroeyeri*
      - *Pyrulofusus deformis*
      - *Retifusus roseus*
- CRUSTACEA
  - CIRRIPEDIA
    - Balanidae
      - *Balanus* spp.
      - *Balanus crenatus*
      - *Balanus rostratus*
  - DECAPODA
    - CARIDEA
      - *Pandalus tridens*
      - *Pandalopsis dispar*
      - *Crangon* spp.
      - *Argis lar*
    - Paguridae
      - *Pagurus* spp.
      - *Pagurus trigonocheirus*
      - *Pagurus townsendi*
    - BRACHYURA
      - *Hyas coarctatus*
      - *Chionoecetes opilio*

- BRYOZOA
        - *Alcyonidium* spp.
        - *Alcyonidium disciforme*
    - Flustrellidridae
        - *Flustra* spp.
- ECHINODERMATA
    - ASTEROIDEA
        - *Leptasterias* spp.
    - OPHIUROIDEA
        - Ophiuridae
            - *Stegophiura nodosa*
            - *Ophiocten sericeum*
            - *Ophiura sarsi*
            - *Ophiopholis aculeata*
        - Amphiuridae
            - *Amphiodia craterodmeta*
    - ECHINOIDEA
        - *Strongylocentrotus droebachiensis*
        - *Echinarachnius parma*
        - *Psolus fabricii*
        - Cucumariidae
            - *Pentamera calcigera*
            - *Chiridota* spp.
            - *Myriotrochus rinkii*
- UROCHORDATA
    - ASCIDIACEA
        - *Chelyosoma* spp.
        - Styelidae
            - *Styela coriacea*
            - *Styela rustica*
            - *Pelonaia corrugata*
            - *Boltenia* spp.
            - *Boltenia ovifera*
            - *Boltenia echinata*
            - *Boltenia villosa*
            - *Halocynthia aurantium*
        - Molgulidae
            - *Molgula* spp.

APPENDIX III:

LIST OF MEIOFAUNAL TAXA COLLECTED DURING THE 2012 CSESP

- PROTOZOA
  - FORAMINIFERA
- CNIDARIA
  - HYDROZOA
    - Corynidae
      - *Sarsia* spp.
- BRYOZOA
- NEMERTEA
- KINORHYNCHA
- NEMATODA
- ANNELIDA
  - POLYCHAETA
    - Pholoidae/Sigalionidae
      - *Pholoe minuta*

    - Nephtyidae
      - *Nephtys spp.*
    - Sphaerodoridae
      - *Sphaerodoropsis* spp.
      - *Sphaerodoropsis minuta*
      - *Sphaerodoropsis sphaerulifer*
    - Dorvilleidae
    - Orbiniidae
    - Chrysopetalidae
      - *Dysponetus pygmaeus*
    - Paraonidae
      - *Aricidea* spp.
    - Apistobranchidae
    - Spionidae
      - *Dipolydora* spp.
    - Cirratulidae
    - Cossuridae
      - *Cossura pygodactylata*
    - Flabelligeridae
    - Scalibregmidae
      - *Scalibregma* spp.
    - Capitellidae
    - Maldanidae
    - Ampharetidae
    - Trichobranchidae
      - *Terebellides* spp.
    - Sabellidae
    - c.f. Nerillidae
      - *Nerilla* spp.
  - OLIGOCHAETA
- MOLLUSCA

- GASTROPODA
  - Buccinoidea
    - *Buccinum polare*
- BIVALVIA
  - Nuculidae
    - *Ennucula tenuis*
  - Yoldiidae
    - *Yoldia* spp.
  - Mytilidae

PYCNOGONIDA

CRUSTACEA
- OSTRACODA
- COPEPODA
  - Harpacticoida
- CIRRIPEDIA
  - Balanidae
    - *Balanus* spp.
    - *Balanus* spp. cyprid
- TANAIDACEA
- ISOPODA

CEPHALORHYNCHA
- PRIAPULIDAE
  - *Priapulus caudatus*

ECHINODERMATA
- HOLOTHUROIDEA