

**CHUKCHI SEA ENVIRONMENTAL STUDIES PROGRAM 2008–2011:
BENTHIC ECOLOGY OF THE NORTHEASTERN CHUKCHI SEA**

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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 ecological baseline conditions within three study areas in the northeastern Chukchi Sea. The research program is managed by Olgoonik-Fairweather LLC. The Klondike, Burger, and Statoil study areas are located where successful lease bids were made in the February 2008 Chukchi Sea Lease Sale 193. 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 2009–2011.

Objectives of the benthic ecology component were to document infaunal community structure within the Klondike, Burger, and Statoil study areas and the Greater Hanna Shoal study area, determine associations of infaunal community structure with environmental factors, evaluate meiofaunal communities, document epifaunal community composition, and investigate benthic food webs. For the first discipline within the benthic ecology study, infauna (sediment-dwelling organisms retained on a 1.0-mm sieve) and environmental parameters were sampled at 70 stations in the Klondike (9 stations), Burger (9 stations), Statoil (21 stations), Transitional (3 stations) and regional (28) study areas. Thirty-nine stations throughout the regional study area were sampled with a HAPS corer to investigate deep-dwelling infauna. In 2011, the benthic ecology component also included a small study to investigate meiofauna. In the second discipline within benthic ecology, epifauna (larger invertebrate organisms residing on the sediment surface) were sampled at 33 stations including the Klondike (4 stations), Burger (2 stations), and Statoil (4 stations) study areas. There was a major change in epifaunal sampling methods in 2011 as digital photography was used to sample all surface-dwelling animals. Evaluation of benthic food web structure was the third discipline within the benthic ecology component. Results from the multi-year investigation of stable carbon isotopes, food web structure, and energy content of dominant organisms are presented. This report summarizes the results of the benthic ecology portion of the 2008–2011 northeastern Chukchi Sea Environmental Studies Program (CSESP), providing insights into multiyear trends.

Environmental characteristics reflected interactions between the pressure-driven northward flow of water and topographic deviations of the submerged continental shelf. Eastward flow of water moving north through the Central Channel moves across the study area

including through a saddle between two small peaks in Klondike and Statoil leading to a trough in Burger. Clockwise circulation of water around Hanna Shoal brings winter water into Burger from the north but interactions with the eastward flow causes a bending and divergence of some of that water to the east. The complex water movements, including the eastward retroflection of the water coming into Burger from the north, are currently being investigated in the physical oceanography component of the CSESP. The divergences meet over Burger and the trough that forms there. The underwater trough has a shape similar to a submerged watershed draining to Barrow Canyon and that is where the currents flow. Burger is deeper and muddier and has colder bottom-water temperatures and higher bottom-water salinity than Klondike which is adjacent to the Central Channel and the northward flowing currents. At the regional scale, water depth is greatest in Burger and along the margins of the regional study area, percent mud is greatest where water depth is deepest, and 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. Thus, the complex flows resulting from topographic control over water movements appears to be the driver for the coinciding environmental and biological differences observed. The small-scale deviations in circulation are being investigated in the 2012 CSESP.

Benthic infauna 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 sample 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 infaunal communities by study area but no clear separation by year. The declines in density and the number of taxa observed in 2010 were reversed in 2011.

At the regional level, the 2011 Chukchi Regional 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 provided a much greater opportunity to better 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 in 2011, and continued in 2012, are of great value.

Overall, there was a trend of declining density, biomass, and diversity from the southwest corner of the regional study area (the South stratum) to the northeast corner (the North stratum). Community structure was correlated with water depth, percent mud, and bottom-water temperature reflecting the influence 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 high in the Central A and B strata.

The strong covariance between hydrodynamics, physical dynamics, sediment characteristics, and biological communities is well-known. Mud is deposited in regions with lower water currents, particulate organic carbon is attracted to mud particles, and deposit-feeding organisms feed on the deposited carbon. As current speeds increase, sediments shift to larger particles and suspension-feeding animals become increasingly common. Thus, the greater proportions of mud and high density and biomass of infauna in Burger are indicative of a depositional environment where organic carbon accumulates. We have not fully identified the process through which food becomes more available to benthic organisms in Burger, nor the underlying oceanographic characteristics driving the differences among study areas. The current deviations suggested as causing the greater deposition in Burger are being investigated further in the 2012 CSESP.

Deep-dwelling infaunal communities were investigated using a HAPS corer that could reach to 26 cm deep, well beyond the 15 cm maximum penetration depth for the van Veen grab. The target organisms were deep-dwelling clams, particularly *Mya*. We did successfully recover one fragment of a large *Mya*. The biomass of the sipunculid worm *Golfingia margaritacea* was three to seven times the biomass collected from van Veen grab samples. Infaunal organisms were common to 10 cm and one *Maldane sarsi* extended to 21-25 cm depth. Further, a number of organisms were found deeper than expected (6-10 cm), including two brittle stars. Measurement of sediment redox potential and determination of chlorophyll concentrations from sediment cores indicate high activity at depth and transport of carbon to 15 cm depth at some stations. Chlorophyll concentrations from cores indicate that the quantity of production stored in the sediments may be substantial but varies greatly among stations.

Meiofauna were abundant and included both permanent and temporary members. Permanent members include harpacticoid copepods, nematodes, and protozoans of the order Foraminifera. Temporary members were juvenile infaunal species such as bivalves and polychaetes. As with the infaunal community, meiofaunal densities were lower in the North stratum.

Population dynamics of a dominant bivalve, *Ennucula tenuis*, were investigated by measuring shell lengths. Bivalve age and length measurements are commonly a part of baseline studies as they can reflect environmental changes. This investigation was prompted by the declines in density observed in 2010. We did not see any indicators of change when comparing 2010 to 2008 and 2009. The recruitment of juvenile bivalves to the sediments in 2011, however, was 10% higher than in prior years, as demonstrated by peaks in lengths from 1 to 3 cm. Prior studies in the Bering Sea demonstrated lengths of about 12 cm. In the Chukchi Sea, lengths were up to 17 cm and age/growth annuli were indistinct (suggesting young, fast growing populations and possibly, no cessation of growth during winter) whereas in the Bering Sea, counting distinct age annuli resulted in ages of up to nine years. Lengths of bivalves were shorter and there were fewer larger *E. tenuis* in Klondike than in Burger or Statoil.

Evaluation of still photos and video demonstrates large differences in habitat and biological characteristics of the study area. Habitat structure in Klondike varies from sporadic rocks with upright epifaunal communities to mud along a 1 km transect. Still photos and video from Burger indicate a homogenous, muddy environment dominated by brittle stars. Images from Statoil showed a similar muddy habitat as seen in Burger, but with fewer brittle stars. The photos from the North stratum indicate widely varying habitat ranging from mud to gravel. Few animals were observed in the North stratum.

Benthic food webs were generally similar among study areas. The isotopic signatures of particulate organic matter varied among study areas with Klondike having fresh POM and Burger and Statoil reflecting a mix of fresh and degraded production as well as an additional source. Sediment isotope signatures were, however, similar indicating that the fresher POM in Klondike is not deposited on the sediment surface. Benthic food webs demonstrated the classic, linear shift among trophic (feeding) levels indicating no real difference among study areas. Nitrogen isotope values of the polychaete *Maldane sarsi* demonstrated a shift among Klondike, Burger and Statoil indicating a more degraded food source in Burger than in Klondike. Energy

content of faunal species demonstrated that the main prey items of marine mammals had the highest energy content, as would be expected. Sediments in Burger had higher energy content than Klondike. The energy content and food web of benthic communities reflected the dense aggregations of deposit-feeding animals and bivalves, especially in Burger.

In summary, trends in the infaunal and epifaunal communities indicate that the 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 invertebrate fauna 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 between 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 oceanographic variables apparently enhances the deposition of food (primary production) in Burger resulting in greater density and biomass of animals.

CHAPTER 1

GENERAL INTRODUCTION

ConocoPhillips (COP), Shell Exploration and Production Company (SEPCO), and Statoil USA E&P are supporting a multi-disciplinary environmental studies program to establish baseline conditions for three study areas in the northeastern Chukchi Sea. The project is managed by Olgoonik-Fairweather LLC (OLF). The study areas are Klondike, Burger, and Statoil (2010–2011 only) where successful lease bids were made in the February 2008 Chukchi Sea Lease Sale 193. The study area was expanded in 2011 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), and oceanographic baseline trends for the Klondike, Burger, and Statoil study areas. The Chukchi Sea Environmental Studies Program (CSESP) was initiated in 2008 and continued in 2009, 2010, and 2011.

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 those interested in extracting 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; Highsmith and Coyle, 1992; Feder et al., 1994a, 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 the northeastern Chukchi Sea. The first study of macrofaunal community structure was performed 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. (1994a). Following the latter study, Grebmeier et al. (1988) documented the strong association between annual pelagic production reaching the bottom and the benthic communities (pelagic-benthic coupling) in the southeastern Chukchi Sea. The infauna of the Chukchi Sea are abundant and biomass high due to the comparatively high quantities of unconsumed primary production (pelagic and ice-edge production) reaching the benthos (Grebmeier et al., 2006). A rich epifaunal 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., 1994b, 2005; Ambrose et al., 2001; Bluhm et al., 2009). 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, Regulation and Enforcement'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 long-term trends with confidence (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 2009–2011 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., 1994a; Blanchard et al., 2011). The combined results from the 2011 investigation will allow for assessment of short-term temporal trends in addition to the evaluation of spatial trends over the larger, regional study area. The results of this four-year investigation in the northeastern Chukchi Sea will contribute to benchmarks for determining potential changes in the benthos from 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 2008–2011 CSESP.

OBJECTIVES

The objectives of the benthic ecology component of the 2011 CSESP were to investigate the benthic ecology of a Chukchi regional study area surrounding Hannah Shoal and temporal variations in the three main study areas. The specific objectives were to:

- Sample infaunal organisms within the Klondike, Burger, Statoil, and the larger regional study area (Hannah South, Central, and North) to document infaunal community structure;
- Sample epifaunal organisms using digital photography and video within the Klondike, Burger, Statoil, and the larger regional study area (Hannah South, Central, and North) to document epifaunal community structure;
- Evaluate spatial and temporal variability in infaunal density and biomass within the three main study areas over 2008–2011;
- Assess infaunal species composition, density, and biomass of benthic communities within the regional study area in 2011 and determine associations of community structures with environmental factors;
- Document the food-web structure of benthic communities within the Klondike, Burger, and Statoil study areas using stable isotopes; and
- Determine caloric content of infaunal and epifaunal marine-mammal prey items within the Klondike, Burger, and Statoil study areas.

METHODS

Nomenclature for the 2008–2011 Sampling Cruises

Vessels are identified by a unique letter code. The M/V Bluefin (BLF) was used for sampling in 2008. The M/V Westward Wind (WWW) was used for sampling in 2009, 2010, and 2011.

Cruises are identified by the ship name, 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 epifaunal sampling

occurring on WWW0902 (August 14-29) and WWW0904 (September 25 - October 10) and infaunal sampling on cruise WWW0903 (September 5-19). Infauna were sampled on cruise WWW1002 (August 5-19) in 2010 and epifauna on cruise WWW1003 (September 1-18). In 2011, benthic fauna were sampled on cruises WWW1102 (August 3-24) and WWW1104 (August 31 to October 5, 2011).

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. Mammal-feeding stations were given the character code TM and the Transitional stations were coded as TF. Samples from the regional study were identified as Hannah South (HS), Hannah Central (HC), and Hannah North (HN).

General Sampling Methods

The term “infauna” is herein limited to invertebrate animals residing in sediments and retained on a 1.0-mm mesh screen. Large, mobile organisms or those not adequately sampled by the van Veen grab (the epifauna) are excluded. The term “macrofauna” is often considered synonymous with “infauna” but the exclusion of mobile and epifaunal organisms in this project favors use of the term “infauna”. 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 “epifauna”, for the purposes of this report is limited to larger invertebrate animals residing on the sediment or closely associated with the surface sediment (e.g., upright organisms or large clams near the surface).

The infauna were sampled using a double van Veen grab with two 0.1 m² adjoining grabs to collect sediments for analyzing sediment grain-size, chlorophyll, sediment and tissue stable isotopes, and infauna. Three replicate grabs were collected at each station (Table 1-1, Fig. 1-1). The infauna was also sampled at 39 stations using a HAPS corer in 2011. The HAPS corer has a longer tube and can reach animals at a greater depth (26 cm) than the van Veen (< 15 cm). Deep-dwelling bivalves were the target for sampling with the HAPS. Three replicate cores were taken at stations selected for sampling with the HAPS corer. The first few centimeters of sediment were also collected from additional van Veen grab samples to determine sediment

grain-size, chlorophyll-*a*, and phaeopigment concentrations. Sediment cores were also collected from the HAPS corer samples for chlorophyll determinations. The redox potential of sediments was measured from HAPS corer samples in 2011. Further details for infaunal sampling and laboratory methods are given in Chapter 2.

Meiofauna were sampled at 65 stations with one replicate collected at each station (Table 1 and Fig. 1). Samples were collected using a 5 cm diameter by 1 cm depth plastic ring (hereafter called “small core”) from the surface layer of the van Veen grab or HAPS core. A piece of plexiglass was slid underneath the small core to lift the sample. Further details for meiofaunal sampling and laboratory methods are given in Chapter 2.

Surface-dwelling fauna were sampled at 33 stations using a drop camera. Further details for video sampling and laboratory methods are given in Chapter 3.

Infaunal and epifaunal organisms were collected and frozen from 2009–2011 for determination of tissue stable isotopes and caloric content. The analysis of invertebrate tissues provides insight into the trophic structure (food web) and 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 isotopic food web and caloric content studies are detailed in Chapters 4 and 5, respectively.

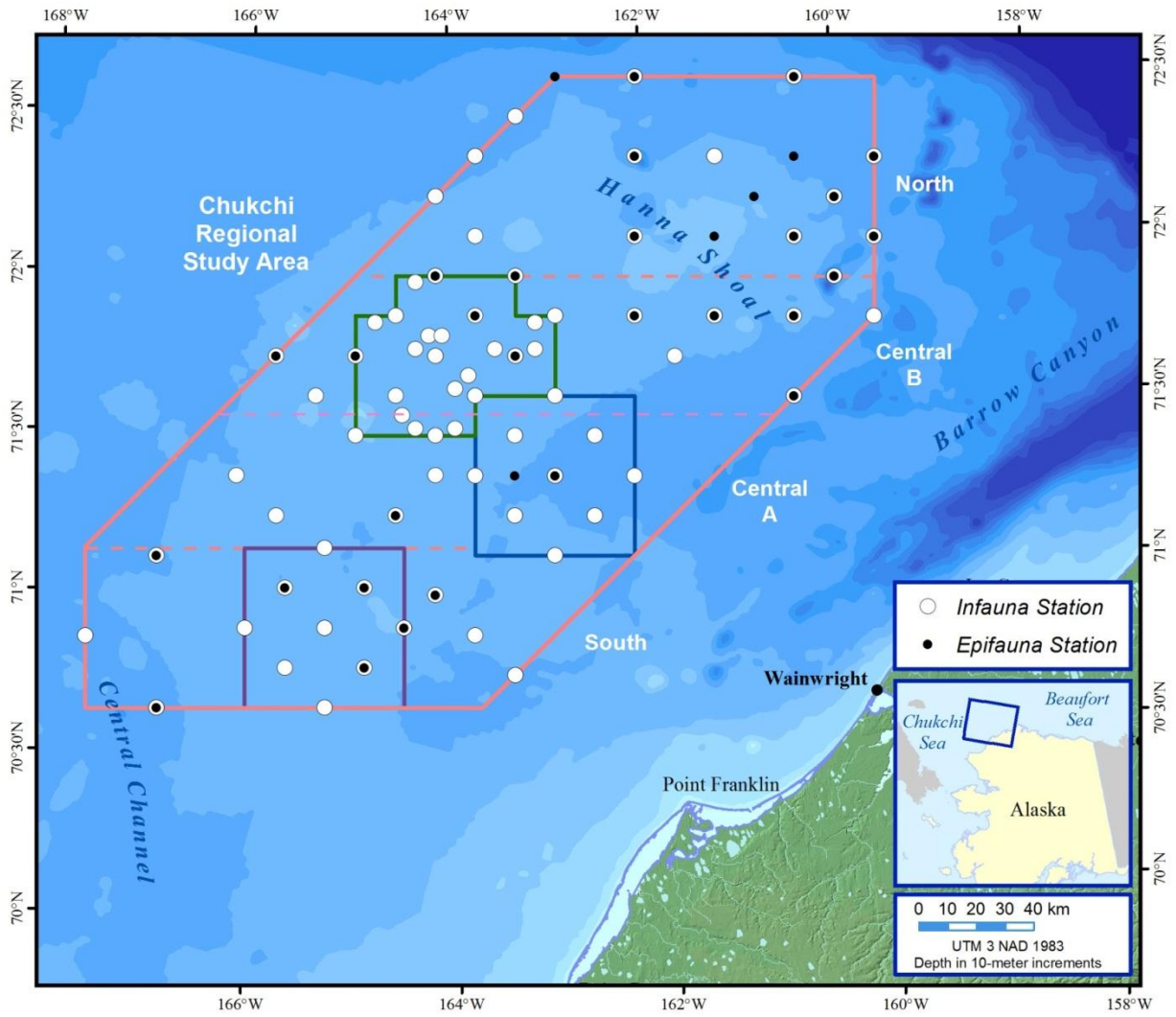


Figure 1-1. Map of all stations sampled during the 2011 CESP benthic surveys.

Table 1-1. Station information for all benthic sampling during the 2011 CSESP regional study. Intended positions (decimal degree format) and type of sampling are given for each station. K = Klondike, B = Burger, S = Statoil, T = transition station between Burger and Klondike, F = fixed station, R = random station, TM = mammal feeding station.

Station	Latitude, N	Longitude, W	Infauna	HAPS		
				Corer	Epifauna	Meiofauna
BF003	71.1134	-163.04	x	x		x
BF007	71.2415	-163.41	x	x		x
BF009	71.2334	-162.64	x	x		x
BF011	71.3689	-163.79	x	x		x
BF012	71.3660	-163.40			x	
BF013	71.3623	-163.01	x	x	x	x
BF015	71.3525	-162.23	x	x		x
BF017	71.4905	-163.39	x	x		x
BF019	71.4822	-162.61	x	x		x
BF021	71.6179	-163.77		x		x
BF023	71.6112	-162.98	x	x		x
HC003	71.247	-165.73	x			x
HC006	71.370	-166.13		x		
HC011	71.6217	-165.35	x			x
HC012	71.7451	-165.75	x		x	x
HC020	71.5718	-160.62	x	x	x	x
HC022	71.7196	-161.78	x			x
HC025	71.8502	-162.16	x	x	x	x
HC026	71.8368	-161.36	x	x	x	x
HC027	71.8201	-160.56	x		x	x
HC028	71.8002	-159.77	x	x		x
HC032	71.9346	-160.14	x	x	x	x
HN002	72.116	-163.74	x			x
HN004	72.0989	-162.12	x		x	x
HN005	72.0853	-161.31			x	x
HN006	72.0684	-160.51	x	x	x	x
HN007	72.0482	-159.7	x	x	x	x
HN008	72.2427	-164.14	x	x		x
HN012	72.2015	-160.88			x	
HN013	72.1828	-160.07	x	x	x	x
HN014	72.365	-163.72	x	x		x
HN016	72.3476	-162.08	x		x	x

Table 1-1. Continued.

Station	Latitude, N	Longitude, W	Infauna	HAPS		
				Corer	Epifauna	Meiofauna
HN013	72.1828	-160.07	x	x	x	x
HN014	72.365	-163.72	x	x		x
HN016	72.3476	-162.08	x		x	x
HN017	72.3339	-161.26	x	x		x
HN018	72.3167	-160.44			x	x
HN019	72.2962	-159.63	x		x	x
HN020	72.4864	-163.30	x			x
HN025	72.6069	-162.87			x	x
HN026	72.5964	-162.04	x	x	x	x
HN028	72.5649	-160.38	x	x	x	x
HS002	70.6395	-166.84	x	x	x	x
HS005	70.8574	-167.53	x	x		x
HS010	71.1144	-166.88	x		x	x
HS013	70.7437	-163.45	x	x		x
HS014	70.871	-163.82	x			x
KF003	70.6486	-165.25	x	x		x
KF007	70.7722	-165.63	x			x
KF009	70.7732	-164.88	x		x	x
KF011	70.895	-166.02	x	x		x
KF013	70.8976	-165.26	x	x		x
KF015	70.8971	-164.49	x	x	x	x
KF017	71.0213	-165.64	x		x	x
KF019	71.0223	-164.87	x		x	x
KF023	71.1467	-165.26	x	x		x
SF001	71.4974	-164.96	x	x		x
SF003	71.618	-163.77	x	x		x
SF005	71.6215	-164.56	x			x
SF007	71.7465	-164.96	x		x	x
SF009	71.7447	-164.16	x	x		x
SF011	71.7396	-163.37	x	x	x	x
SF013	71.871	-164.96	x			
SF014	71.8714	-164.55	x	x		x
SF016	71.867	-163.76	x		x	x
SF018	71.8603	-162.96	x	x		x

Table 1-1. Continued.

Station	Latitude, N	Longitude, W	Infauna	HAPS Corer	Epifauna	Meiofauna
SF020	71.9937	-164.15	x	x	x	x
SF022	71.9885	-163.35	x		x	x
SR005	71.5174	-164.37	x			
SR008	71.5157	-163.98	x			
SR013	71.5593	-164.5	x			
SR035	71.6402	-163.97	x			
SR051	71.681	-163.84	x			
SR077	71.7665	-164.36	x			
SR083	71.7622	-163.57	x			
SR086	71.7588	-163.17	x			
SR093	71.8075	-164.23	x			
SR094	71.8069	-164.1	x			
SR104	71.8504	-164.76	x			
SR116	71.8418	-163.16	x			
SR137	71.974	-164.36	x			
TF001	70.9975	-164.19	x		x	x
TF003	71.2479	-164.57	x		x	x
TF006	71.3711	-164.18	x			x

Quality Assurance Procedures

The TigerObserver system was developed for the CSESP to assist with data collection in the field while simultaneously linking field data with the ship's navigation system. This allows for real-time geographic coordinates and oceanographic conditions to be linked with biological data. Data managers onboard the vessels were able to perform onsite quality control checks to assist with minimizing input errors of the data. The TigerObserver system transcribed the data into a Microsoft® (MS) Access database which was archived along with the raw datasheets at the University of Alaska Fairbanks (UAF) Institute of Marine Science (IMS).

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

Quality control procedures were followed in processing infaunal 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. One hundred percent 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 2011 CSESP were compared to the voucher collection from the 1986 investigation by Feder et al. (1994a) 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 current 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 infaunal 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. Taxonomic information of epifaunal data sets was also scrutinized for consistency and pelagic and obvious infaunal taxa were excluded from data sets analyzed.

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. (1994a) 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 and transits the Chukchi Shelf 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 with 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, or the Bering Land Bridge, that was 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 providing a connection between Alaska and Siberia. When submerged, the 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 (e.g., Taylor columns; Martin and Drucker, 1997), the dominant topographic features on the northeastern Chukchi Sea seafloor.

Sampling in 1986 was performed to determine broad-scale ecological conditions with sampling stations dispersed across the northeastern Chukchi Sea (Fig. 1-2; Feder et al., 1994a). Sampling locations were selected based on known variations in sediment types, bathymetry, and mean summer ice position. General trends in the northeastern Chukchi Sea follow the expected increase in depth and associated increase in percent mud of sediments with greater distance offshore. There is also a trend of increasing percent mud, increasing bottom-water salinity, and decreasing bottom-water temperatures with increasing latitude. Feder et al. (1994a) 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.

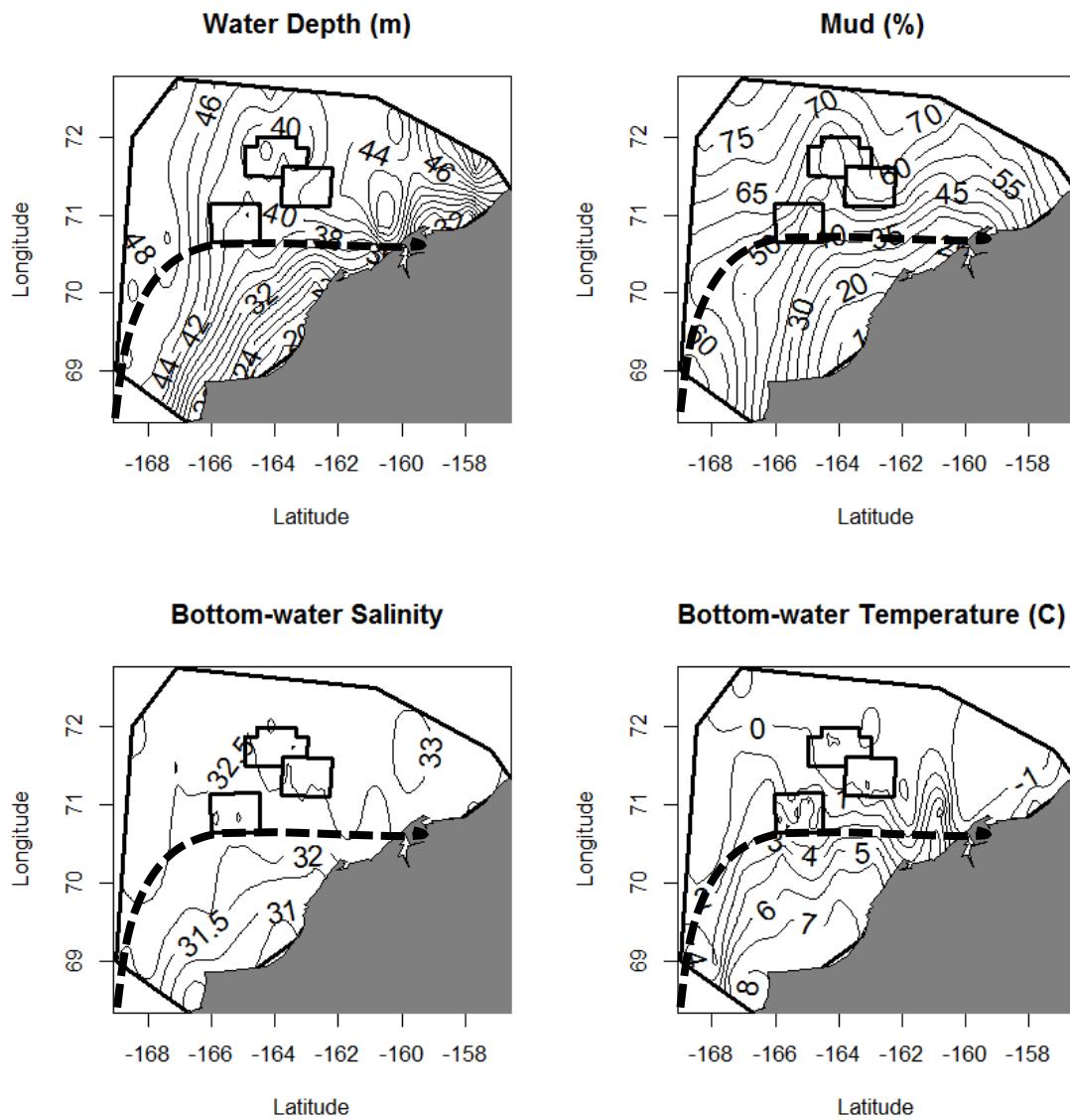


Figure 1-2. Geospatial models of water depth, percent mud, and bottom-water salinity and temperature for the northeastern Chukchi Sea. Data are from 1986 (Feder et al., 1994) and values averaged from 2008–2010 for the CSESP. The dotted line denotes the bottom-water front identified by Feder et al. (1994).

The CSESP study area lies 100 to 200 km northwest of the village of Wainwright, Alaska, on the northwestern coast of Alaska along the northeastern Chukchi Sea (Fig. 1-1; Day et al., in preparation). The 2008–2010 study region encompassed three small study areas,

Klondike, Burger, and Statoil, where successful lease bids were made during the February 2008 Chukchi Sea Lease Sale 193. The 2011 study area encompassed a larger region from Klondike to 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 for northward-flowing water (called the Central Channel) and has coarse sediments whereas Burger is a depositional area with muddy sediments and a submarine valley forms in the area. Cold, saline winter-water remains longer in Burger than in Klondike reflecting complex water movement in the former area. 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., in preparation). The Statoil study area is adjacent to Burger to the northwest 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 2008–2011:

Association of Infaunal Community Structure with Environmental Variables

By Arny L. Blanchard, Ann L. Knowlton, Marissa Hajduk, and Steven Savard

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 comparatively nutrient poor (Feder et al., 1994; Codispoti et al., 2005; Grebmeier et al., 2006). The water mass differences are associated with substantial differences in benthic community structure (Feder et al., 1994; Grebmeier et al., 2006). 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 sediment organic carbon to nitrogen ratios (C/N ratio) (Feder et al., 1994). Sediment granulometry reflects a number of environmental processes, such as hydrodynamics (strong currents, storm effects, ice gouging, etc.), sediment deposition, and proximity to sediment sources. Prior studies in the Chukchi Sea have been focused on large-scale variations of faunal communities and little information is available on small-scale factors structuring faunal distributions. Topographic control over water circulation may be a key source for spatial variations of infaunal communities as circulation divergences can result in greater food availability via increased deposition for deposit-feeders or within the water column for suspension feeders.

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 results in strong pelagic-benthic coupling because of the large flux of uneaten phytoplankton reaching the benthos resulting in a very abundant and diverse

infaunal community (Dunton et al., 2005; Grebmeier et al., 2006). As a result, interannual variability in primary production and zooplankton communities 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 the ecological importance of ice algae needs to be established for the Chukchi Sea (Ambrose et al., 2001, 2005).

Benthic communities are often categorized by size, sampling gear, and life-habits. Large, mobile animals captured by trawling are considered epifauna or megafauna and generally live on the sediment surface. The infauna, also called macrofauna, includes smaller animals on the sediment surface and those living in the sediments; infaunal 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- or 1.0-mm mesh but retained on smaller sieves such as a 64- μ m mesh. Smaller-sized organisms are preyed upon by larger organisms throughout the community linking each of the separate benthic communities. Epifauna and infauna 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 was to document species composition, density, and biomass of infaunal communities within the study areas, and determine associations of communities with environmental characteristics. Specific objectives of the benthic ecology component of the 2011 CSESP were:

- 1) To describe environmental gradients over the regional study area.
- 2) To test the hypothesis that there is significant temporal variability of repeatedly sampled communities, presumably associated with oceanographic variability.
- 3) To test the hypothesis that spatial variability of faunal communities over the regional study area is associated with measured environmental factors.
- 4) To sample deeper-dwelling infaunal communities with a HAPS corer to test the hypothesis that bivalve prey of walrus are present at deeper depths in the sediment column (to 26 cm).
- 5) To document meiofaunal species present and test the hypothesis that meiofaunal densities vary across the regional study area.

METHODS

Infaunal Sampling Methods

Sampling for infauna with the van Veen grab in 2011 included 70 stations from the regional study area (Fig. 2-1). Sampling occurred from August 3 to 24 (cruise WWWW1102) and from August 31 to October 5, 2011 (cruise WWWW1104). Nine fixed stations were sampled at both Klondike and Burger, 21 at Statoil, 3 Transitional stations, and 28 stations were visited interspersed within the regional sampling area. The study design for the larger regional study in 2011 included three strata; South, Central, and North. The central study region was broken into two substrata, Central A and Central B, for this report to better match the scale of benthic biological and environmental processes in the study region. See Blanchard et al. (2011) for details of sampling cruises from 2008–2010.

Infauna were sampled using a double van Veen grab with two 0.1 m² adjoining grabs to collect sediments for analyzing sediment grain-size, chlorophyll, sediment stable isotopes, and infauna. Three replicate samples were collected at each station. Material collected from each grab for infauna 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). The top few centimeters of sediment were collected from grab samples to determine chlorophyll *a* concentration and frozen for transport to the laboratory. In the laboratory, sediment samples were thawed and soaked in acetone. After centrifuging, the leachates were analyzed for chlorophyll *a* and phaeopigment concentrations using a Turner Trilogy fluorometer.

A HAPS corer was deployed at 39 sites to sample sediments for animals living deeper than the maximum 15 cm collection/penetration depth of the van Veen grab (Table 1-1). Three replicate cores were collected and sediments were sieved over a 3.0-mm mesh screen and residuals preserved. Samples were sorted and animals identified according to methods for the van Veen samples.

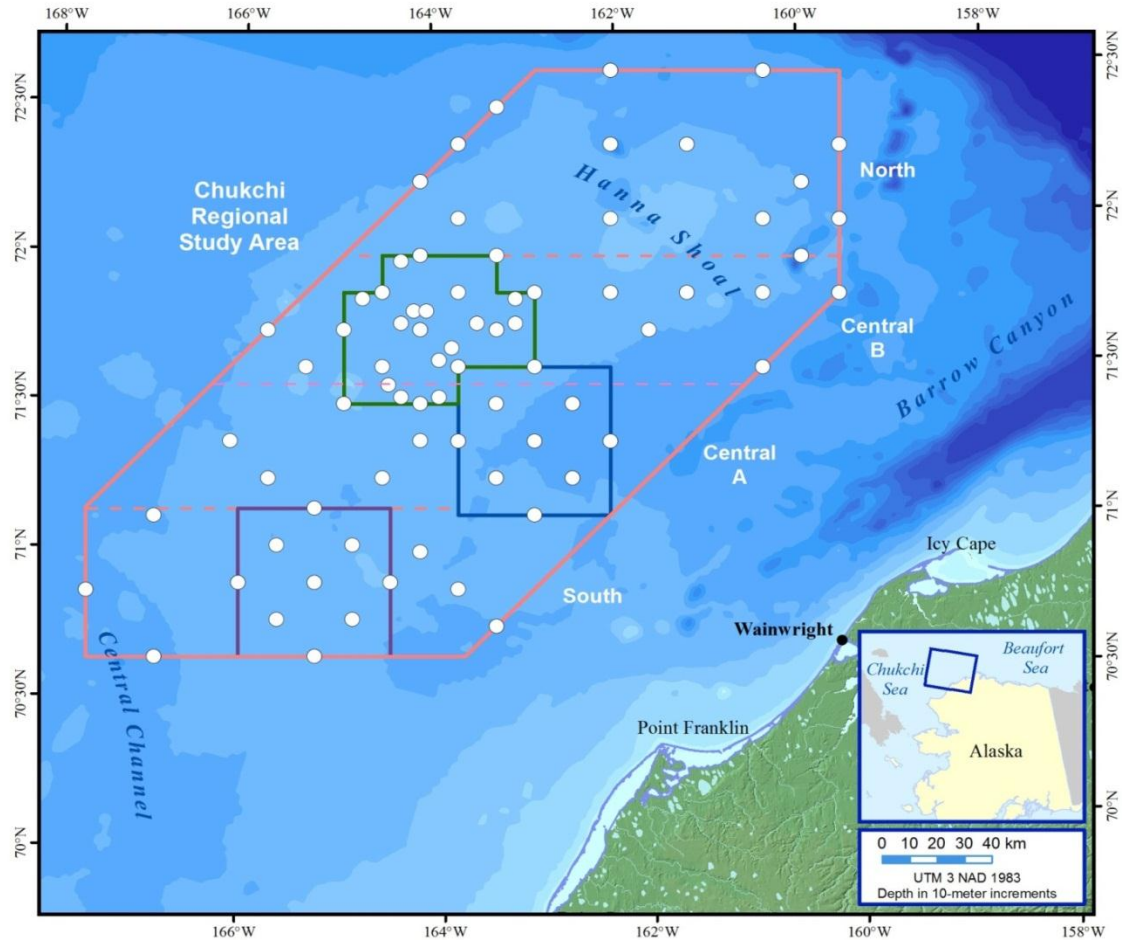


Figure 2-1. Map of stations sampled for infauna during 2011 CSESP survey.

Sampling with the HAPS corer allowed measurements of sediment voltage to determine the redox potential profile at depths to 20 cm. The redox potential discontinuity layer is the boundary between aerobic (oxidative reactions with positive voltage) and anaerobic (reduction reactions with negative voltages) processes and marks a shift in biological processes and in habitable sediments (Valiela, 1984; Lenihan and Micheli, 2001). The compounds accumulating in the layer below the redox boundary are toxic to many invertebrates. The redox potential layer is closer to the surface when there is low sediment porosity and water exchange (muddy sediments) and will be deeper as sediment porosity increases (sandy or gravelly sediments). Animals can alter toxic conditions and extend to deeper depths by irrigating their burrows to increase oxygen availability and with substantial irrigation, sediments may grade from oxidative to a reducing environment and then back to an oxidative state. Thus, determining the depth of

the redox potential boundary provides a baseline for the depth of aerobic processes and provides insights into activities of deep-dwelling organisms or those with deep burrows that may increase the oxygen content of sediments at depth through burrowing activities. To measure the redox potential, sediments from the HAPS corer samples were carefully extruded from the sampling tube. A handheld VWR® sympHony® multiparameter meter with an epoxy combination redox electrode was used to measure the redox potential (Eh) as millivolts with the redox probe inserted into the sediments every 5 cm along the length of the sediment core and voltages recorded. The data were plotted to generate a redox profile (a plot of changes with depth in the sediment column).

Sampling with the HAPS corer also allowed measurements of chlorophyll pigment concentrations at depths to 20 cm. A number of infaunal organisms have been identified that transport particulate organic carbon from the surface to deep sediments. These include maldanid polychaetes and sipunculid worms (Romero-Wetzel, 1987; Levin et al., 1997; Shields and Kędra, 2009). Understanding the extent of biologically-mediated sediment exchange to depth can provide insights into the transport and persistence of food resources at depth. Chlorophyll cores were collected by two methods (methods were adapted in the field). In the first approach, the tube method, sediment cores were collected by inserting a plastic tube (diameter approximately 2 cm) into the sediments from the HAPS corer samples. Cores were then frozen for transport to the laboratory. In the laboratory, the cores were cut into pieces 2 cm long and analyzed for chlorophyll concentrations using a Genesys 10S VIS spectrophotometer. In the second approach, the plug method, a syringe was used to collect samples to 1 cm deep in the side of the core and these plugs were taken every 5 cm as sediments were extruded from the HAPS corer sampling tube. These sediment plugs were then analyzed for chlorophyll concentrations using the spectrophotometer.

Meiofaunal samples were collected from sixty-five stations sampled with a double van Veen grab and HAPS bottom corer, with one replicate collected at each station (Table 1-1). Samples were collected using a 5 cm diameter by 1 cm depth plastic ring (hereafter called “small core”). The small core was pressed down 1 cm into the surface layer of the van Veen grab or HAPS core, and a piece of plexiglass slid underneath the small core to lift the sample. The sediment sample was then transferred from the small core to a Whirl-Pak bag and preserved in 10% formalin-seawater buffered with hexamine. In the laboratory, samples were rinsed through

a 64- μ m mesh screen and transferred to containers with 50% isopropyl alcohol and rose Bengal stain. Samples were sorted under a dissecting microscope and meiofauna identified and counted. Identifiable tissue fragments were grouped together and recorded as a count of 1.

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 limpets and *Mytilus trossulus* from Port Valdez (Blanchard and Feder, 2000 a and b).

The 2008-2010 CSESP studies demonstrated significant temporal variability with a sharp decline of infaunal density (Blanchard et al., 2011). 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 and widths 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 interannually. 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.

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 repeated measures ANOVA (rm ANOVA) with the statistical program R (www.r-project.org). 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.

RESULTS

Environmental Characteristics of the Study Area

General Trends in the Regional Study Area

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). No significant differences among regions were apparent for chlorophyll from comparisons of confidence intervals (Table 2-1 and Fig. 2-2). The spatial model for total chlorophyll demonstrates a decline in chlorophyll with greater distance north (Fig. 2-3). No significant differences among regions were apparent for percent sand and values vary by station (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. Percent mud is higher along the margins of the study region and in Burger, reflecting the covariance of mud with water depth. 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).

Redox Measurements and Chlorophyll Sediment Cores

Measurements of the voltage of sediments were made to determine the redox potential of sediments and the depth of the redox potential discontinuity layer. The plot of average redox potential curves demonstrates that the average depth of the redox discontinuity layer is approximately 9 cm (Fig. 2-4). There was great variability in the redox measurements with some stations not demonstrating a redox discontinuity layer until 15 cm (e.g., KF015; Appendix I) and others demonstrating a shift to reducing conditions (negative voltages) and a second shift back to oxidizing conditions (positive voltages) (e.g., HS010; Appendix I).

Concentrations of chlorophyll pigments in sediment cores were measured to understand the movement of carbon through the sediment column. The plug method demonstrated highest average chlorophyll concentration at the sediment surface with values lower at depth (Fig. 2-5). The tube method demonstrated highest average chlorophyll concentration at 4 to 8 cm below the sediment surface (Fig. 2-5). There was substantial variation in patterns though, with many stations indicating chlorophyll concentrations first declining and then increasing at depth (e.g., KF011 in 2011; Appendix II). For the most part, chlorophyll concentrations were highest in the top 5 cm of the sediment column reflecting the immediate deposition and assimilation of annual production (e.g., BF015 in 2011; Appendix II). There were a few exceptions where concentrations increased at depth (e.g., HS002; Appendix II). Chlorophyll *a* (fresh chlorophyll) generally declined with depth with pigments reflecting mostly phaeopigments (degraded chlorophyll) although chlorophyll *a* was greater at depth at stations where total chlorophyll increased (Appendix II).

Table 2-1. Summary of environmental characteristics for the strata sampled for infauna during the 2011 CSESP study. Chlorophyll *a* and total chlorophyll (chlorophyll *a* plus phaeopigment) are in pg cm^{-3} , bottom-water temperature is in degrees C, and water depth is in meters.

Variable	South				Central A			
	Ave.	SD	n	95% CI	Ave.	SD	n	95% CI
Total								
Chlorophyll	29.62	6.21	15	(26.18, 33.06)	27.29	3.93	16	(25.2, 29.39)
Water Depth	40.89	4.03	15	(38.66, 43.12)	41.94	1.31	16	(41.24, 42.64)
% Sand	54.07	16.24	15	(45.08, 63.06)	42.17	10.82	16	(36.41, 47.94)
% Mud	36.99	14.42	15	(29, 44.97)	56.37	12.76	16	(49.58, 63.17)
Temperature	2.80	1.03	15	(2.28, 3.37)	0.24	1.15	16	(-0.37, 0.86)
Salinity	31.88	0.20	15	(31.77, 32)	32.34	0.22	16	(32.22, 32.45)

Variable	Central B				North			
	Ave.	SD	n	95% CI	Ave.	SD	n	95% CI
Total								
Chlorophyll	28.26	4.91	30	(26.43, 30.09)	25.51	4.62	13	(22.72, 28.3)
Water Depth	39.18	3.08	30	(38.03, 40.33)	40.15	5.59	13	(36.77, 43.53)
% Sand	50.11	14.40	30	(44.73, 55.48)	47.65	16.33	13	(37.79, 57.52)
% Mud	44.24	15.46	30	(38.47, 50.01)	49.57	18.46	13	(38.42, 60.73)
Temperature	-0.14	0.81	30	(-0.45, 0.16)	-0.05	0.70	13	(-0.48, 0.37)
Salinity	32.47	0.18	30	(32.4, 32.54)	32.52	0.19	13	(32.4, 32.63)

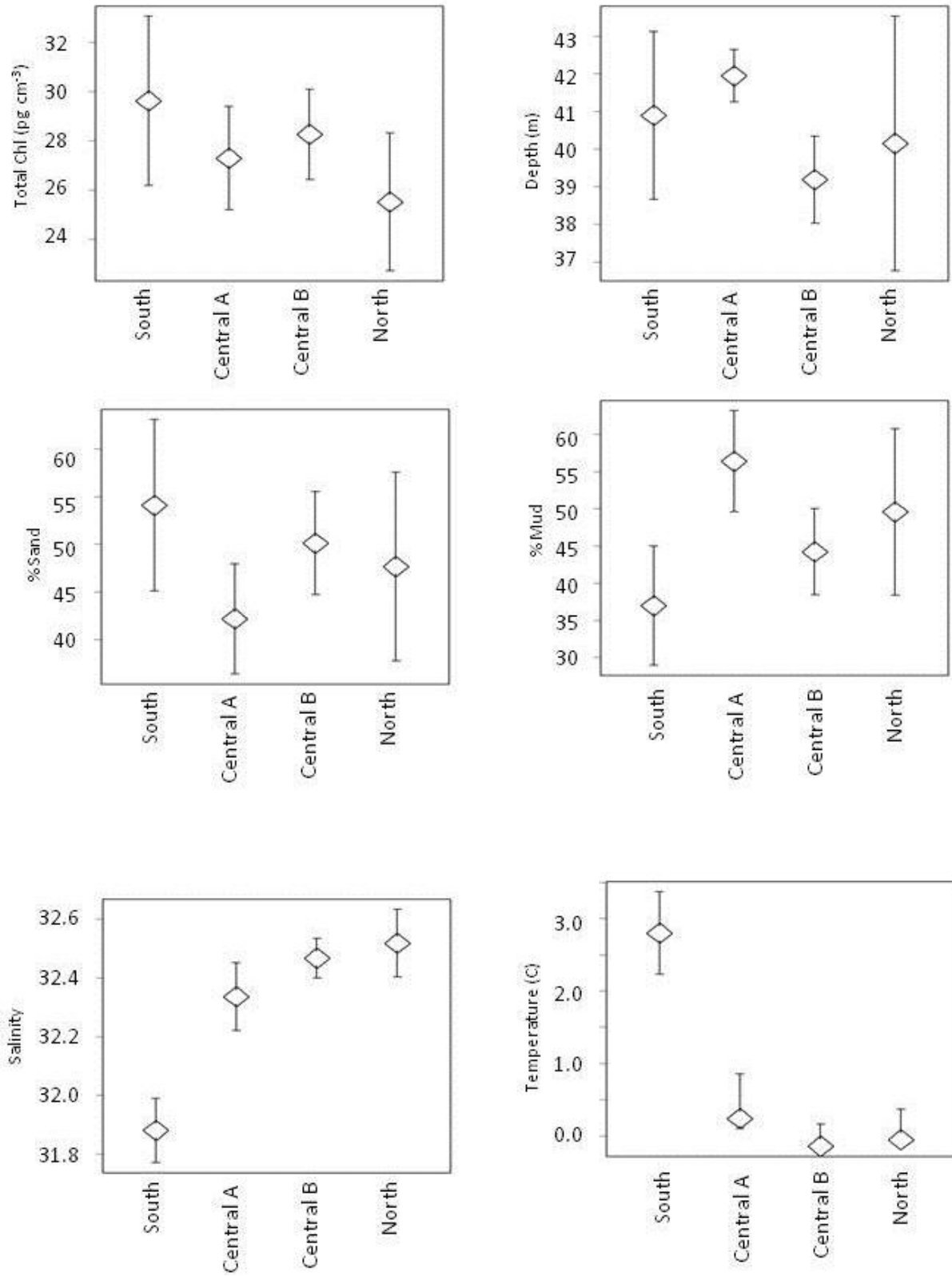


Figure 2-2. Whisker plots of environmental variables by sampling region of the 2011 CESP.

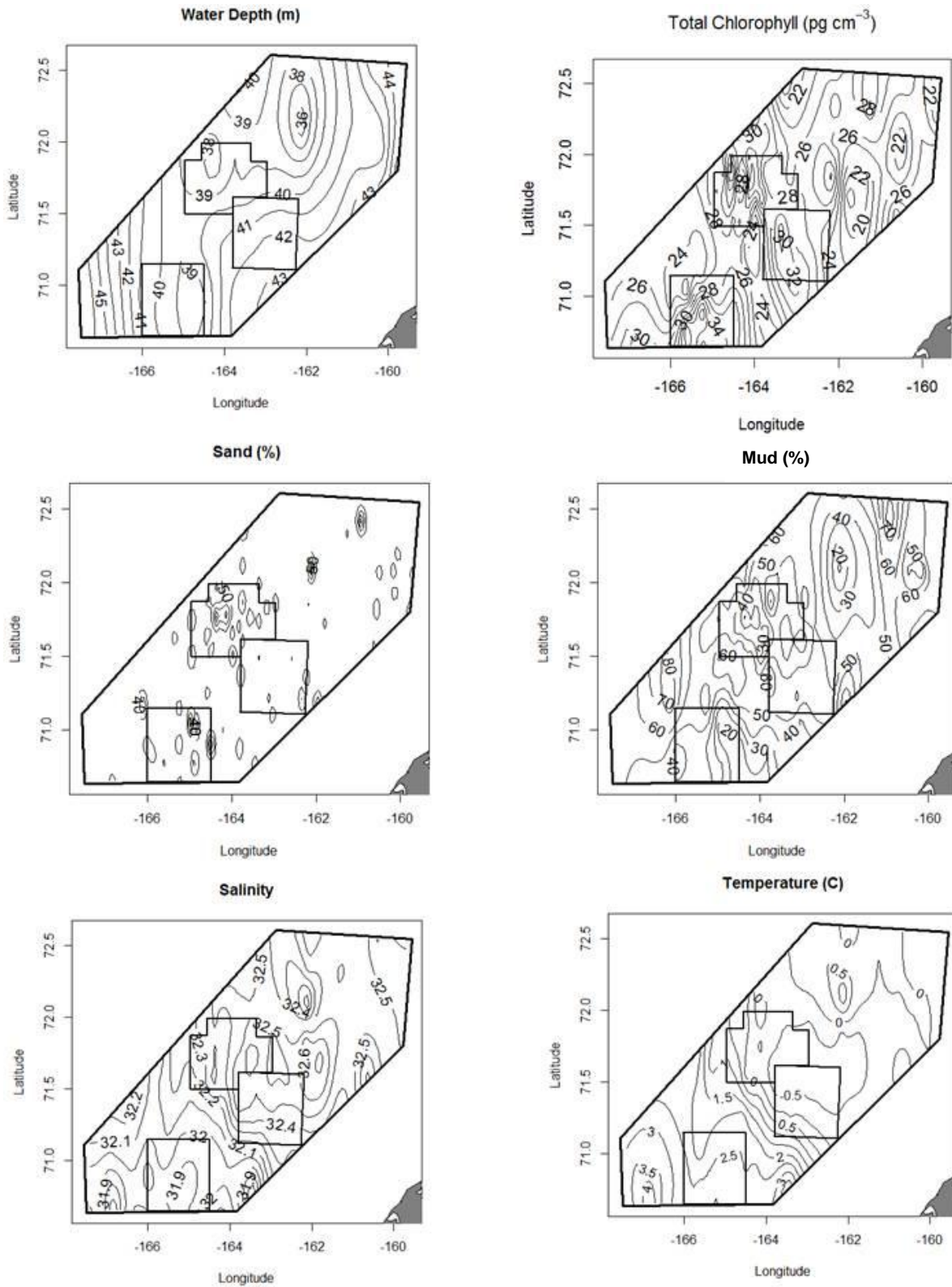


Figure 2-3. Geostatistical analysis of environmental variables sampled during the 2011 CESP.

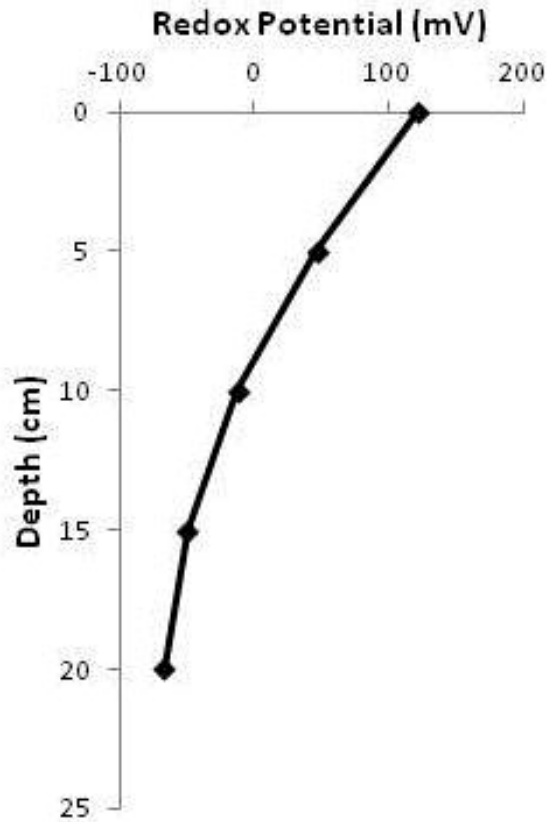


Figure 2-4. Average redox potential (mV) for all stations and gear for the 2011 CESP.

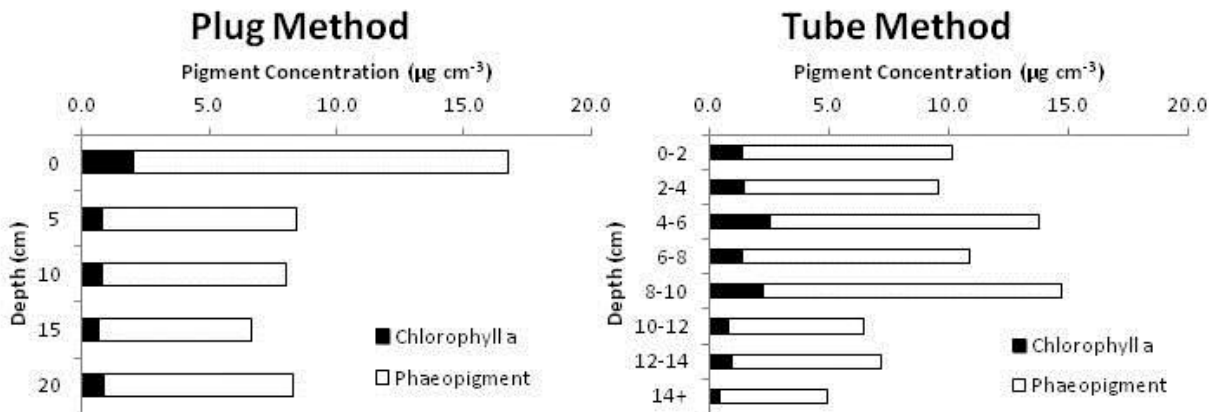


Figure 2-5. Average chlorophyll concentrations by depth for the 2011 CESP. Results from the two sampling methods used are presented.

Spatial and Temporal Variability of Infauna in the 2008–2011 CSESP

Average infaunal density (ind. m⁻²) in the main study areas from 2008–2011 ranged from 794 (Klondike 2008) to 4,659 (Burger 2011) (Table 2-2). Biomass (g m⁻²) for the main study areas ranged from 115.0 (Klondike 2009) to 388.3 (Burger 2011). The total number of taxonomic categories identified in the main study areas ranged from 210 for Klondike stations in 2011 to 288 for Klondike in 2009 with no temporal trend (Appendix III). Total taxonomic categories for Burger stations indicate a decrease in number of taxa since 2008, from 268 categories to 212 different taxonomic categories in 2011. The total number of taxonomic categories for Statoil stations has remained similar, at 220 taxa categories in 2010 and 219 categories in 2011 (Table 2-2).

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 with 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).

Animals with highest density in Klondike include the bivalve *Ennucula tenuis*, polychaetes of the family Cirratulidae, and the amphipod *Melita* spp. (Table 2-3). Dominants in Burger include the bivalve *Ennucula tenuis*, the polychaete *Maldane sarsi*, and ostracods. Statoil had the same top three dominants as Burger, although in a different order. By biomass, the numerical dominants in Klondike include *M. sarsi*, the bivalve *Macoma calcarea*, and the sipunculid worm *Golfingia margaritacea*. Animals with the greatest biomass in Burger were *M. sarsi* and the bivalves *Astarte borealis* and *M. calcarea*. Biomass in Statoil includes the three bivalves *M. calcarea*, *A. borealis*, and *Yoldia hyperborea*.

Comparisons of biological measures indicate significant differences among study areas from 2008 to 2011. Repeated measures analysis of variance (rm ANOVA) of data from

Klondike and Burger 2008–2011 indicated significant study area by year interactions for density and the number of taxa, and significant study area and year main effects for biomass (Table 2-4). Whisker plots of the raw data with 95% confidence intervals demonstrated the significant trends and indicated that overall, Klondike had lower average density, sample number of taxa (replicate averages), and biomass than Burger, (Table 2-2 and Fig. 2-6). The significant study area by year interactions for average density and the number of taxa arise from significantly lower values for 2010 which declined sharply in Burger. The lower values in Burger in 2010 demonstrated a much larger change from 2008 and 2009 than in Klondike thus resulting in statistically-significant interaction effects (Fig. 2-6). Density and the number of taxa both increased sharply for Klondike and Burger in 2011. Biomass was significantly higher in Burger than Klondike and significantly lower in 2009. In general, during years of low density and number of taxa, biomass has been high (2008 and 2010; Fig. 2-6). Alternatively, during years of high density and number of taxa, biomass has been low. These interannual variations in biomass reflect benthic communities shifting from more numerous, smaller organisms, to communities with fewer but larger organisms. The exception to this case is Burger 2011, where density, number of taxa, and biomass were all higher than the previous three years.

Analysis of density of the major taxonomic groups, amphipods, bivalves, gastropods, and polychaetes, by rm ANOVA for Burger and Klondike 2008–2011 indicated significant study area by year interaction effects for all groups (Table 2-4). All four groups demonstrated higher values from 2008 to 2009 and 2011 with lower values in 2010 (Fig. 2-7). The density of bivalves and amphipods was significantly greater in 2011 for Burger than in 2010 and density of bivalves was significantly greater in 2011 in Klondike than in prior years. The response was not as strong in Klondike as in Burger.

Table 2-2. Summaries of biotic variables for the study areas sampled for infauna during the 2008–2011 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 Variable	<u>Klondike</u>		<u>Burger</u>		<u>Statoil</u>	
	Ave.	SD	Ave.	SD	Ave.	SD
Density	793.8	334.3	2,784.3	1,608.35	ns	ns
Biomass	178.8	175.01	333.2	177.41	ns	ns
Sample # Taxa	34.3	9.65	51.6	8.53	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	1,119.7	685.6	3,979.1	2,723.8	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	191.5	105.3	285.3	86.4	355.4	286.7
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	2029.3	1420.0	4,659.0	4,331.3	1,360.0	859.2
Biomass	157.5	83.9	388.29	142.7	259.6	194.1
Sample # Taxa	50.6	13.5	56.17	8.6	37.0	10.0
Total # Taxa	210	--	212	--	219	--
Shannon Diversity	4.22	--	3.05	--	3.95	--
Simpson's Evenness	0.97	--	0.84	--	0.96	--

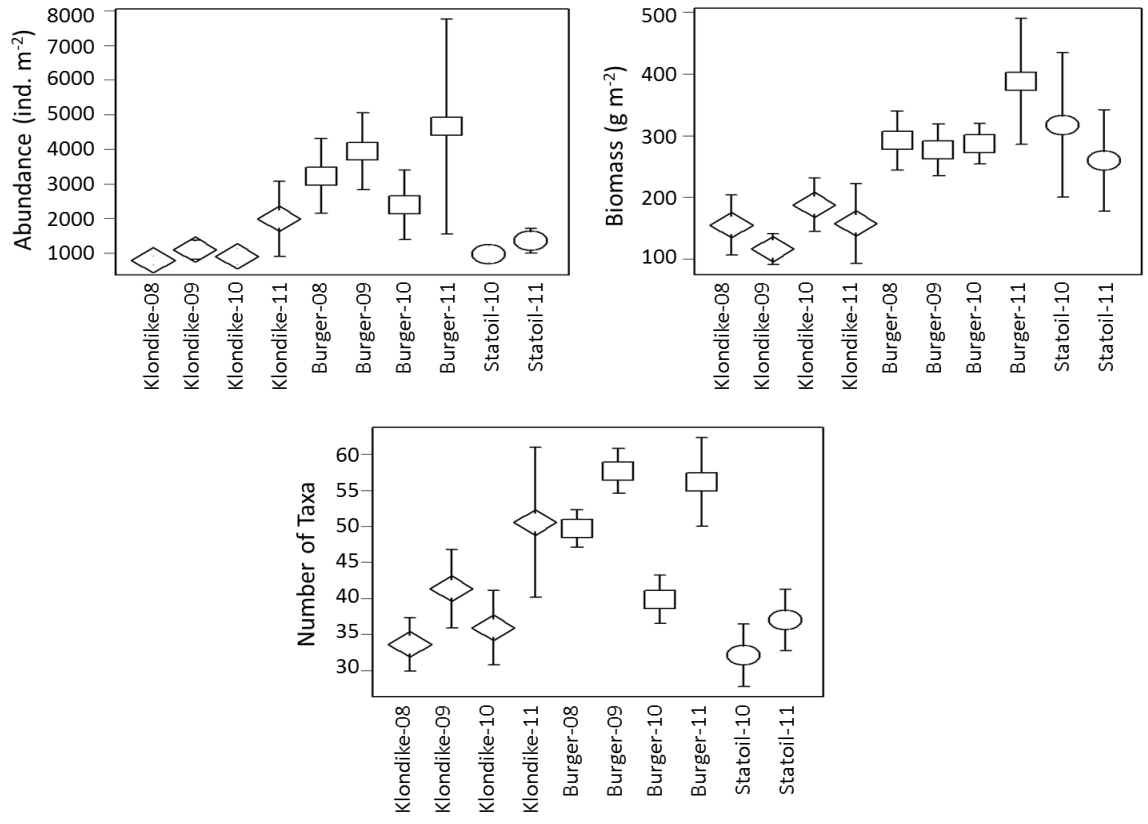


Figure 2-6. Plots of means and 95% confidence intervals based on the raw data for biological summary measures in study areas over the 2008–2011 CSESP study.

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

Study Area	Taxon	Density	Taxon	Biomass
Klondike	<i>Ennucula tenuis</i>	172	<i>Maldane sarsi</i>	34.4
	Cirratulidae	144	<i>Astarte borealis</i>	23.3
	<i>Melita</i> spp.	92	<i>Macoma calcarea</i>	14.1
	<i>Nuculana</i> spp.	84	<i>Cyclocardia crassidens</i>	7.3
	Capitellidae	72	<i>Neptunea ventricosa</i>	7.1
	<i>Maldane sarsi</i>	66	<i>Axiothella catenata</i>	6.6
	<i>Macoma</i> spp.	65	<i>Nephtys paradoxa</i>	6.3
	<i>Protomedeia</i> spp.	62	<i>Serripes groenlandicus</i>	6.2
	<i>Barantolla americana</i>	62	Maldanidae	4.6
	<i>Cistenides granulata</i>	42	<i>Ennucula tenuis</i>	3.5
Burger	<i>Maldane sarsi</i>	1,788	<i>Maldane sarsi</i>	74.4
	Ostracoda	415	<i>Macoma calcarea</i>	61.5
	<i>Ennucula tenuis</i>	312	<i>Golfingia margaritacea</i>	52.7
	<i>Photis</i> spp.	150	<i>Ennucula tenuis</i>	38.1
	<i>Lumbrineris</i> spp.	141	<i>Astarte borealis</i>	28.2
	<i>Paraphoxus</i> spp.	129	<i>Protomedeia</i> spp.	12.1
	<i>Ektondiastylis robusta</i>	120	<i>Axiothella catenata</i>	11.6
	<i>Myriochele heeri</i>	87	<i>Neptunea heros</i>	10.7
	<i>Macoma</i> spp.	64	<i>Macoma moesta</i>	6.7
	<i>Leitoscoloplos pugettensis</i>	63	<i>Astarte montagui</i>	6.7
Statoil	<i>Ennucula tenuis</i>	153	<i>Macoma calcarea</i>	41.9
	<i>Maldane sarsi</i>	114	<i>Yoldia hyperborea</i>	35.0
	Ostracoda	113	<i>Astarte borealis</i>	32.8
	<i>Yoldia</i> spp.	72	Hydrozoa	21.9
	Cirratulidae	61	<i>Golfingia margaritacea</i>	20.6
	<i>Lumbrineris</i> spp.	48	<i>Macoma moesta</i>	16.1
	<i>Yoldia hyperborea</i>	43	<i>Maldane sarsi</i>	14.8
	<i>Praxillella praetermissa</i>	41	<i>Ennucula tenuis</i>	10.8
	<i>Paraphoxus</i> spp.	39	<i>Nuculana pernula</i>	9.1
	<i>Macoma</i> spp.	38	Maldanidae	6.1

Table 2-4. Repeated measures analysis of variance of summary statistics and density (ind. m⁻²) of major taxonomic groups for 2008–2011 CSESP studies in the Klondike and Burger study areas only. Values significant at $\alpha = 0.05$ are in bold type.

<u>Summary Statistics</u>					
Density	F-value	p-value	Biomass	F-value	p-value
Study Area	44.4	< 0.0001	Study Area	66.8	< 0.0001
Year	21.3	< 0.0001	Year	4.2	0.0072
Study:Year	22.1	< 0.0001	Study:Year	1.2	0.3034

Taxa	F-value	p-value			
Study Area	24.6	< 0.0001			
Year	52.7	< 0.0001			
Study:Year	13.5	< 0.0001			

<u>Key Taxa</u>					
Amphipoda	F-value	p-value	Gastropoda	F-value	p-value
Study Area	32.1	< 0.0001	Study Area	7.5	0.0082
Year	23.3	< 0.0001	Year	22.1	< 0.0001
Study:Year	24.2	< 0.0001	Study:Year	4.8	0.0035

Bivalvia	F-value	p-value	Polychaeta	F-value	p-value
Study Area	56.6	< 0.0001	Study Area	21.6	< 0.0001
Year	30.1	< 0.0001	Year	5.7	0.0011
Study:Year	6.4	< 0.0001	Study:Year	14.4	< 0.0001

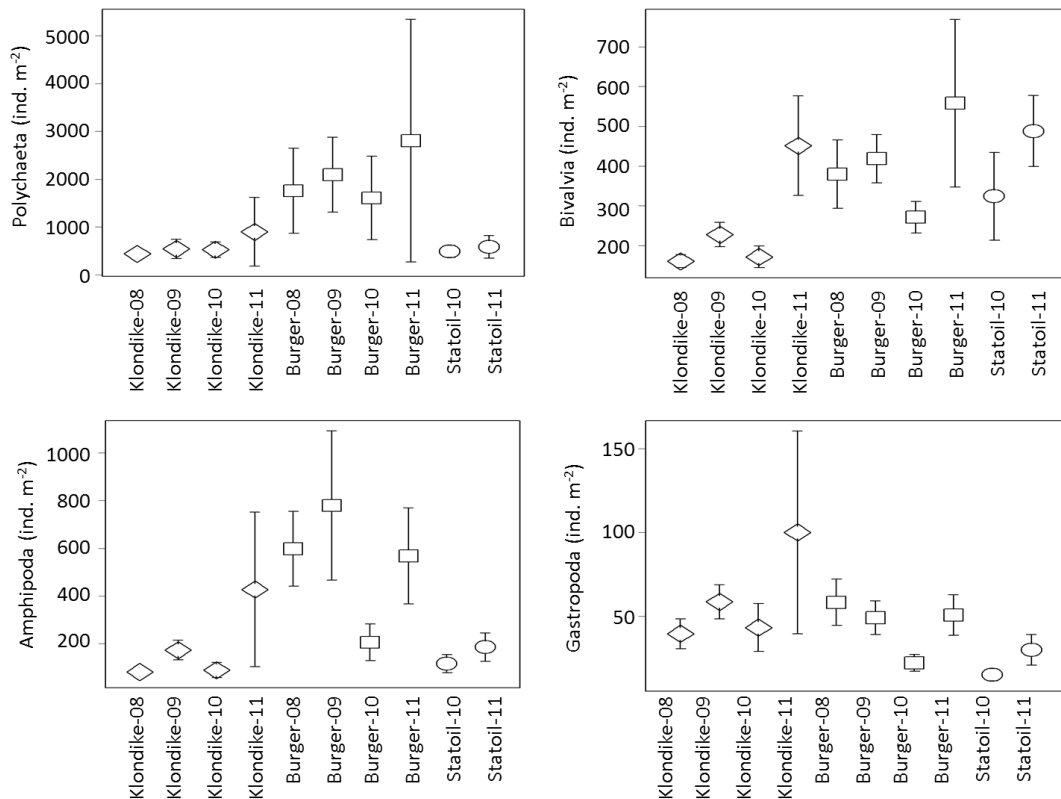


Figure 2-7. Plots of means and 95% confidence intervals based on the raw data of the density of major taxonomic groups in study areas over the 2008–2011 CESP study.

When comparing data for Klondike, Burger, and Statoil from 2010 to 2011, the rm ANOVA indicated significant study area by year interactions for density and the number of taxa, and significant study area main effects for biomass (Table 2-5). Statoil, sampled in 2010 and 2011, was intermediate between Klondike and Burger with lower density and average number of taxa, similar to Klondike, and higher biomass like Burger (Table 2-2 and Fig. 2-6). Similar to results from the rm ANOVA for Klondike and Burger 2008–2011, significant study area by year interactions were observed for average density and the number of taxa. The interactions were primarily driven by the larger magnitude changes in Burger from 2010 to 2011. Whisker plots illustrate the increase in density and number of taxa from 2010 to 2011 across all three study areas (Fig. 2-6). From 2010 to 2011, biomass decreased in Klondike and Statoil while biomass in Burger increased in 2011. The repeated measures analysis also indicated significant study area by year interaction effects for amphipods and gastropods (Table 2-5 and Fig. 2-7). Bivalve density differed significantly by year and by study area. Polychaetes displayed no significant

differences among the three study areas or by year. Variations in density of the taxon groups did not follow a common pattern. Densities of amphipods, bivalves, and polychaetes were higher in Burger than Klondike and densities of amphipods and gastropods were higher in Burger than Statoil. Densities for all groups in 2010 were generally lower than in other years and densities were increased again in 2011. The densities of amphipods, bivalves, and gastropods in Klondike in 2011 were higher than in all prior years.

Table 2-5. Repeated measures analysis of variance of summary statistics for 2010-2011 CSESP studies, including Statoil.

<u>Summary Statistics</u>					
Density	F-value	p-value	Biomass	F-value	p-value
Study Area	19.0	< 0.0001	Study Area	9.9	0.0002
Year	21.0	< 0.0001	Year	0.1	0.8180
Study:Year	4.7	0.0143	Study:Year	1.2	0.3214

Taxa	F-value	p-value			
Study Area	4.5	0.0144			
Year	47.4	< 0.0001			
Study:Year	6.1	0.0049			

<u>Key Taxa</u>					
Amphipoda	F-value	p-value	Gastropoda	F-value	p-value
Study Area	10.7	< 0.0001	Study Area	16.3	< 0.0001
Year	25.7	< 0.0001	Year	20.8	< 0.0001
Study:Year	11.5	< 0.0001	Study:Year	4.7	0.0151

Bivalvia	F-value	p-value	Polychaeta	F-value	p-value
Study Area	9.5	0.0002	Study Area	2.6	0.0803
Year	69.5	< 0.0001	Year	1.6	0.2198
Study:Year	0.5	0.6100	Study:Year	1.5	0.2413

Multivariate analysis of infaunal community composition (density) for all CSESP sampling years (2008–2011) indicates separations by study area but not by years (Fig. 2-8). Klondike stations cluster to the bottom right, Burger stations cluster above and to the left of the Klondike stations, and Statoil stations are positioned above the Klondike stations and to the right of Burger stations with some mixing with the other study areas. Thus, the MDS ordination for the infauna reflects the strong influence of environmental gradients in the region (Fig. 2-3). There is not a clear separation by year for any of the study areas as within a study area, all years overlap.

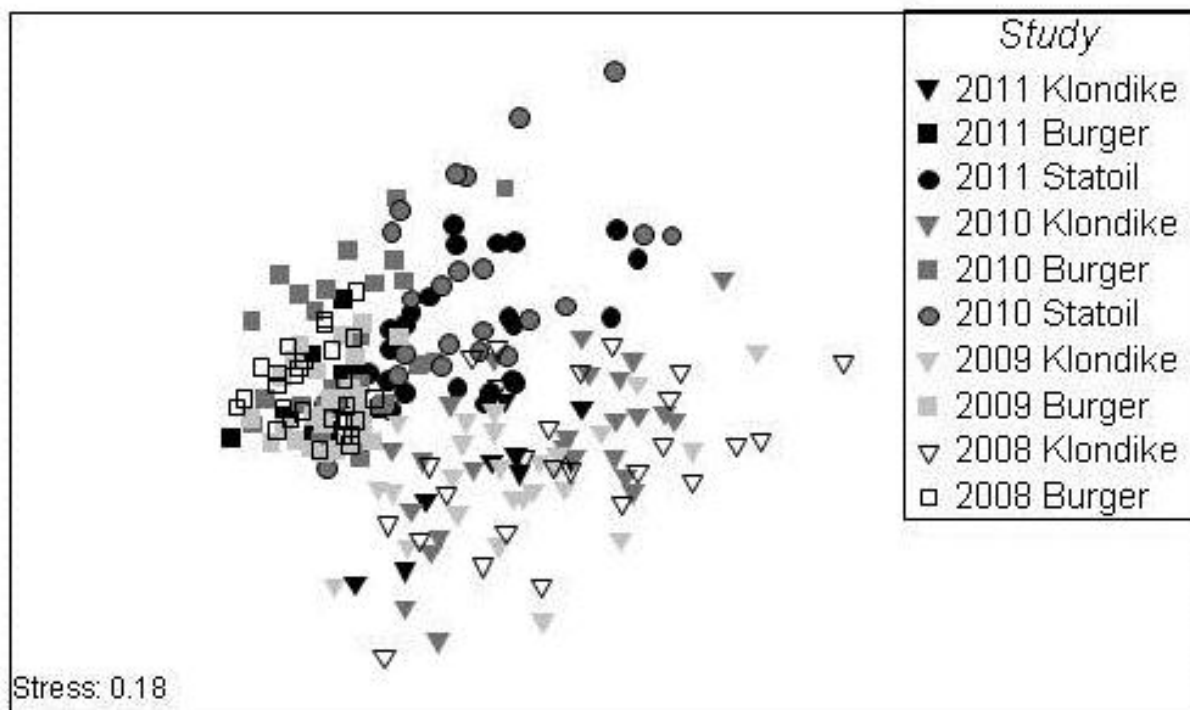


Figure 2-8. Nonmetric multidimensional scaling ordination plot of Bray-Curtis similarities for $\ln(X+1)$ -transformed benthic density data from 2008–2011 CSESP sampling.

To further investigate the 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 in Klondike stations were the bivalves *E. tenuis* (2008–2011) and *Macoma* spp. (2011) and the polychaetes *Barantolla americana* (2008 and 2011), Cirratulidae (2009–2010), and *M. sarsi* (2008–2010) (Table 2-6). Animals contributing most to within-study area similarity by density in Burger were the amphipod *Photis* spp. (2009), *E. tenuis* (2010–2011), ostracods (2008–2010), and the polychaetes *Lumbrineris* spp. (2008) and *M. sarsi* (2008–2011). In the Statoil study area, the taxa contributing to study area similarity include the bivalves *E. tenuis* (2010–2011), *Macoma* spp. (2011), *Yoldia hyperborea* (2010), and *Yoldia* spp., and malidanid polychaete *Praxillella praetermissa* (2010).

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

2008 Klondike Average similarity = 41.95			2010 Klondike Average similarity = 43.78		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Maldane sarsi</i>	70.51	6.22	<i>Ennucula tenuis</i>	112.31	10.50
<i>Ennucula tenuis</i>	67.95	7.96	Cirratulidae	59.49	3.66
<i>Barantolla americana</i>	43.97	3.26	<i>Maldane sarsi</i>	47.05	3.15
2009 Klondike Average similarity = 44.46			2011 Klondike Average similarity = 44.76		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Ennucula tenuis</i>	112.31	10.50	<i>Ennucula tenuis</i>	172.22	9.59
Cirratulidae	59.49	3.66	<i>Barantolla americana</i>	61.85	3.28
<i>Maldane sarsi</i>	47.05	3.15	<i>Macoma</i> spp.	65.19	2.90
2008 Burger Average similarity = 38.27			2010 Burger Average similarity = 34.14		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Maldane sarsi</i>	748.39	2.68	<i>Maldane sarsi</i>	1084.74	6.15
Ostracoda	286.67	3.98	Ostracoda	135.26	2.59
<i>Lumbrineris</i> spp.	188.51	4.34	<i>Ennucula tenuis</i>	130.90	5.41
2009 Burger Average similarity = 40.30			2011 Burger Average similarity = 36.57		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Maldane sarsi</i>	749.62	2.53	<i>Maldane sarsi</i>	1788.33	5.41
Ostracoda	289.49	3.47	<i>Ennucula tenuis</i>	312.33	4.85
<i>Photis</i> spp.	212.05	0.90	Ostracoda	415.00	3.84
2010 Statoil Average similarity = 35.06			2011 Statoil Average similarity = 37.72		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Ennucula tenuis</i>	87.08	5.93	<i>Ennucula tenuis</i>	159.44	10.38
<i>Yoldia hyperborea</i>	65.97	1.22	<i>Yoldia</i> spp.	74.72	2.68
<i>Praxillella praetermissa</i>	59.86	3.11	<i>Macoma</i> spp.	39.17	2.39

Associations between Biological and Environmental Characteristics of the Regional Study Area

A total of 318 taxonomic categories of infaunal organisms were identified within the Chukchi regional study area. The study area was split into four strata: South, Central A, Central B, and North. The taxonomic categories that comprised the majority of the density (ind. m⁻²) were polychaetes and bivalves. Polychaetes comprised 41.12% of the total density in the southern stratum, 55.61% in Central A, 34.55% in Central B, and 32.52% in the North. Bivalves comprised 21.4% of total density in South, 14.53% in Central A, 44.02% in Central B, and 41.67% in the North strata. Amphipods comprised 22.78% of the total density in the South stratum, 10.96% in Central A, 12.67% in Central B, and 19.4% in North. The dominants in terms of biomass (g m⁻²) in each stratum were polychaetes, bivalves, and sipunculids. In the southern region, polychaetes comprised 42.9% of the total biomass, 31.56% in Central A, 16.16% in Central B, and 13.8% in North. Bivalves contributed to 44.69% of total biomass in South, 39.32% in Central A, 68.16% in Central B, and 78.61% in North. Sipunculids were mostly a contributing factor in the Central A region, comprising 16.48% of the total biomass.

Average density in the study region ranged from 645 in the North to 3,582 in Central A, while biomass ranged from 137.1 in the North to 328.7 in Central B (Table 2-7). The sample number of taxa declined from south to north from a high of 81 taxa in South and Central A to a low of 43 in the North stratum. The total number of taxa also declined with greater distance north from 246 taxon categories in South to 157 in North. The contour plot of geostatistical predictions for density indicate greatest density in Burger with values declining to the south, west, and north of Burger (Fig. 2-9). The geostatistical model for biomass indicates a peak in biomass occurs just to the east of Burger extending slightly to the north with low values in the southern and the northeastern regions (Fig. 2-9). Bivalve biomass and density peak just to the east of the Burger study area (Fig. 2-10). Polychaete density peaks in Burger and biomass peaks south of Burger (Fig. 2-10).

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

By biomass, South was dominated by *A. borealis*, *A. catenata*, and *M. sarsi* (Table 2-8). Dominants in Central A were *G. margaritacea*, *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*.

Table 2-7. Average and standard deviations of total density and biomass between the four strata (South, Central A, Central B, and North). 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.

Variable	<u>South</u>		<u>Central A</u>		<u>Central B</u>		<u>North</u>	
	Ave.	SD	Ave.	SD	Ave.	SD	Ave.	SD
Density	1938.4	1290.0	3581.5	3731.0	1285.6	564.8	644.5	281.5
Biomass	227.3	204.0	301.4	158.7	328.7	227.7	137.1	46.9
Sample # Taxa	82.1	30.5	82.4	17.4	60.5	17.1	42.7	12.6
Total # Taxa	246	--	221	--	227	--	157	--

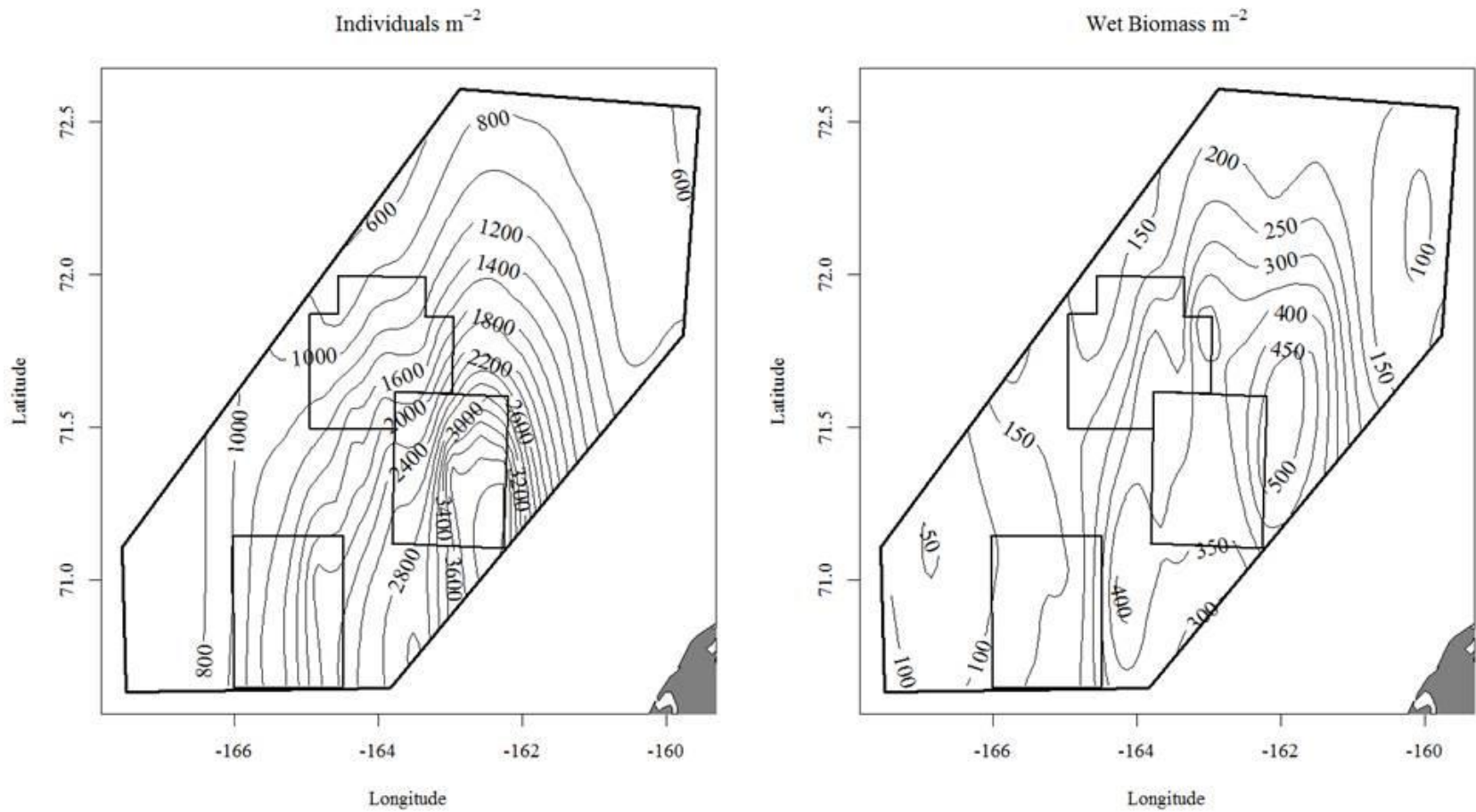


Figure 2-9. Geostatistical models for density (ind. m⁻²) and biomass (g m⁻²) for the regional study area of the 2011 CESP.

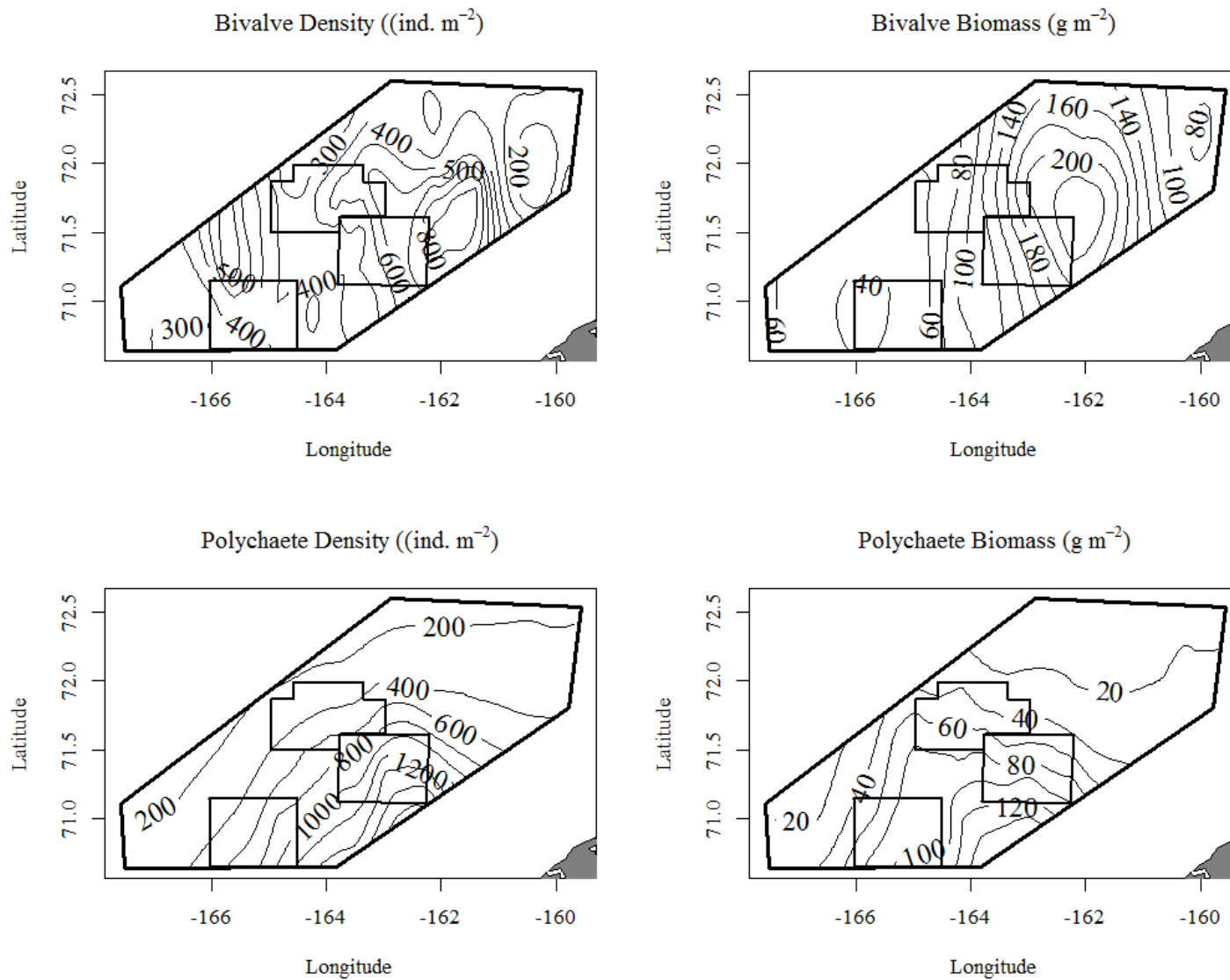


Figure 2-10. Geostatistical models for bivalve and polychaete density (ind. m⁻²) and biomass (g m⁻²) for the regional study area of the 2011 CESP.

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

Stratum	Taxon	Density	Taxon	Biomass
South	<i>Ennucula tenuis</i>	189	<i>Astarte borealis</i>	46.8
	Cirratulidae	97	<i>Maldane sarsi</i>	39.5
	<i>Maldane sarsi</i>	96	<i>Axiothella catenata</i>	17.1
	<i>Melita</i> spp.	60	<i>Macoma calcarea</i>	16.6
	<i>Macoma</i> spp.	59	<i>Golfingia margaritacea</i>	10.7
	Capitellidae	58	<i>Ennucula tenuis</i>	7.0
	<i>Dyopedos arcticus</i>	57	Maldanidae	6.9
	<i>Barantolla americana</i>	50	<i>Musculus niger</i>	5.4
	<i>Protomedeia</i> spp.	47	<i>Astarte montagui</i>	4.9
	<i>Nuculana</i> spp.	44	<i>Cyclocardia crassidens</i>	4.4
Central A	<i>Maldane sarsi</i>	1,263	<i>Golfingia margaritacea</i>	49.1
	Ostracoda	422	<i>Maldane sarsi</i>	40.1
	<i>Ennucula tenuis</i>	261	<i>Macoma calcarea</i>	39.3
	<i>Photis</i> spp.	101	<i>Ennucula tenuis</i>	26.1
	<i>Paraphoxus</i> spp.	84	<i>Astarte borealis</i>	24.9
	<i>Ektondiastylis robusta</i>	80	<i>Axiothella catenata</i>	11.9
	<i>Lumbrineris</i> spp.	76	<i>Yoldia hyperborea</i>	8.2
	<i>Barantolla americana</i>	58	<i>Protomedeia</i> spp.	7.6
	<i>Myriochele heeri</i>	55	<i>Neptunea heros</i>	6.7
	<i>Macoma</i> spp.	54	Maldanidae	6.5
Central B	<i>Ennucula tenuis</i>	184	<i>Macoma calcarea</i>	75.5
	<i>Yoldia</i> spp.	81	<i>Yoldia hyperborea</i>	32.8
	Cirratulidae	81	<i>Astarte borealis</i>	25.2
	<i>Macoma calcarea</i>	57	<i>Nuculana pernula</i>	22.7
	<i>Lumbrineris</i> spp.	49	<i>Ennucula tenuis</i>	22.2
	<i>Macoma</i> spp.	45	<i>Maldane sarsi</i>	19.4
	<i>Yoldia hyperborea</i>	38	<i>Macoma moesta</i>	18.4
	<i>Nuculana pernula</i>	30	Hydrozoa	17.7
	<i>Paraphoxus</i> spp.	27	<i>Golfingia margaritacea</i>	14.0
	<i>Macoma moesta</i>	27	<i>Serripes groenlandicus</i>	5.4
North	<i>Ennucula tenuis</i>	83	<i>Macoma calcarea</i>	38.5
	<i>Macoma</i> spp.	43	<i>Yoldia hyperborea</i>	20.8
	Cirratulidae	34	<i>Nuculana pernula</i>	15.0
	<i>Ampelisca</i> spp.	26	<i>Ennucula tenuis</i>	10.8
	<i>Yoldia</i> spp.	25	<i>Astarte borealis</i>	7.8
	<i>Ampelisca eschrichti</i>	24	<i>Musculus niger</i>	4.5
	<i>Nuculana pernula</i>	22	<i>Nephtys punctata</i>	4.4
	<i>Nephtys punctata</i>	20	<i>Serripes groenlandicus</i>	2.8
	<i>Byblis</i> spp.	18	<i>Liocyma fluctuosa</i>	2.7
	<i>Macoma calcarea</i>	18	<i>Maldane sarsi</i>	2.6

Comparisons of biological measures indicate significant differences among strata. Analysis of variance indicated that both density (F-value = 14.91, $p < 0.0001$) and biomass (F-value = 4.2, p -value = 0.0086) were significantly different between strata. Multiple comparisons reveal that there was a significantly lower density in the North stratum as compared to the others (Central A vs. North, p -value < 0.0001 ; Central B vs. North, p -value = 0.0080; South vs. North, p -value = 0.0003), as well as a significant difference between the two central strata, with Central B having lower density than Central A (p -value = 0.0004) (Fig. 2-9). In terms of biomass, again there was significantly less biomass in North as compared to the two central strata (Central A vs. North, p -value = 0.04; Central B vs. North, p -value = 0.01) (Fig. 2-11).

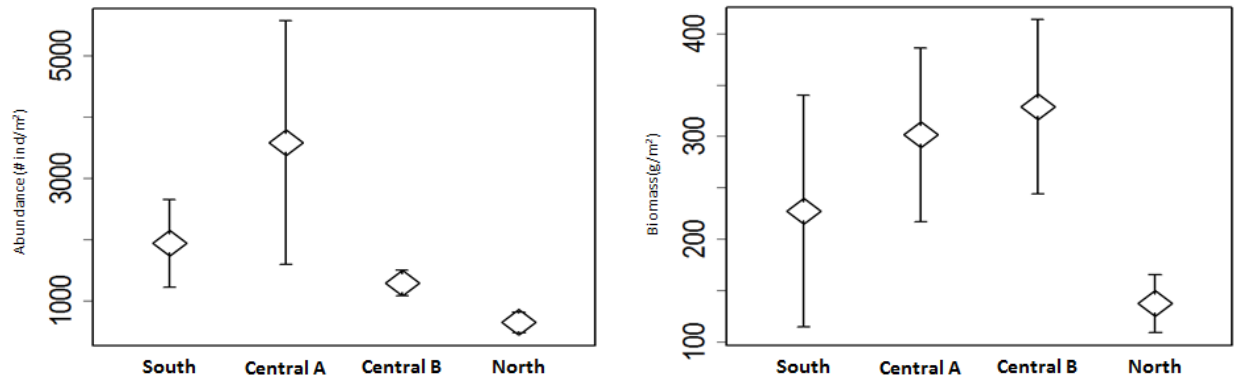


Figure 2-11. Plot of mean density (ind. m⁻²) and biomass (g m⁻²) with 95% confidence intervals.

Multivariate analysis of infaunal density indicated a gradient following the latitudinal shift between strata from the upper left corner to the lower right (Fig. 2-12). The South stations cluster in the upper left corner and spread to the right along the top, followed by Central A, then Central B, and finally the North stratum in the bottom. This gradient reflects the strong influence of known environmental gradients from the southwest of Hanna Shoal to the northeast (Fig. 2-3). Percent mud had the highest correlation with MDS axis 1 and bottom water temperature had the highest correlation with MDS axis 2. The overlay of fitted correlations on the MDS ordination shows stations increasing in percent mud positioned to the right of the plot and stations with higher bottom-water temperature towards the top.

The BIOENV shows that bottom temperature had the highest correlation with the biotic structure captured in the MDS ($\rho= 0.25$), but the variable combination with the highest overall correlation was water depth, percent mud, and bottom temperature ($\rho= 0.31$) (Table 2-9).

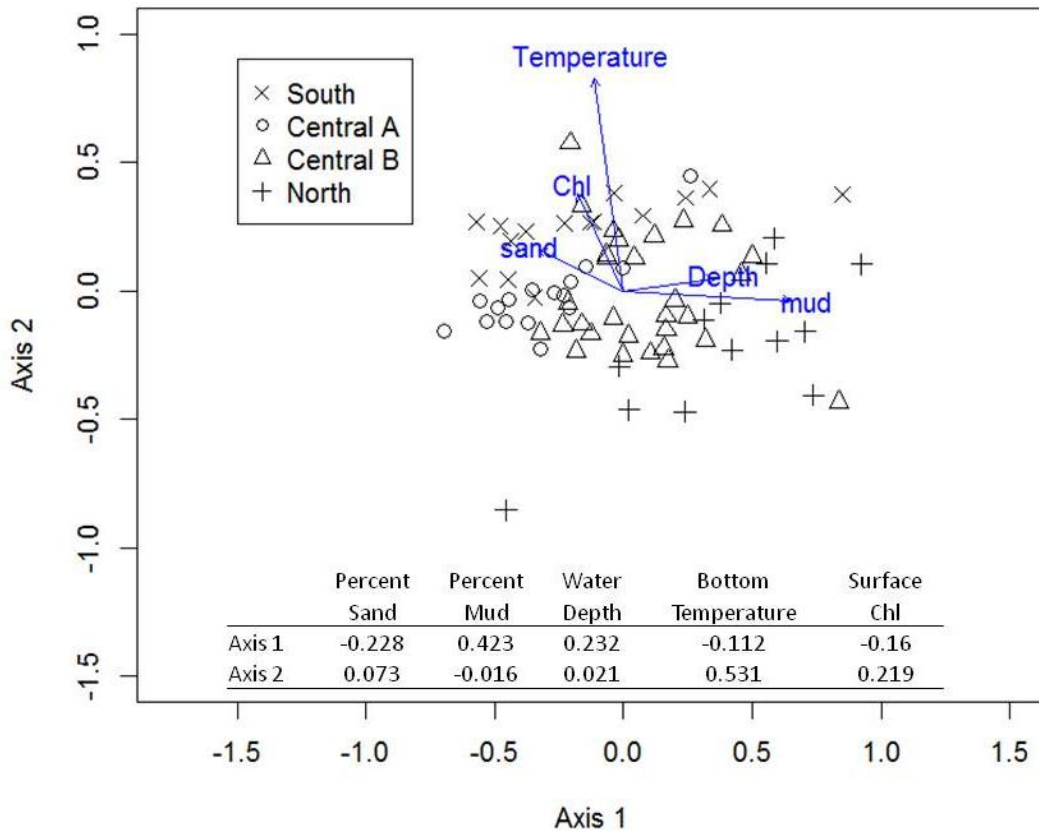


Figure 2-12. Nonmetric multidimensional scaling ordination plot of Bray-Curtis similarities for $\ln(X+1)$ -transformed infaunal density data. Overlays of environmental variables and their correlations (Spearman’s ρ) with the MDS axes are presented.

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
Bottom Temperature	0.25
% Mud, Bottom Temperature	0.29
% Mud, Water Depth, Bottom Temperature	0.31
% Mud, Water Depth, Bottom Temperature, Total Chl volume (pg cm^{-3})	0.27

The taxon contributing most to regional similarity by density within all strata was *E. tenuis* (Table 2-10). *Macoma* spp. and Cirratulidae were the next greatest contributors to density in South and Central B. In Central A, Ostracoda and *M. sarsi* were important contributors, while in the North stratum Cirratulidae and *Lumbrineris* spp. were important.

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

Density			Central B		
South			Central B		
Average similarity = 46.38			Average similarity = 49.02		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Ennucula tenuis</i>	188.67	3.16	<i>Ennucula tenuis</i>	185.89	3.89
<i>Macoma</i> spp.	58.67	2.14	<i>Macoma</i> spp.	45.67	2.98
Cirratulidae	97.33	2.11	Cirratulidae	83.78	2.84

Central A			North		
Average similarity = 53.46			Average similarity = 41.75		
Taxon	Density	Sim	Taxon	Density	Sim
<i>Ennucula tenuis</i>	256.46	3	<i>Ennucula tenuis</i>	83.08	4.43
Ostracoda	421.67	2.45	Cirratulidae	34.29	2.9
<i>Maldane sarsi</i>	1263.12	2.01	<i>Lumbrineris</i> spp.	17.37	2.72

Sampling of Deeper Sediments with HAPS Corer

Station rankings of dominant species found in HAPS corer samples were broadly similar to those from the van Veen grab (Table 2-11). The focus was on larger organisms that may be dwelling just beyond the reach of the van Veen grab. Without too much detail, the predominant taxa in these samples by density and biomass shares dominants from the van Veen grab samples including *A. borealis*, *E. tenuis*, *G. margaritacea*, maldanid polychaetes (Maldanidae and *M. sarsi*), *M. calcarea*, and *Y. hyperborea* (Tables 2-8 and 2-11). Most importantly, the target organism, the deep-dwelling bivalve *Mya*, a known walrus prey item, was rare and only one *Mya* sp. fragment was collected at station HC032 with a biomass of 5.51 g in the sample for an estimated weight of 118.4 g m⁻² at that station. The biomass of *G. margaritacea* in the HAPS corer samples from the South, Central A, and Central B strata was three to seven times the

biomass in samples collected from the van Veen grab while biomass of *Macoma calcarea* from the HAPS samples for the North strata was 2 times that found in the grab samples. Some of the HAPS corer samples were sectioned by depth resulting in 5-cm sections to 25 cm. The 0–5 cm sections included a range of organisms, as expected. The 6–10 cm section contained the amphipod *Ampelisca eschrichti*, bivalves *E. tenuis* and *Macoma calcarea*, and various polychaetes including *M. sarsi* (Table 2-12). Unexpectedly, the 6–10 cm core segments also contained brittle stars (*Amphiura sundevalli* and *Ophiura sarsi*). The 11–15 cm core segment contained the sipunculid worm *Golfingia margaritacea* and the polychaetes Capitellidae and *M. sarsi*. No organisms were noted in the 16–20 cm segments and one *M. sarsi* was found in the 21–25 cm segment.

Population Dynamics of Ennucula tenuis

Spatial and temporal variability in the length-frequency distributions of *E. tenuis* were high (Fig. 2-13). Overall, the bivalve populations were unimodal to bimodal with peaks at 2–3 mm and around 12–13 mm. Length-frequency distributions for 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. 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 the curve was dominated by a peak at about 2–3 mm.

There were differences among summary statistics among study areas. Average and median lengths of *E. tenuis* in Klondike (median from 3.05 to 4.24 mm) from 2008 and 2010 were smaller than those found in Burger (median from 7.24 to 8.01 mm) and Statoil (7.38 mm). In 2011, all sites had higher relative frequencies of small bivalves (new recruits) and lengths were smaller than in prior years (median lengths of 2.70, 5.15, and 2.49 for Klondike, Burger, and Statoil, respectively). Presuming that the peaks in bivalve lengths at 2–3 mm were cohort 1 bivalves (experiencing their first year's growth after late-winter/early-spring recruitment), then the second peak in the histograms may reflect a second year's growth.

Table 2-11. Rankings by density (ind. m⁻²) and biomass (g m⁻²) of dominant animals (top ten) by strata for HAPS Corer samples collected during the 2011 CSESP regional study.

Stratum	Taxon	Density	Taxon	Biomass
South	<i>Maldane sarsi</i>	37	<i>Golfingia margaritacea</i>	71.77
	Maldanidae	23	<i>Astarte borealis</i>	42.57
	<i>Paradiopatra parva</i>	11	<i>Maldane sarsi</i>	18.45
	<i>Praxillella praetermissa</i>	11	<i>Nephtys</i> spp.	10.51
	<i>Golfingia margaritacea</i>	9	Maldanidae	10.25
	<i>Nephtys</i> spp.	9	<i>Paradiopatra parva</i>	2.81
	<i>Macoma calcarea</i>	9	<i>Macoma calcarea</i>	2.74
	<i>Sternaspis fossor</i>	6	<i>Proclea emmi</i>	2.47
	<i>Ennucula tenuis</i>	6	<i>Sternaspis fossor</i>	2.43
	<i>Astarte borealis</i>	3	<i>Astarte montagui</i>	2.43
Central A	<i>Maldane sarsi</i>	259	<i>Golfingia margaritacea</i>	135.63
	<i>Ennucula tenuis</i>	67	<i>Macoma calcarea</i>	41.90
	<i>Paradiopatra parva</i>	23	<i>Ennucula tenuis</i>	22.35
	Maldanidae	15	<i>Maldane sarsi</i>	14.20
	<i>Ampelisca eschrichti</i>	15	<i>Cyclocardia crebricostata</i>	13.62
	<i>Golfingia margaritacea</i>	13	Maldanidae	6.53
	<i>Praxillella praetermissa</i>	13	<i>Macoma moesta</i>	5.63
	<i>Macoma calcarea</i>	10	<i>Astarte borealis</i>	5.30
	<i>Macoma moesta</i>	8	<i>Paradiopatra parva</i>	4.31
	<i>Cyclocardia crebricostata</i>	6	<i>Ampelisca eschrichti</i>	3.05
Central B	<i>Ennucula tenuis</i>	84	<i>Macoma calcarea</i>	90.01
	<i>Macoma calcarea</i>	69	<i>Golfingia margaritacea</i>	32.65
	<i>Nuculana pernula</i>	19	<i>Ennucula tenuis</i>	32.43
	<i>Maldane sarsi</i>	13	<i>Nuculana pernula</i>	27.57
	<i>Liocyma fluctuosa</i>	11	<i>Liocyma fluctuosa</i>	19.90
	<i>Macoma moesta</i>	10	<i>Astarte borealis</i>	10.54
	<i>Golfingia margaritacea</i>	8	<i>Macoma moesta</i>	10.11
	Maldanidae	8	<i>Mya</i> sp. (fragment)	9.87
	<i>Paradiopatra parva</i>	8	<i>Astarte montagui</i>	6.88
	<i>Cistenides granulata</i>	8	Maldanidae	6.20
North	<i>Macoma calcarea</i>	29	<i>Macoma calcarea</i>	65.13
	<i>Proclea</i> spp.	14	<i>Nuculana pernula</i>	12.51
	<i>Owenia fusiformis</i>	13	<i>Nephtys paradoxa</i>	11.23
	<i>Nuculana pernula</i>	13	Nemertea	6.90
	<i>Ennucula tenuis</i>	13	<i>Lumbrineris fragilis</i>	4.16
	Nemertea	7	<i>Ennucula tenuis</i>	2.69
	<i>Maldane sarsi</i>	7	<i>Nuculana</i> spp.	2.60
	<i>Nuculana</i> spp.	6	<i>Maldane sarsi</i>	2.35
	<i>Bivalvia</i>	4	<i>Paradiopatra parva</i>	2.01
	<i>Nephtys paradoxa</i>	3	<i>Proclea</i> spp.	1.49

Table 2-12. Raw density and biomass for HAPS corer samples separated by depth strata. No organisms were found between 16 and 20 cm. One *Maldane sarsi* was found at 21-25 cm depth at station BF013 with a weight of 0.005 g. F = fragment. R = replicate, Den = density, and Biom = biomass.

Station	R	0-5 cm		6-10 cm			11-15 cm			
		Organism	Den	Biom	Organism	Den	Biom	Organism	Den	Biom
BF011	3	<i>Phascolion strombus</i>	2	0.026	<i>Petaloproctus tenuis</i>	1	0.003	<i>Golfingia margaritacea</i>	1	6.003
		<i>Terebellides stroemi</i>	1	0.123	<i>Ampelisca eschrichti</i>	1	0.012			
		<i>Ampelisca eschrichti</i>	1	0.203	<i>Ennucula tenuis</i>	1	0.224			
		<i>Ennucula tenuis</i>	1	0.204						
		<i>Ophiura sarsi</i>	1	0.012						
		<i>Cyclocardia crebricostata</i>	1	2.853						
BFO13	3	<i>Maldane sarsi</i>	3	0.041	<i>Amphiura sundevalli</i>	1	0.057	Capitellidae	1	0.007
		<i>Ophiura sarsi</i>	1	0.257	<i>Ophiura sarsi</i>	1	0.462	<i>Maldane sarsi</i>	F	0.13
					<i>Ampelisca eschrichti</i>	1	0.255			
					<i>Petaloproctus</i> sp.	2	0.007			
					<i>Ennucula tenuis</i>	2	0.425			
					<i>Maldane sarsi</i>	41	0.887			
BF015	3	<i>Ampelisca macrocephala</i>	1	0.061	<i>Macoma calcarea</i>	1	4.017	None		
		<i>Maldane sarsi</i>	2	0.037						
		<i>Astarte montagui</i>	1	1.076						
		<i>Macoma moesta</i>	1	0.148						
		<i>Ennucula tenuis</i>	2	0.513						
		<i>Ophiura sarsi</i>	2	0.978						

Table 2-12. Continued.

Station	R	0-5 cm		6-10 cm		11-15 cm				
		Organism	Den	Biom	Organism	Den	Biom	Organism	Den	Biom
BF021	3	None			Maldanidae	F		None		
					<i>Terebellides</i>					
					<i>stroemi</i>	1				
HC006	3	<i>Nuculana pernula</i>	1					None		
HC020	3	None			<i>Yoldia hyperborea</i>	1		None		
					<i>Macoma calcarea</i>	1				
					<i>Ennucula tenuis</i>	3				
HC028	3	None			<i>Macoma calcarea</i>	1	1.446	None		
KF011	3	<i>Praxillella</i>								
		<i>praetermissa</i>	1	0.082				None		
		<i>Oenopoda excurvatus</i>	1	0.749	<i>Proclea</i> sp.	1	0.591			
SF018	3	<i>Macoma calcarea</i>	1	1.002	<i>Ennucula tenuis</i>	2	0.916	None		
		<i>Nuculana pernula</i>	1	0.912						
		<i>Ennucula tenuis</i>	1	0.613						
		<i>Cyclocardia</i>								
		<i>crebricostata</i>	1	1.152						

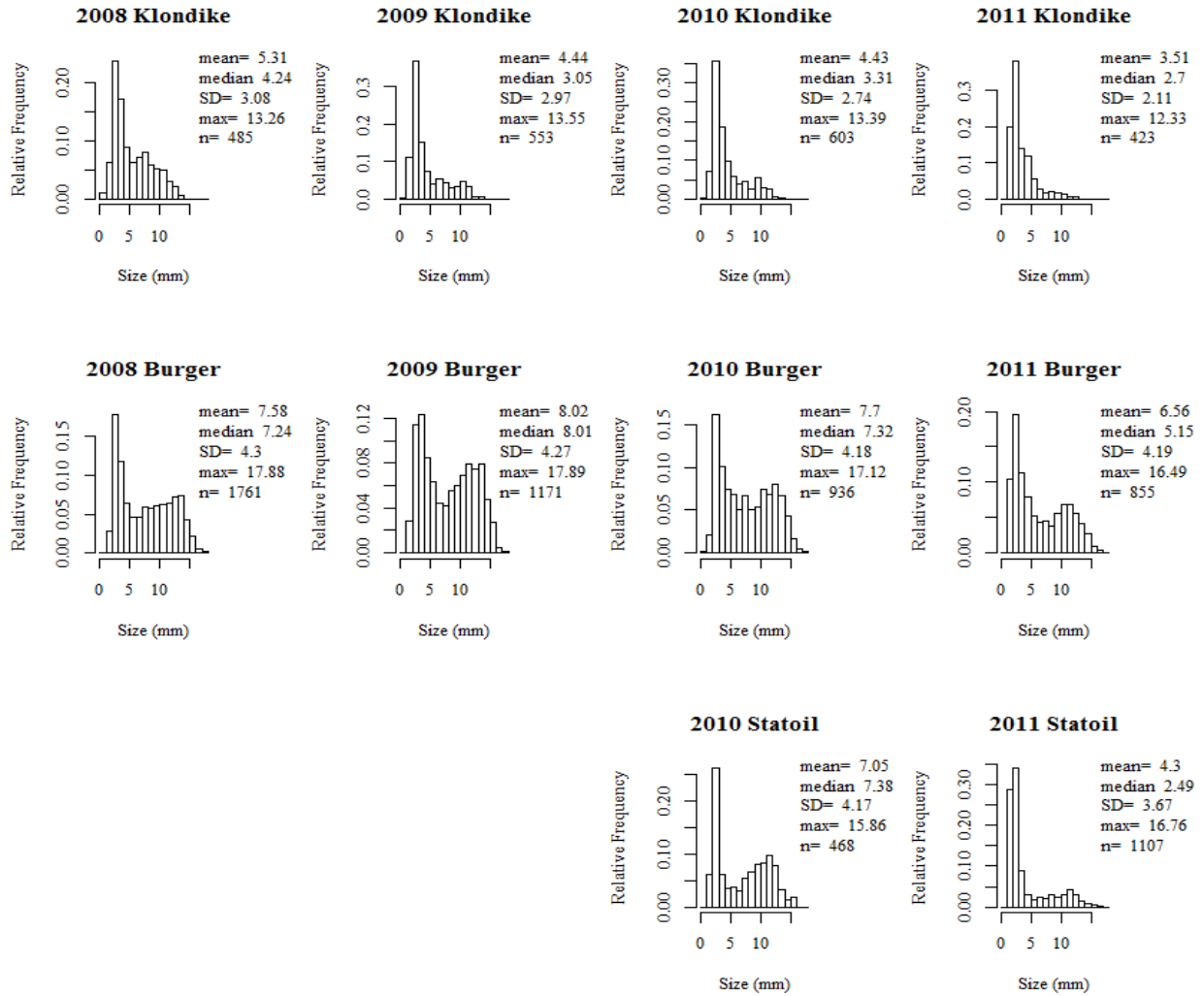


Figure 2-13. Relative length-frequency histograms of *Ennucula tenuis* for the Klondike, Burger, and Statoil study areas, 2008–2011.

Meiofauna of the Regional Study Area

A total of 137 taxonomic categories of meiofaunal organisms were identified from the 2011 CSESP regional study. By strata, the total number of taxonomic categories identified ranged from 50 for North to 89 for Central B (Table 2-13). The total number of taxa was highest in the South and Central B strata. These areas coincide with the main study areas Klondike (South), and the majority of Statoil plus the very northern section of Burger (Central B) (Figure 2-1). Central A (containing most of Burger, Transitional sites, and the northernmost portion of Klondike) had slightly fewer taxa compared to South and Central B. The North stratum (Hanna Shoal) had the lowest number of taxa of the four strata, with a total of 50 taxa (Table 2-13).

The meiofaunal taxa for the 2011 regional study area included permanent and transitory taxa. Nematodes, a permanent meiofaunal group, had the highest density across all four strata, ranging from approximately 10 to 33 ind. cm⁻², with higher densities in Central B than the other three strata (Table 2-14 and Fig. 2-14). Harpacticoid copepods, also permanent meiofauna, had the second highest densities ranging from 2 to 5 ind. cm⁻² with higher densities in Central B compared than the other strata. The permanent meiofaunal group Foraminifera had its highest densities in Central A and lowest in the North stratum with densities ranging from 0.6 to 5 ind. cm⁻². Transitory meiofaunal taxa (juvenile infauna) observed included bivalves (including *E. tenuis*), and polychaetes (including *Cossura* spp., *Nephtys* spp., and *Prionospio steenstrupi*), and all occurred with densities less than 1.0 ind. cm⁻².

Table 2-13. Summaries of biotic variables for regional strata sampled for meiofauna during the 2011 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.

Variable	South		Central A		Central B		North	
	Ave.	SD	Ave.	SD	Ave.	SD	Ave.	SD
Density	34.7	28.3	39.3	52.9	46.3	36.6	15.2	10.6
Sample # Taxa	24.1	5.3	20.3	5.5	19.5	4.9	13.5	4.3
Total # Taxa	86	--	71	--	89	--	50	--

Table 2-14. Meiofaunal groups (top ten) ranked by density (ind. cm⁻²) and strata within the 2011 CSESP regional study.

Stratum	Taxon	Density	Stratum	Taxon	Density
South	Nematoda	22.9	Central B	Nematoda	33.4
	Harpacticoida	3.9		Harpacticoida	5.0
	Foraminifera	3.1		Foraminifera	2.7
	Ostracoda	1.0		Ostracoda	0.8
	Tanaidacea	0.5		<i>Ennucula tenuis</i>	0.6
	<i>Ennucula tenuis</i>	0.5		Bivalvia	0.5
	<i>Cossura</i> spp.	0.4		Kinorhyncha	0.3
	Bivalvia	0.3		Cirratulidae	0.3
	Cirratulidae	0.2		<i>Cossura</i> spp.	0.2
	<i>Nephtys</i> spp.	0.2		<i>Prionospio steenstrupi</i>	0.1
Central A	Nematoda	26.0	North	Nematoda	9.8
	Foraminifera	4.6		Harpacticoida	1.8
	Harpacticoida	3.4		Nemertea	1.2
	Ostracoda	0.7		Foraminifera	0.6
	Tanaidacea	0.7		<i>Ennucula tenuis</i>	0.4
	Bivalvia	0.4		Cirratulidae	0.2
	<i>Cossura</i> spp.	0.4		Ostracoda	0.2
	<i>Ennucula tenuis</i>	0.4		<i>Cossura</i> spp.	0.1
	Kinorhyncha	0.3		Bivalvia	0.1
	<i>Nephtys</i> spp.	0.1		Kinorhyncha	0.1

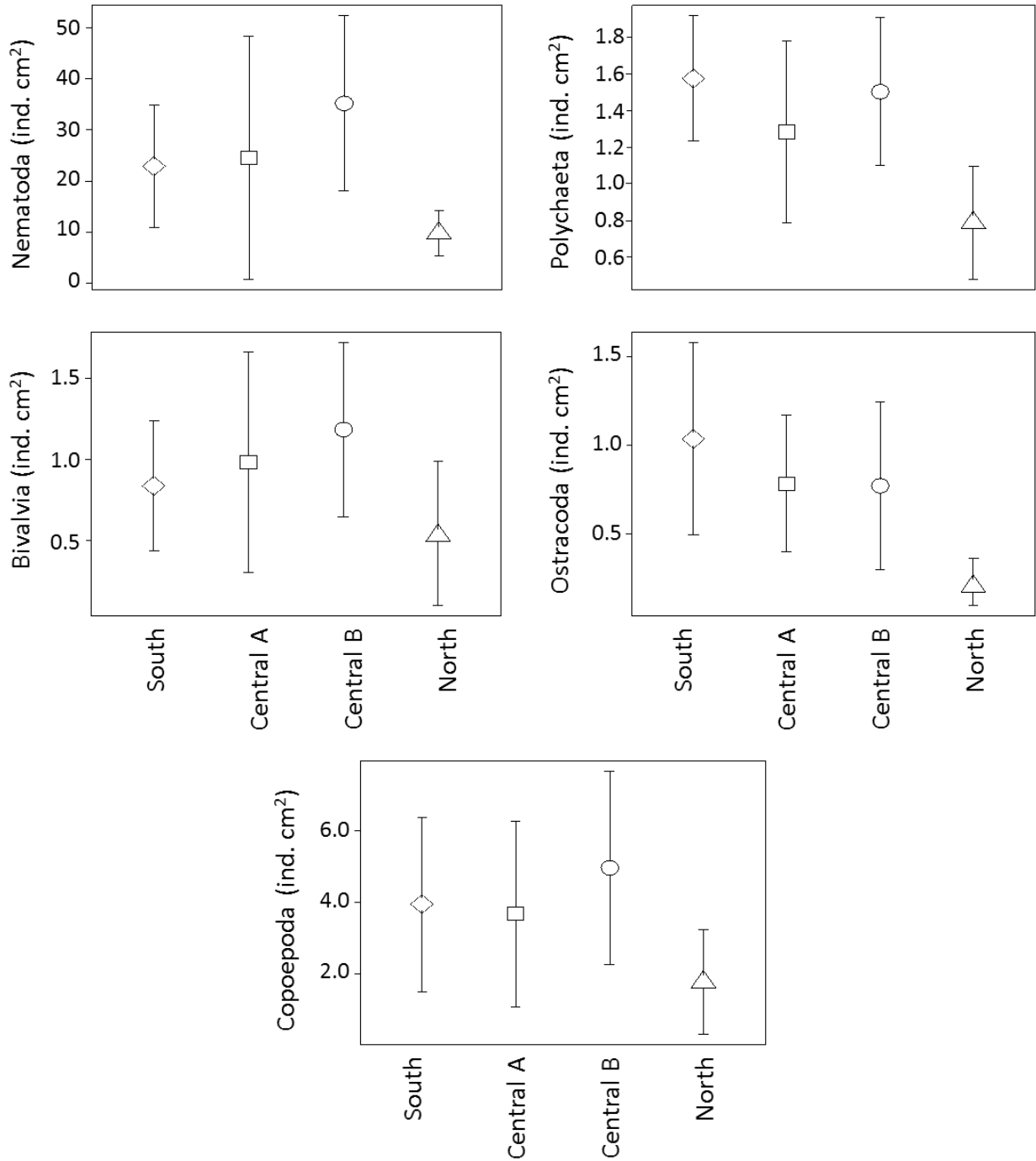


Figure 2-14. Plots of means and 95% confidence intervals by strata based on density of major meiofaunal taxonomic groups from the 2011 CSESP study.

DISCUSSION

Benthic Ecology of the Northeastern Chukchi Sea

The 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). Fauna within the study area include all major groups found in Alaskan waters and are dominated by polychaetes and bivalves (Feder et al., 1994). The high density and biomass of the communities in the study areas indicate that a large amount of seasonal production is reaching the benthos. The benthic infaunal community in Burger has higher density and biomass. Burger also has deeper water depth and a longer persistence of 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; Weingartner et al., in preparation; Blanchard et al., 2011). Feder et al., (1994) also demonstrated higher biomass for stations closest to the Burger study area related to environmental differences. The high density and biomass values in Burger (adjacent to a documented biological hot spot) presumably reflect the concentration of food resources within the sediments due to interactions of the bottom topography with water currents, as reflected in its greater depth.

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 infauna. 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; Snelgrove and Butman, 1994; Lenihan and Micheli, 2001; Bluhm and Gradinger, 2008). 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 muddy sediments indicate lower physical dynamics. Higher proportions of particulate organic carbon are found with greater percent mud (organics bind to mud) which then leads to deposit-

feeding behaviors. 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 may be driven by interactions between seafloor geomorphology and water movements. Distance from shore, increasing water depth, and declining disturbance from storms and ice gouging also contribute to measurable environmental and biological gradients. Topographic control over water current 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 infaunal communities in the northeastern Chukchi Sea include sediment grain-size, sediment organic carbon concentrations, and water mass characteristics (Feder et al., 1994; Grebmeier et al., 2006). In the present study, the Burger study area lays in a trough to the south of Hanna Shoal with Klondike stations to the southwest. Weingartner et al. (2009, 2010, and 2011) demonstrated higher water temperature and salinity values for the Klondike study area, 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 study, benthic community structure is most highly correlated with percent mud and bottom water temperature. In general, water depth is greater, bottom water temperatures colder, salinity highest, and sediments muddier where density and biomass are highest (Figs. 2-3 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.

Capturing the environmental gradients associated with the large spatial variations in dominant biological characteristics such 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* (Fig. 2-9). Similarly, data and analyses show high biomass in the Central stratum just to the east of Burger extending to the north towards Hanna Shoal and down to the Transitional stations (Fig.

2-9). The high biomass values across the central portion of the study area are due to the bivalves *Astarte borealis*, *Macoma calcaria*, and *Yoldia hyperborea* and the sipunculid worm *Golfingia margaritacea*. The MDS analysis for the regional study indicated bottom water temperature as 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 2-9).

Temporal Variability

The seasonal ice cover and influx of water from the North Pacific Ocean through the Bering Strait are major influences on the productivity of 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., Hopcroft et al., 2009). The mismatch of zooplankton community development 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 other pelagic systems such as Port Valdez, Alaska, can consume much of the primary productivity and very little phytoplankton may reach the sea floor (Blanchard et al., 2010). Patterns of seasonal production and zooplankton community development in the study area are dependent on the environmental characteristics of the water column and large, interannual differences of zooplankton density can result from environmental variations, as observed by Questel et al. (in preparation) over the study period 2008-2010. Zooplankton community composition and lower production in 2009 reflected 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 changes in melt patterns (Weingartner et al., in preparation).

Water temperature changes influence benthic communities through altering survival of pelagic larvae as well as causing 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 calcaria* in the Chukchi Sea (Pearson and Barnett, 1987;

Sirenko and Gagaev, 2007). The declines in density and diversity (number of taxon) of infaunal animals in the study area in 2010 and increases in 2011 reflect observations of change in oceanographic conditions and zooplankton communities, 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 suggests a loss of smaller, less competitive species from the community rather than the larger, multi-year animals dominating biomass. The communities returned to prior levels of density in 2011 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 infauna density in Port Valdez, Alaska, indicating that benthic communities throughout Alaska are very responsive to oceanographic variability.

Deep-dwelling Infaunal Communities

Biological factors can also be important determinants of animal/sediment interactions as the disruption of sediments by animals as they feed, build tubes, and move (bioturbation) can result in a well-mixed sediment column with reduced layering of sediments, transport of surface carbon downward, and increased water circulation and greater oxygenation at depth (Snelgrove and Butman, 1994; Lenihan and Micheli, 2001; Levin et al., 1997; Shields and Kędra, 2009). Animals associated with carbon and oxygen transport to depth in sediment include a number of abundant worms found in the northeast Chukchi Sea. Maldanid worms (e.g., *Maldane sarsi* in the current study) and a sipunculid worm *Nephasoma* sp. are shown to transport sediments and carbon between the sediment surface to a suitable feeding depth, with transport of carbon going both ways (e.g., Levin et al., 1997; Shields and Kędra, 2009). The burrows and feeding activities of burrowing animals enhance the exchange of oxygen and water-borne nutrients within sediments while at the same time the worms subduct a portion of annual primary production into their burrows (down to 25 cm in the present study). Burrowing sipunculid worms can be ecologically important by mixing the sediment column and facilitating transport of oxygen, nutrients, and organic carbon down to at least 50 cm depth (Romero-Wetzel, 1987). The

specimens of *Golfingia margaritacea* found in this study were very large measuring up to 2 cm wide and 17 cm long (~0.75 X 6.75 inches) and have a large potential for bioturbation as they were observed at depth during sampling (H. Nichols, personal observation).

Deep-dwelling infaunal organisms were sampled using a HAPS corer in 2011. The communities sampled by HAPS corer were generally similar to those sampled by van Veen grab and no additional animals were added to the overall species list by sampling down to 25 cm. A fragment of one deep-dwelling organism known as the preferred prey for walrus, the bivalve *Mya*, was captured. Large siphon holes were only rarely observed in the video investigations of the epifauna suggesting that *Mya* are not common (Chapter 3). The sipunculid worm *Golfingia margaritacea* was found with three to seven times greater biomass in the HAPS corer samples than the van Veen samples. Apparently, the van Veen grab does not adequately sample deeper-dwelling organisms and their biomass is underestimated. Activity deep in the sediment column is also suggested by the redox and chlorophyll core profiles (Appendices I and II). The redox potential depth profile curves for a number of stations demonstrate a shift from an oxidative state (positive Eh values) to a reducing state (negative Eh values) but then back to an oxidative state. Likewise, a number of chlorophyll cores demonstrate increased chlorophyll pigments at depth. Nelson et al. (1994) sampled the Chukchi Sea infauna with a box corer and found open burrows, live *G. margaritacea*, and live *Macoma* at depth (8 to 55 cm) to 35 cm deep. *Macoma* and *G. margaritacea* were common in box corer samples from the region but *Mya* was recorded infrequently.

Population Dynamics of Ennucula tenuis

The length-frequency histograms of *E. tenuis* in the present 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 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 within the middle of the 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. 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). The meiofaunal sampling connects with the *E. tenuis* histograms as very small juveniles would pass through the 1.0-mm mesh sieves used for infaunal sampling. The meiofaunal data suggests 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. The Klondike study area had smaller lengths than Burger and Statoil (Fig. 2-13). Burger and Statoil were similar. The lower medians reflect dominance of the bivalve population by smaller bivalves (new cohorts) at Klondike. The very small peaks at larger lengths in Klondike suggest either lower survival or lower recruitment rates in Klondike than Burger or Statoil. Burger and Statoil had more balanced distributions with strong peaks around 12-13.0-mm lengths (the second-year cohort). Variations in shell growth by location are common and were also identified for blue mussels in Port Valdez related to environmental conditions (Blanchard and Feder, 2000). The smaller shell lengths of recruits in Klondike reflect the distinctly different environmental conditions between the study areas.

The investigation of shell lengths was initiated following the observations of significant temporal trends in total density between Klondike and Burger (Blanchard et al., 2011). The significant drop in density, and much greater change in Burger, prompted a question. Can we see change in the growth of a dominant bivalve? In the present study, we see little change between Klondike and Burger from 2008 to 2010. In 2011, however, length-frequency histograms were dominated by juveniles of the first length cohort resulting in a 10% increase in Klondike, Burger, and Statoil of the 2-3.0-mm length class over prior years. This coincides with an increased infaunal density at all study areas in 2011 over 2010.

Only a few bivalve species have been studied in detail in Alaska including the blue mussel from Port Valdez. Mussels increase storage of energy required for reproduction in summer and these energy stores are maintained through the winter until needed (Blanchard and Feder, 1997). Reproductive tissues begin to develop in midwinter with spawning beginning as early as March and April. First spawning events are coincident with the spring bloom as energy is allocated for gamete development and release, although spawning extends throughout the

summer. Juveniles recruit to hard substrates throughout the summer when food is available in the water column. Following a fall to early winter spawning period, juvenile limpets (*Lottia persona*) settle out into benthic habitats as early as November to graze on subtidal rocks. The large numbers of juvenile *E. tenuis* in sediments in August suggest a late winter to summer spawning period (presuming pelagic larval stages) with juveniles recruiting to sediments in summer, as mussels do.

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 the age classes in the Bering Sea study were right skewed 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 observed 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, so 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 great, as occurred 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). The increase in *E. tenuis* length of 10 mm from one length cohort to the next is possible in environments with unrestricted food resources. The maximum lengths of 17 mm are 5 mm longer than the maximum observed 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 by predators in the present study whereas the

Bering Sea study suggested little predation occurred. In the presence of substantial predation in the Chukchi Sea, ages of 3–5 years seem reasonable whereas the absence of predation in the Bering Sea is suggested as allowing survival to nine years (McDonald et al., 1981). Determination of age annuli via an acetate-peel method could be a direction for further research.

Meiofauna

Meiofauna are not well-known from Alaskan waters. A few studies are available documenting seasonal and spatial trends in a glacial fjord (Jewett and Feder, 1977; Feder and Paul, 1980) but little else is published from Alaska. Meiofauna are known as possibly the most productive faunal group within sediments as they can be found in extremely high densities. Though they have low biomass, permanent meiofauna populations can reproduce and turn over quickly making them an ecologically-significant source of secondary production. Some Alaskan meiofauna are reproductively active year-round while others have distinct reproductive periods (Jewett and Feder, 1977; Feder and Paul, 1980). The summer meiofaunal population of the CSESP study area includes permanent and transitional infaunal organisms. 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). The permanent meiofauna in the study area occurred in very high densities compared to the infauna (1 to 23 ind. cm^{-2} translating to 10,000 to 230,000 ind. m^{-2} ; biomass wasn't measured in 2011).

The transitory meiofauna (juvenile infaunal organisms) included common infaunal species. The transitory meiofauna occurred at lower densities than the permanent meiofauna taxa (generally less than 1.0 ind. cm^{-2} translating to less than 10,000 ind. m^{-2}). The transitory meiofauna included juvenile *Ennucula tenuis*, polychaetes (e.g., Cirratulidae, *Cossura* sp., and *Nephtys* sp.), other bivalves, and other taxa. The presence of juvenile infauna in the meiofauna, suggests that some infaunal species are probably timing reproduction so that juveniles have settled to the bottom when seasonal production becomes available (see discussion below). Periodically, polychaete and bivalve larvae are numerous in the plankton in summer as well (Hopcroft et al., 2012).

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 infaunal assemblages of 2008–2011 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 (1994). Although average density of infauna 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 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 2008–2011 were associated with climatic variations influencing the Chukchi Sea, which likely altered larval survival and recruitment.

Deep-dwelling infaunal communities include the bivalve *Mya* and sipunculid worms. Sampling with a HAPS corer demonstrated that *Mya* are present but rare. Photographic evidence did not reveal abundant large siphon holes indicative of large *Mya* populations. Biomass estimates of *Golfingia margaritacea* are much larger in the HAPS corer samples suggesting that distributions of deep-dwelling animals are poorly estimated by sampling with the van Veen.

Meiofaunal organisms are numerous and reflect the communities observed elsewhere in Alaska. Juvenile infaunal organisms were observed. Further investigation of meiofaunal organisms in 2012 will provide greater insights into the ecology of these organisms.

Length-frequency distributions of *Ennucula tenuis* did not reflect the changes in the infaunal communities observed in 2010. Numbers of juveniles were, however, higher in 2011 than in prior years indicating a strong recruitment event/year.

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CHAPTER 3
BENTHIC ECOLOGY 2011:
Regional Examination of Benthic Community Structure

By Ann L. Knowlton and Army L. Blanchard

INTRODUCTION

Invertebrate organisms fill an enhanced ecological role in the Chukchi Sea as a result of strong linkages with primary production. The reduced numbers of water-column grazers and relatively shallow depths result in strong pelagic-benthic coupling with the large flux of unconsumed production to the benthos driving very abundant and diverse macrofaunal assemblages (Ambrose et al., 2001; Dunton et al., 2005; Grebmeier et al., 2006). Production in the Chukchi Sea is supported by the advection of nutrient-rich waters from the Bering Sea. The abundant infauna is comprised of large individuals and is a major prey resource and critical habitat for benthic-feeding marine mammals. The epifaunal communities also have important roles in ecological processes of the Chukchi Sea including consumption as prey by marine mammals, predation on the infaunal communities, and mineralization of nutrients (Lowry, et al., 1980; Feder et al., 2005, 2007; Ambrose, et al., 2001). The reduced fish communities within the Chukchi Sea, particularly the northeastern part, may allow larger roles for invertebrate epifauna to exploit resources, as compared to the Bering Sea (Feder et al., 2005). The epifaunal communities in this area may, thus, provide important top predators in the system, although the importance of epifauna to the food web in the northeast Chukchi Sea is still being investigated.

The Chukchi Sea is strongly influenced by waters derived from the Pacific Ocean entering through the Bering Strait (Weingartner et al., 2005). The northward movement of water is driven by sea-height differences between the Bering Sea to the Arctic Ocean (Weingartner et al., 2005). These water masses, the nutrient-rich Anadyr water, nutrient-poor Alaska Coastal water (ACW), and Bering Shelf water, of southern origin transport heat, nutrients, carbon, and animals to the Chukchi Sea and Arctic Ocean and are vitally important for maintenance of the ecological structure of the region (Weingartner et al., 2005; Grebmeier et al., 2006; Feder et al., 2007; Hopcroft et al., 2010, 2011). The combined effect of seasonal ice cover and the influx of water through the Bering Strait is a major influence on the productivity of the Chukchi Sea.

Melting sea ice stratifies the water column creating conditions favorable for the primary production that results in a summer bloom supported by the nutrient-rich, Bering Sea water (e.g., Hopcroft et al., 2010, 2011). The combined influences of the absence of zooplankton grazers at the onset of the bloom and shallow water depths result in much of the primary production reaching the benthos of the Chukchi Sea. The strong pelagic-benthic coupling resulting from the increased proportion of production reaching the sediments (relative to other systems) supports rich benthic communities.

ConocoPhillips (COP), Shell Exploration and Production Company (SEPCO), and Statoil USA E&P are sponsoring the multi-disciplinary Chukchi Sea Environmental Studies Program (CSESP) to establish ecological conditions for three survey areas in the northeastern Chukchi Sea 2008–2011 and their relationship to the larger surrounding area. The primary survey areas are Klondike, Burger, and Statoil, where successful lease bids were made in the February 2008 Chukchi Sea Lease Sale 193. The overall research program will provide information on physical, chemical, biological (including zooplankton and benthic ecology), and oceanographic baseline trends for the Klondike, Burger, and Statoil survey areas, as well as the regional study area established in 2011. The objective of this portion of the benthic ecology component of the CSESP is to assess species composition, and density of benthic fauna within the regional survey area with special interest in the lease sale areas, as well as examine small scale habitat and benthic community structure along one kilometer transects.

METHODS

Benthic Fauna Sampling Methods

Thirty-three stations were targeted for sampling of benthic fauna with video within the Chukchi Sea regional study area August 3-24 (WWW1102) and August 31 to October 5, 2011 (WWW1104) (Table 1-1 and Figure 3-1). Stations sampled included a subset from each of the primary study areas (Klondike, Burger, and Statoil) from prior CSESP surveys. At 21 stations, sampling only occurred at the intended station coordinates, while at 12 stations sampling occurred along a transect starting at the intended station coordinates (0 m). Sampling continued along the transect at 50, 100, 250, 500, and 1000 m distances.

A major change in sampling strategy and methodology occurred for the 2011 survey. Epifauna were sampled with a plumb-staff beam trawl from 2009 to 2010 (Blanchard et al., 2010b, 2011). In 2011 benthic fauna was sampled using a non-destructive imaging system. High definition digital video was recorded using a frame mounted camera (AOS HD1080i 1,000m Imaging System). External lights were mounted on the frame to provide illumination, including two lasers with a 10 cm separation distance to provide a size reference within the camera's field of view. At designated stations the camera was lowered to the seafloor and allowed to rest on the bottom for approximately 5 seconds before being raised a few meters off the bottom and repositioned. Ideally, 3-5 "touchdowns" were made at each station or distance along a transect before the camera was brought back up to the surface. Video footage was recorded for all bottom time and processed in the laboratory afterwards.

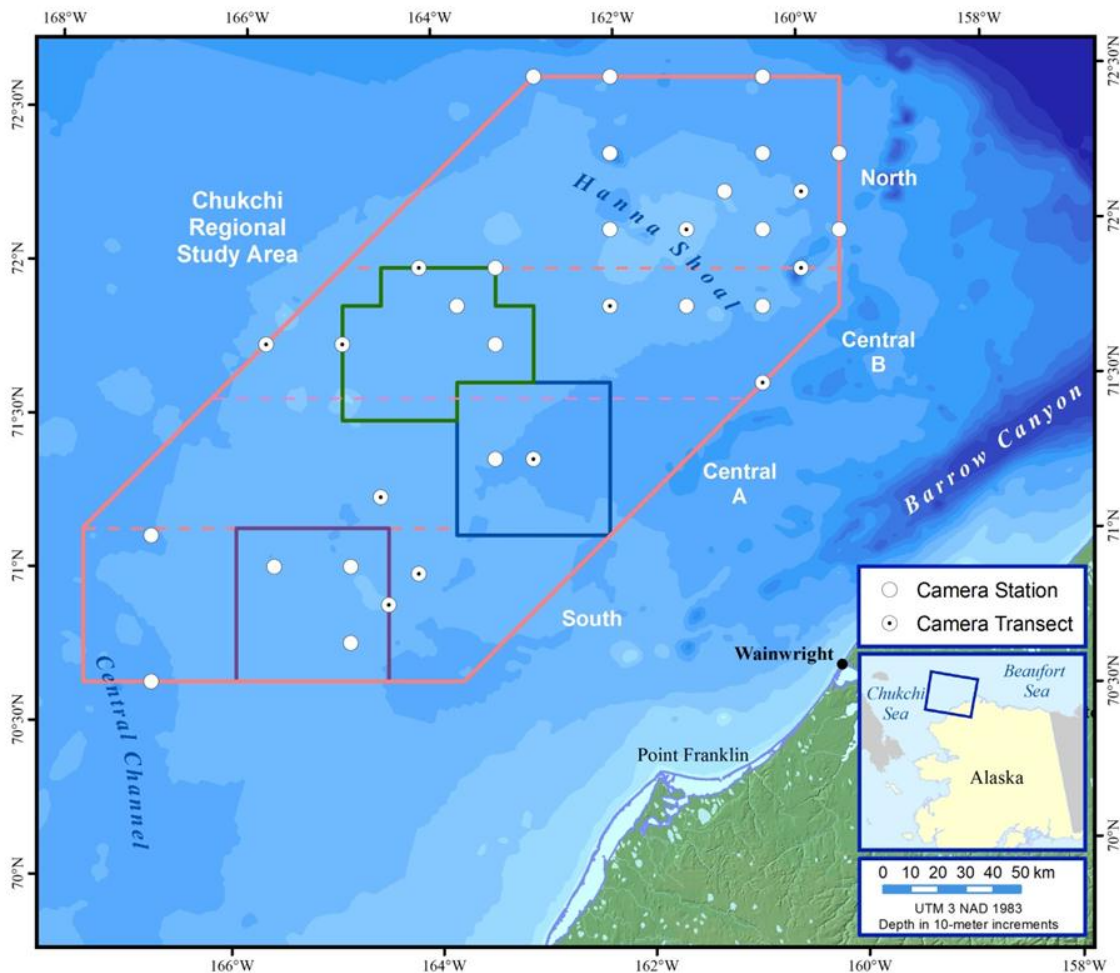


Figure 3-1. Map of camera survey stations for the 2011 CESP study.

Post-cruise processing included logging all video segments with notations on camera touchdowns, video quality, sediment type, and interesting biological observations. Still-frames were extracted from the video footage for all touchdowns using freely available software (VLC Media Player, www.videolan.org). The area of the seafloor surface imaged in each frame was measured using image analysis software (Image J, rsbweb.nih.gov/ij/) and calibrated against the known 10 cm distance separating the laser dots in each frame. A team of taxonomists analyzed the images for living organisms. Conservative identifications of all invertebrates detected were made to the lowest taxonomic level possible and counts were recorded. Most colonial organisms such as ascidiaceans, hydrozoans, bryozoans, and sponges and other hard to count invertebrates were noted for presence. A few colonial organisms that form discrete colonies and were easy to identify (e.g. *Gersemia rubiformis*, *Alcyonidium disciforme*) were given counts. Additionally, ecologically interesting and relevant observations were recorded in the dataset, such as sediment type and the presence of worm tubes.

Quality Assurance Procedures

Each frame extracted from the video footage was evaluated for suitability for further analysis (Table 3-1). General image quality was scored on a scale of 1 to 5 with higher numbers indicating a better image (Figure 3-2). Criteria included sharpness of focus or, alternately, degree of blurriness, obstruction of view (e.g. sediment clouds, deep shadows, etc.), and distance above the sediment surface. This score was determined by a single individual to maintain consistency for all images. Only images with a score of 3 or greater were included in quantitative analyses of biological communities. Data from frames that were partially obscured by a sediment cloud or deep shadow, but otherwise acceptable could be retained for quantitative analyses if (1) the sediment cloud covered less than 50% of the frame area, (2) no data were collected from anything seen through the sediment cloud, and (3) the area obscured was subtracted from the total frame area to get an adjusted frame area. Other criteria used for identifying usable frames were that no two frames could overlap in coverage of the seafloor. In the case of two overlapping images, the frame with the higher image quality score was retained. If they had the same score, the frame without sediment clouds or shadows and that had the expected frame area was chosen. If both frames were deemed equivalent for all criteria, then one frame was chosen at random to be retained for quantitative analyses. Since there was no

Table 3-1. Summary of video frame grabs by stratum based on 33 stations surveyed during the 2011 CSESP survey. Values in parentheses are standard deviations. "--" = not calculated.

	South	Central A	Central B	North	Total
Overall					
Stations	7	3	11	12	33
Transects	2	2	6	2	12
Total Frames	73	53	178	125	429
Unusable Frames	9	23	39	19	90
Usable Frames	64	30	139	106	339
Ave. Usable Frames/Station					
Stations without Transects	5.8 (1.8)	4.0 (--)	3.3 (1.5)	5.3 (1.0)	5.0 (1.5)
Stations with Transects	17.5 (3.5)	13.0 (5.7)	18.0 (8.7)	26.5 (6.4)	17.5 (3.5)
All Stations	9.1 (6.1)	10.0 (6.6)	12.6 (10.1)	8.8 (8.5)	9.1 (6.1)
Ave. Image Quality	4.2 (1.0)	2.8 (0.9)	3.4 (1.1)	4.0 (1.2)	3.7 (1.2)
Obscured Frames	5	5	21	15	46
Ave. % Area Obscured/Frame	20.3 (5.8)	31.7 (24.4)	33.3 (26.1)	29.9 (24.1)	30.6 (23.6)
Usable Frames Only					
Area Imaged (m ²)	10.79	5.89	22.24	16.73	55.66
Ave. Area/Frame (m ²)	0.17 (0.03)	0.20 (0.09)	0.16 (0.11)	0.16 (0.02)	0.16 (0.08)

minimum defined separation distance between frames, two adjacent, but not overlapping, frames would both be included in analyses.

Identification of organisms was performed by a team of three senior scientists, including two senior taxonomists. A consensus of all three was needed on identifications. This led to a highly conservative approach with many identifications left at higher taxonomic levels than in previous years. Three categories for unidentifiable organisms were included in order to capture the overall density of organisms in the video survey in spite of not being able to classify them

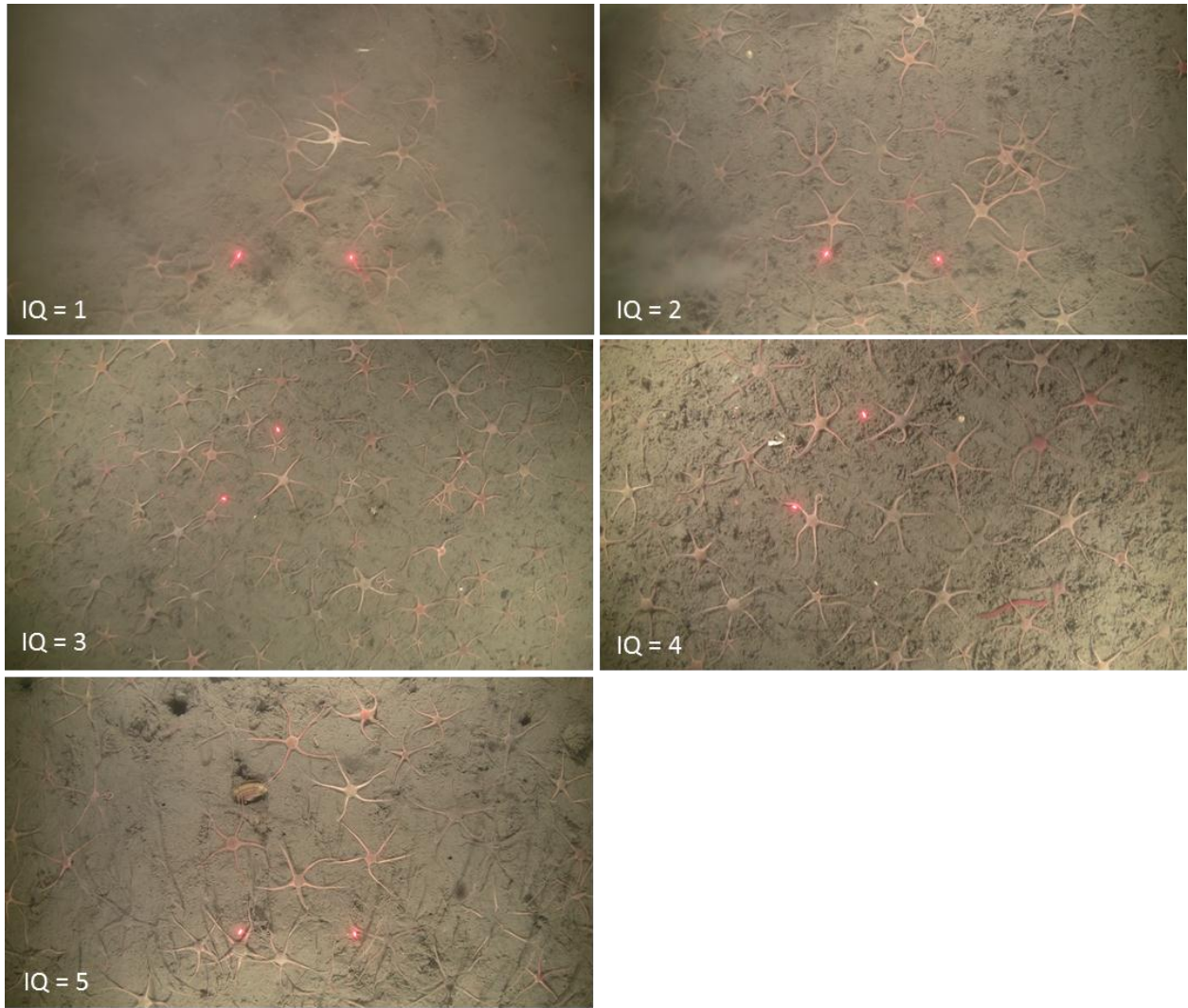


Figure 3-2. Example photos of each image quality (IQ) score used for determining usability of still photos for data analyses. Photos from similar habitats were specifically chosen to reduce perceived influences caused by habitat and community composition differences.

taxonomically. These categories were “Unidentified Animal” for discrete individuals, “Unidentified Colony” for colonial or hard to count organisms, and “Unidentified” for organisms where it could not be determined if they were discrete individuals or colonies. Variable video quality, and therefore variable still frame quality, contributed to the conservative approach. The original video footage was used in tandem with extracted still frames since movement of individuals and multiple perspectives became important factors in making identifications.

Descriptive summaries of the data provide insights into survey area variability and include sediment characteristics and average density.

RESULTS

Analysis of the 2011 Video Data

Environmental characteristics of the regional strata showed greater variability in sediment characteristics in the South and North than in Central A or B (Table 3-2). The South stratum had predominantly mud interspersed with gravel and rock, while the North had sand and mud with coarser sediments occurring or mixed in at lower frequencies. Average water depth was similar between all regions with Central A being the deepest and least variable. The North stratum was most variable with respect to water depth, having both the deepest and shallowest stations (HN028, 48.7 m; HN005, 27.3 m, respectively).

Benthic fauna in the regional study area were identified to 54 taxonomic categories (Appendix V). Most categories were at the family level. A few highly recognizable taxa were identified to genus or species. Average density ranged from 342.6 individuals per m² in Central A to 30.3 individuals in Central B (Table 3-2). The total number of taxonomic categories ranged from 17 in the Central B stratum to 42 in the South (Table 3-2). The dominant taxa for South were brittle stars, shrimps, and amphipods (Table 3-3). Central A was dominated by brittle stars, shrimp, and unidentified epifaunal animals. Brittle stars, amphipods, and polychaete worms were the dominant groups in Central B, while brittle stars, polychaete worms, and amphipods dominated North (Table 3-3). Taxa common to all strata included brittle stars, shrimps, amphipods, and polychaete worms. Brittle stars occurred at high densities in Central A and present in moderate and low densities in the other three regions (Fig. 3-3). A high density of brittle stars seemed to exclude the presence of amphipods and shrimps, while moderate or low

densities did not (Fig. 3-3). Polychaete worms were present in high densities when brittle stars were in low densities (Fig. 3-3).

Table 3-2. Regional summary of environmental and biological characteristics from photographic sampling of benthos during the 2011 CSESP survey. Values in parentheses are standard deviations.

	South	Central A	Central B	North	Overall
% Frequency Sediment Types					
Mud	83	100	96	61	83
Sand	0	0	0	25	8
Gravel	1	0	0	1	1
Sand/Mud	0	0	4	4	3
Gravel/Mud	11	0	0	8	4
Rock/Mud	5	0	0	1	1
Ave. Depth (m)	39.0 (3.6)	43.1 (0.6)	40.2 (3.7)	37.6 (7.3)	39.4 (5.1)
Ave. Density (ind. m ⁻²)	159.8 (206.4)	342.6 (154.5)	30.3 (29.9)	46.3 (33.8)	84.2 (144.3)
# Taxa	42	17	32	22	54

Table 3-3. Regional ranking of benthic faunal groups (top 10) by average density (ind. m⁻²).

Stratum	Taxon Group	Ave. density
South	Ophiuroidea	63.0
	Caridea	7.3
	Amphipoda	3.1
	Unidentified epifauna	2.5
	Hydrozoa/Bryozoa complex 1	1.5
	Unidentified animal epifauna	1.3
	Paguridae	1.2
	<i>Gersemia rubiformis</i>	0.6
	Hydrozoa/Bryozoa complex 2	0.6
	Unidentified animal infauna	0.5
Central A	Ophiuroidea	262.6
	Caridea	3.1
	Unidentified animal epifauna	1.9
	Amphipoda	1.8
	Echinodermata	0.7
	<i>Gersemia rubiformis</i>	0.5
	Asteroidea	0.4
	Unidentified animal infauna	0.4
	Actinaria	0.4
	Unidentified epifauna	0.4
Central B	Ophiuroidea	6.2
	Amphipoda	4.2
	Polychaeta	4.2
	Caridea	2.4
	Unidentified animal epifauna	1.1
	Unidentified animal infauna	0.7
	Paguridae	0.7
	Hydrozoa/Bryozoa complex 1	0.6
	Unidentified epifauna	0.6
	Actinaria	0.5
North	Ophiuroidea	7.2
	Polychaeta	5.1
	Amphipoda	3.8
	<i>Alcyonidium disciforme</i>	2.5
	Caridea	2.4
	Unidentified animal epifauna	1.4
	Unidentified animal infauna	1.4
	Actinaria	1.0
	Paguridae	0.5
	Actiniidae	0.4

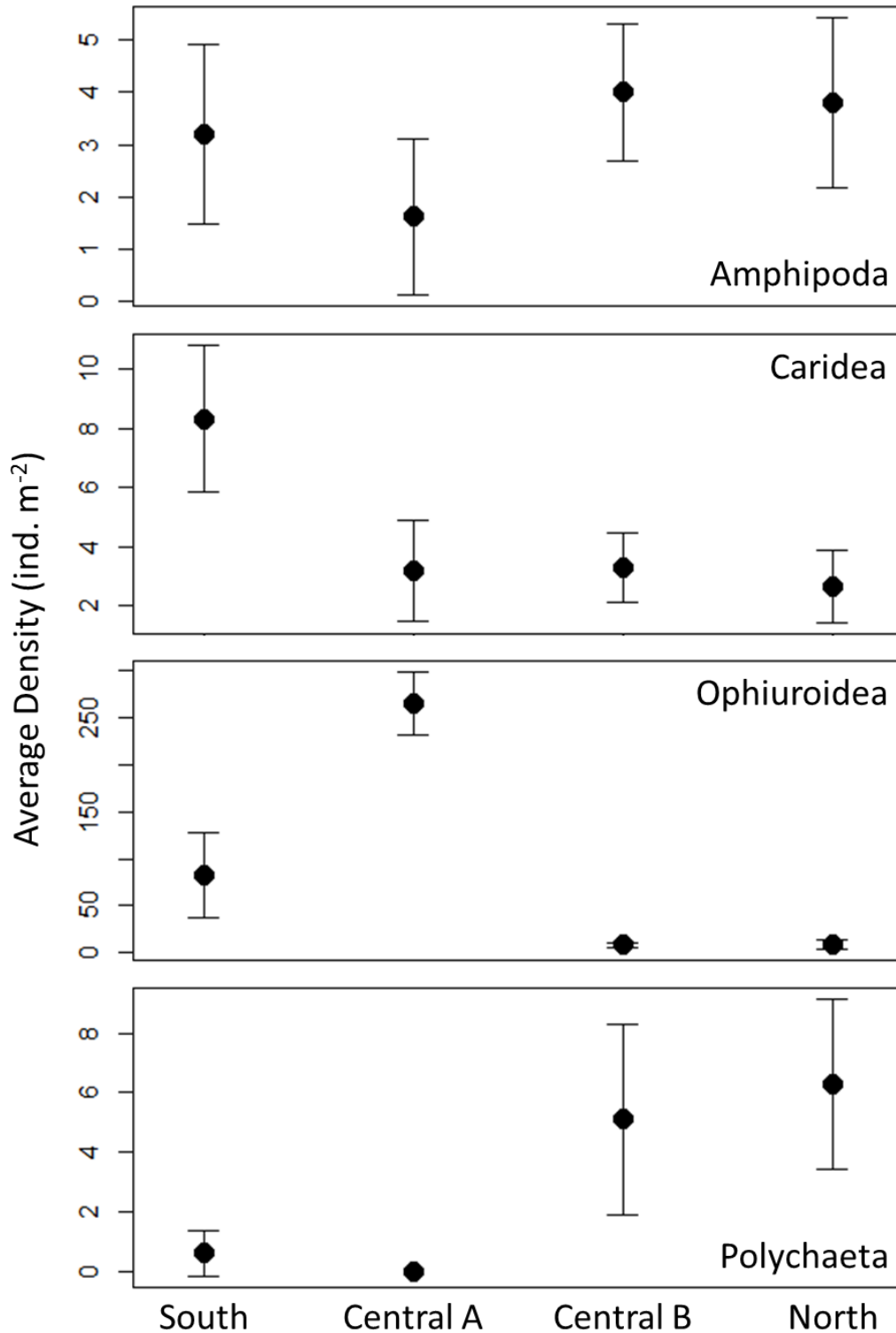


Figure 3-3. Average density of dominant taxa by stratum for 2011 CSESP epifauna sampling. Amphipoda (amphipods), Caridea (shrimps), Ophiuroidea (brittle stars), and Polychaeta (polychaete worms) were selected because they were present in all regions.

Video Transects

Environmental parameters measured along one kilometer transects included water depth and sediment type (Table 3-4). Within an individual transect water depth showed little variation. The transect at HN005 had the greatest depth variation with an approximately 2 m rise at the 500 m site along the transect (Appendix VI). All other water depth measurements along this transect were within 0.3 m. Sediment variations were most evident in the North transect, with moderate variation in the South transect and generally homogenous sediment types for the Central A and Central B transects (Table 3-4). One exception to the trend was found at HC032 where the substrate type at 0m was different than at all other transect distances, causing all frames from 50-1000m to be marked as habitat deviations. If looked at from the other direction (i.e. starting at 1000m), the habitat changes would be 16%.

Biological characteristics along each transect generally followed the patterns of the regional biological characteristics with highest densities found along the Central A transects (BF013) and greatest number of taxa found along the South transect (KF015) (Table 3-2, 3-4). The number of taxonomic categories varied more between the Central B transects than within the other strata (Table 3-4). Central B and North transects consistently had lower densities of benthic fauna (Table 3-4).

Table 3-4. Summary of environmental and biological variations along video transects in the northeastern Chukchi Sea collected during the 2011 CSESP. Habitat changes were determined by the percentage of frames along a transect that deviated from the dominant substrate type found at 0 meters. Values in parentheses are standard deviations. “na” = data not available.

	Habitat Changes from 0m (%)	Ave. Depth (m)	# Taxa	Ave. Density (ind. m ⁻²)
South				
KF015	25	36.3 (0.2)	28	41.4 (24.8)
TF001	0	40.1 (0.1)	16	263.6 (53.1)
Central A				
BF013	0	na	12	317.6 (43.8)
TF003	0	43.4 (0.0)	8	239.4 (53.1)
Central B				
HC012	0	40.7 (0.1)	3	6.3 (0.2)
HC020	0	47.5 (0.1)	9	36.7 (20.2)
HC025	0	40.0 (0.1)	25	23.4 (6.8)
HC032	84	36.7 (0.2)	21	47.4 (11.1)
SF007	0	38.1 (0.1)	11	9.7 (4.0)
SF020	0	37.2 (0.0)	12	11.2 (5.7)
North				
HN005	35	27.3 (0.8)	11	22.4 (5.5)
HN013	5	42.3 (0.3)	16	23.8 (7.1)

DISCUSSION

Benthic Fauna of the CSESP Regional Study Area

Videographic surveys of the CSESP regional study area in 2011 resulted in similar conclusions regarding habitat and community composition as in prior years. The benthic fauna are representative of mixed Arctic and northern Pacific benthic assemblages found throughout the Bering and Chukchi seas (Feder et al., 1994b, 2005, 2007; Blanchard et al., 2010a). Brittle stars, primarily *Ophiura sarsi*, were dominant components of the benthos in all survey areas in the present study, consistent with observations by Feder et al. (1994b), Ambrose et al. (2001), and Bluhm et al. (2009). The dominance of echinoderms in the Chukchi Sea increases with latitude relative to crustaceans and fishes such that the dominant echinoderms switch from sea stars in the southeastern Chukchi Sea to brittle stars in the north, possibly resulting from a lack of predation on brittle stars by flatfishes and large *Chionoecetes opilio* (present in southern waters) in the north (Feder et al., 1994b; Feder et al., 2007; Bluhm et al., 2009). Shrimps and amphipods were the next most common taxa, and were overall a small proportion of the benthic community compared to brittle stars, although variability between strata regions exists. Most benthic species were common within all strata although species compositions shifted with region-specific habitat characteristics. The north Pacific benthic species are maintained in the areas by the transport of larvae north with the movement of water which is established because of the pressure gradient from the Bering Sea to the Arctic Ocean (Weingartner et al., 2005; Feder et al., 2005). The movement of species northward does come at a cost for some species such as the snow crab, *C. opilio*, which are reduced in size relative to populations in southern waters due to physiological growth limits in cold water (Bluhm et al., 2009). In spite of the colder water, however, benthic communities in the northeast Chukchi Sea are diverse and large animals were abundant.

The high density of benthic communities in the Chukchi Sea result from the high productivity in the nutrient-rich waters from the Gulf of Anadyr and Bering Sea (Grebmeier et al., 2006; Sirenko and Gagaev, 2007; Bluhm et al., 2009). The shallow water depths, lack of pelagic consumers, transport of nutrients from the Bering Sea, and seasonal ice cover results in tight pelagic-benthic coupling in the Chukchi Sea. Feder et al. (1994b) also indicated that the transport of POC-rich water from the Bering Sea supplements local primary production thereby providing year-round availability of carbon and a persistent food source for benthic communities in the northeast Chukchi Sea. Extremely high density values have been identified in areas with

gyres resulting from the concentration of nutrients and food resources for benthic-feeding animals (Feder et al., 1994b; Grebmeier et al., 2006; Sirenko and Gagaev, 2007). The benthic faunal density of the CSESP study was comparable to values found by Bluhm et al. (2009) although values in the Burger survey area were even higher than those recorded earlier. The extremely high densities of brittle stars in the muddy Central A stratum are consistent with the increased biomass of infaunal organisms found there resulting from the deposition of fine sediments and organics (Grebmeier et al., 1988; Feder et al., 1994a and b; Feder et al., 2007). Brittle stars are common worldwide and they can dominate epibenthic communities in various habitats including some polar shelves (Piepenburg and von Juterzenka, 1994; Piepenburg and Schmid, 1996; 1997; Piepenburg et al., 1997, Starmans et al., 1999; Ambrose et al., 2001). Overall, the density of benthic invertebrates in the northeast Chukchi Sea shown in this project were within the ranges reported for other Arctic shelf areas (Piepenburg and Schmid, 1996; 1997; Starmans et al., 1999).

The 2011 CSESP video survey provided continued support for the conclusion of variable benthic communities previously described by this project for the South, Central A, and Central B strata (Blanchard et al., 2010b, 2011). The benthic communities were dominated by a few organisms (brittle stars, shrimps (Caridea)) with brittle star density particularly high in the Central A stratum (Burger) (Table 3-3). The North stratum (Hanna Shoal area) was dominated by brittle stars, shrimps and amphipods, plus the bryozoan *Alcyonidium disciforme* which was rarely observed elsewhere. Overall, the variations in biological characteristics reflected environmental differences. The South stratum had variable sediment characteristics that ranged from expanses of mud inhabited by few benthic organisms to rocky patches that supported a broad array of upright epifauna. Central A contained primarily muddy habitat dominated by brittle stars, while Central B was muddy but supported a different, and lower density, soft sediment community. The expansion of the CSESP study area northward around Hanna Shoal added a new region. The North stratum included sandy habitats that were as variable as seen in the South stratum, with communities of slightly different composition and density.

Small spatial scale variability in density and community structure were investigated along one kilometer transects within each stratum. Habitat variability changed depending on stratum. Central A and Central B showed no little to no habitat variability and correspondingly little variation in benthic community composition. The South and North regions showed greater

habitat variability and a greater variability in benthic community composition. As concluded in prior years, a connection between underlying mechanisms structuring a habitat and the organisms that live there is evident.

Comparison of Benthic Sampling Methods

Sampling methods and devices vary in their abilities to reliably capture representative samples of biological communities. A comparison of three benthic sampling methods employed during the CSESP program highlights some of the differences (Table 3-5). While infaunal organisms were the target groups for sampling with the van Veen grab, epifaunal organisms were sampled as by-catch. The beam trawl specifically targeted epifauna, while the camera captured epifauna and elements of the infaunal community. Area of the seafloor sampled by each device

Table 3-5. Comparison of average density of dominant benthic fauna within each lease sale area obtained by three sampling methods used during the 2008–2011 CSESP surveys. All density values have been scaled to individuals per square meter.

Area	Faunal Group	van Veen Grab	Beam Trawl	Camera
Klondike	Brittle Stars	55.0	17.0	5.9
	Crabs	0.9	0.4	0.9
	Hermit Crabs	5.5	0.0	0.9
	Shrimps	0.3	2.1	9.0
	Snails	3.2	0.4	0.4
Burger	Brittle Stars	285.8	86.1	313.2
	Crabs	0.6	0.5	0.0
	Hermit Crabs	0.4	0.0	0.0
	Sea Cucumbers	24.6	3.1	0.2
	Shrimps	0.6	1.9	1.0
	Snails	2.6	3.5	0.0
Statoil	Barnacles	2.3	0.7	0.0
	Brittle Stars	34.4	12.4	1.8
	Crabs	0.5	0.2	0.1
	Hermit Crabs	0.3	0.0	0.3
	Sea Cucumbers	4.7	0.3	0.0
	Shrimps	1.1	0.9	1.1
	Snails	1.4	0.7	0.0

varied. The van Veen grab and the camera sampled on similar spatial scales (0.1 m² and 0.18 m², respectively) while the beam trawl sampled a much larger area of seafloor (on the order of 1000 m²).

The ability and efficiency of a sampling device to catch a particular type of organism depends on factors including mesh size relative to organism size, method and speed at which devices are deployed, suitability of the sampling device for the substrate being sampled, and relative mobility and patchiness of target organisms. Based on CSESP data, the sampling method employed during the 2011 study is generally comparable to other sampling methods. In general, the camera and van Veen grab provide somewhat similar results, though the van Veen grab gives higher estimates for the density of brittle stars in some cases. When brittle stars occur in high densities, beam trawls underestimate population densities, likely due to escape of small individual through the mesh and breakage of individuals. In general, the beam trawl tends to miss or under estimate smaller epifaunal organisms, suggesting that it might be better to rely upon data from the van Veen grab or camera for these groups. Larger colonies that are often not sampled by the van Veen grab are captured by both the camera and the beam trawl. The beam trawl is much more useful for documenting diversity of the broadly scattered, upright epifaunal communities.

CONCLUSIONS

Benthic communities in the CSESP Regional study area reflect the high production in the nutrient-rich water and short food chains in the relatively shallow water of the Chukchi Sea (Grebmeier et al., 2006). Although the density of benthic fauna was higher in Central A than in the South, Central B, or North strata, the assemblages in all regions were similar (containing most of the same species). Small scale variability of habitat and benthic faunal density along one kilometer transects reflected trends similar to within-stratum variation. Environmental gradients were associated with trends in benthic community structure reflecting associations of benthos with food supply, oceanographic conditions, and physical characteristics of the study area. As seen in past years, the benthic invertebrate communities appear to be largely structured by the environmental variables associated with the geologic structure and covarying with other environmental gradients and oceanographic characteristics.

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CHAPTER 4
BENTHIC ECOLOGY 2011:
Food Web Analysis of Benthic Communities in the Northeastern Chukchi Sea

By Kelley Tu and Arny L. Blanchard

INTRODUCTION

The Chukchi Sea shelf is highly productive with high density and benthic faunal biomass (Grebmeier et al., 2006). Although numerous publications are available for the southern Chukchi Sea, less research has been published from the northeastern Chukchi Sea. The few investigations available generally found that the characteristics and distributions of benthic macrofauna and megafauna in the northeastern Chukchi Sea were associated with sediment characteristics, as proxies for larger environmental features (Stoker, 1978; Grebmeier et al., 1989 and 2006; Feder et al., 1994a; Bluhm et al., 2010). The high standing stock of the benthos was partially attributed to particulate organic carbon (POC) advected into the area from the highly productive northern Bering and southern Chukchi seas, thereby supplementing locally available carbon (Grebmeier et al., 2006). Results from the 2008–2011 Chukchi Sea Environmental Studies Program (CSESP) corresponded with these findings as benthic faunal assemblages were diverse and robust, reflecting the high productivity in the area (Blanchard et al., 2011; this report). The latter study also found significant faunal variability associated with landscape-scale environmental gradients that altered processes delivering carbon to the benthos.

Benthic fauna play a large role in food webs and ecosystem functions in the Arctic due to tight pelagic-benthic coupling (Iken et al., 2010). The high density and biomass of benthic fauna provide an abundant food resource for top trophic levels, including marine mammals, which feed directly on primary consumers on many arctic shelves (Dehn et al., 2007). Relatively little research has been conducted, however, on benthic food-web structure in the Chukchi Sea and scales of variability in food-web structure of the region have not been well documented (Iken et al., 2010). Dunton et al. (1989) assessed isotopic gradients in plankton through analysis of benthic fauna from the eastern Beaufort, Chukchi, and Bering seas and found that trophic relationships were similar although there was considerable variability in carbon isotopic signatures. Feder et al. (2011) examined isotope feeding guild positions across the Chukchi

Shelf, Chukchi Bight and Kotzebue Sound and found few ecologically-significant differences between sites, although some variability within each region was related to differing sources of carbon and levels of terrestrial inputs. At a slightly larger scale, tissue isotope measurements in food-web analyses in the southern Chukchi Sea vary at the regional scale due to water mass characteristics (Iken et al., 2010). The role of benthic fauna in food webs of the northeastern Chukchi Sea is poorly described. The effect of small-scale environmental variations on food webs has not been evaluated in this region either.

The Chukchi Sea Environmental Studies Program (CSESP) is a multi-disciplinary research project with the aim of understanding the ecology of the northeastern Chukchi Sea. The CSESP includes nine disciplines encompassing bird and mammal distributions, oceanographic characteristics, and benthic ecology. Sampling has occurred over a four-year period at the Klondike, Burger, and Statoil sites (2010 and 2011 only), and across the regional scale of Hanna Shoal (2011 only). Ecological information from the CSESP research in the northeastern Chukchi Sea will be used to provide a baseline prior to potential gas and oil exploration activities in the area. The CSESP will provide insights on scales appropriate for understanding the ecology of benthic organisms and their interactions with the physical characteristics of the study area. The 2008–2011 CSESP provides an important opportunity to assess food-web structure of the northeastern Chukchi Sea in detail by examining and comparing food webs at a much higher resolution than previous, broadly-focused studies in the U.S. Arctic.

The purpose of this component of the CSESP is to determine and compare food webs of the Klondike, Burger, and Statoil study areas using stable isotope techniques. The 2008–2011 CSESP included sampling of infauna (smaller invertebrates living within the sediments) and epifauna (larger invertebrates living on the sediment surface) for determination of community structure and the factors associated with spatial and temporal variations. The present study fills in gaps in the CSESP benthic ecology studies by providing detailed isotopic determinations of both infaunal and epifaunal organisms from the Klondike, Burger, and Statoil study areas, and several stations in the Central and North strata of the 2011 Chukchi regional study area, to document the food-web structure within the region. Elucidating food-web structure will provide useful information when predicting the effects of environmental change in the northeastern Chukchi Sea. Ecologically-significant community-level differences were observed in the benthic ecology component of the CSESP related to physical qualities of the study area (spatial

variability) and annual differences in oceanographic characteristics (temporal variability) (Blanchard et al., 2011; Chapter 2). The strong variations in faunal characteristics between the study areas resulting from differences in physical and oceanographic characteristics may be reflected in benthic food webs. We hypothesize that there are differences between food webs of the three study areas in regards to structure, carbon transfer and variability, and linkages between major feeding guilds. To evaluate the hypothesis, data on sediment isotopic determinations from sediments, particulate organic carbon, and benthic animal tissues were measured to determine patterns in diets of benthic animals. Diet patterns were then compared between study areas to assess small-scale differences.

METHODS

Stable Isotopes in Ecology and Food Webs

Stable isotope analysis is a commonly used tool in food-web studies that provides a deeper look into an organism's diet, reflecting feeding patterns older than what has been recently consumed by the animal (Peterson and Fry, 1987; Iken et al., 2005) and can provide information on the trophic level (position within the food web) of the organism (Hobson and Welch, 1992). It is especially useful in situations where feeding observations are not possible, or stomach contents do not provide adequate dietary information. Stable isotope analyses for food-web determinations rely on two naturally occurring isotope ratios, denoted as $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$. These measurements are the ratio of the heavy isotope to the light isotope in a given material, with respect to internationally recognized standards (Fry, 2006). The carbon isotope, ^{13}C , has one extra proton relative to the normal carbon atom (^{12}C) and the nitrogen isotope, ^{15}N , has one extra proton relative to the normal nitrogen atom (^{14}N). As a general rule, the heavier isotope tends to accumulate in animals because the lighter isotope will react faster in kinetic reactions (Fry, 2006) and can be excreted more quickly than the heavier isotope. This difference in isotope behavior is called fractionation, and is essentially the separation of heavy and light isotopes through natural processes (Fry, 2006). Fractionation causes a differential distribution of the heavy and light isotopes in nature through biological processes and is the basis of stable isotope ecology. As organisms consume other animals from the trophic levels below them, fractionation results in the progressive accumulation of heavier isotopes in animals. Thus, fractionation of carbon and

nitrogen isotopes provides the basis for evaluating the position of an animal within a food web, and identifying primary production base carbon entering the food web.

Carbon and nitrogen stable isotopes are equally important when examining food webs because they each reveal something different about an organism's behavior. An animal's carbon isotopic composition will be similar to its dietary carbon (a small fractionation), but the animal will have a heavier nitrogen isotopic composition (a larger fractionation) than its dietary nitrogen (Peterson and Fry, 1987). Thus, carbon isotope measurements can be linked to carbon sources that an animal feeds upon and are useful for examining carbon flow through a system. For example, one can determine from analysis of the carbon isotopes whether an animal is feeding on marine or terrestrial food sources. Carbon isotopes can still be used as indicators of feeding (trophic) level in a food web as a 1.5‰ increase in $\delta^{13}\text{C}$ has been shown to indicate an increase in one trophic level in food webs of the Bering Sea (McConnaughey and McRoy, 1979). Nitrogen isotopes, however, are more widely used as indicators of trophic level because consumers will consistently have a higher ratio of the heavy nitrogen isotope to the lighter nitrogen isotope in relation to their food source than carbon isotopes. A 3–4‰ increase in $\delta^{15}\text{N}$ values indicates an increase in one trophic level (e.g., from a primary consumer to a predator of a primary consumer) making trophic level determinations easier, as compared to the smaller changes in the carbon isotopes (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Fry, 1988).

Sampling and Laboratory Methods

Invertebrate samples were collected during the 2009–2011 CSESP sampling cruises for isotopic analyses (Fig. 4-1). Samples of infauna were collected in the field using a double van Veen grab. Grabs were rinsed through 1.0-mm mesh screens and remaining organisms and debris were collected into jars and frozen for transport to the lab. Epifauna were collected by beam trawls during 2009 and 2010 cruises. Epifauna were sorted, identified to genus and species when possible, placed into labeled WhirlPak bags, and frozen for transport to the lab. Whole organisms were partially thawed in the laboratory, rinsed to remove debris, and then freeze-dried. Freezing and freeze-drying do not significantly alter sample isotope compositions (Bosley and Wainwright, 1999; Barrow et al., 2008). Multiple organisms were composited for isotopic analysis when single individuals were too small to provide sufficient mass for processing. Stable

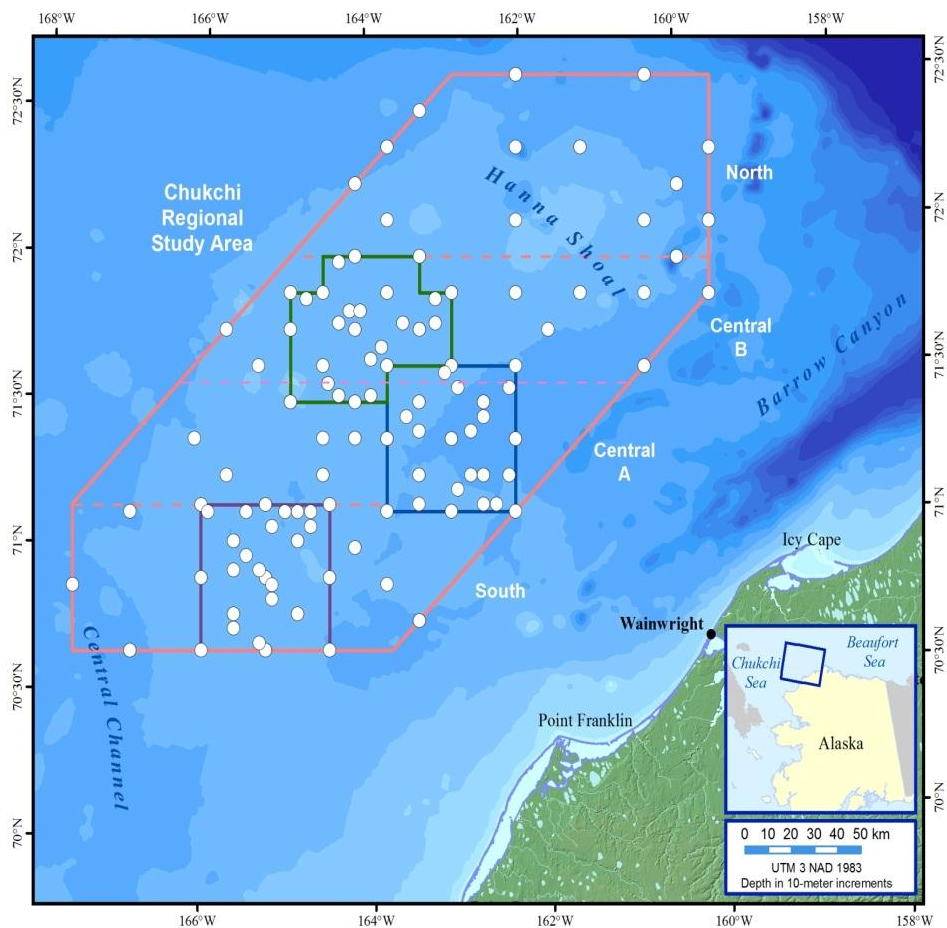


Figure 4-1. Map of stable isotope sampling locations in the northeastern Chukchi Sea, 2009–2011.

isotope measurements can be biased depending on tissue type due to differences in tissue turnover rates, therefore freeze-dried samples were prepared for isotope analysis using whole animals to obtain an average isotope signature for all tissues, regardless of turnover rates (Peterson and Fry, 1987; Michener and Lajtha, 2007). All samples large enough to yield sufficient mass for processing were homogenized with mortar and pestle in preparation for stable isotope analysis. Individuals that were too small were processed whole.

Carbonaceous material was digested by soaking homogenized organisms with 1 N hydrochloric acid (HCl) until bubbling ceased (Iken et al., 2010) to eliminate the bias that carbonate material has on carbon isotope measurements. Carbonate has a $\delta^{13}\text{C}$ measurement of 0‰ and will bias carbon isotope measurements towards 0 if it is not removed. Samples were rinsed with deionized water until the solvent tested neutral on litmus strips, indicating complete

removal of HCl which would also bias isotope measurements. Solvent was siphoned off by pipet and samples were frozen and then freeze-dried to remove all remaining solvent. Acidification has no significant effect on $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values (Bosley and Wainwright, 1999).

Following digestion in HCl, lipids were removed from the tissues to eliminate bias that the fats have on carbon isotope determinations. Lipids are generally 6‰ more negative in their $\delta^{13}\text{C}$ measurements than tissues, and can bias carbon isotope measurements. Most lipid extractions in published studies use a combination of chloroform and methanol, as was used in the present study (Newsome et al., 2010). Lipid extraction was performed by soaking organisms in a 2:1 chloroform-methanol solution. Each sample was subjected to a minimum of three 24 hour soaks, with as many additional soaks as needed until a clear solvent was observed (indicating that all lipids had been removed). Solvent was siphoned off by pipet. Samples were frozen and then freeze-dried to remove all remaining solvent. Once the lipid extraction was completed, a 0.1–0.5 mg subsample from each organism was weighed into tin capsules for stable isotope analysis.

There are conflicting views on whether or not lipid extraction is a suitable method for removing the lipid bias in food-web analyses. Mintenbeck et al. (2008) found that lipid extraction had an effect on $\delta^{15}\text{N}$ measurements in fish muscle tissue, which makes it undesirable for nitrogen isotope analyses. Graeve et al. (1997) found that lipid content was low in Arctic shelf benthic taxa, suggesting it may not be necessary to lipid extract. A subset of 29 taxa, encompassing various benthic and epibenthic fauna were used for a lipid extracted vs. non-lipid extracted comparison. Taxa were prepared with acidification as outlined above. Samples were split at the lipid extraction phase and only half of each individual was lipid extracted. Stable isotope analysis was performed and a comparison was made between lipid extracted and non-lipid extracted values to see if this type of preparation had any effect on $\delta^{15}\text{N}$ measurements. Comparisons were made using a paired t-test, which showed there was a significant difference between lipid-extracted and non-lipid-extracted samples ($p = 0.001$) but the mean difference between the two treatments was 0.6‰, not high enough to be considered biologically relevant (< 1‰). Samples were lipid extracted throughout the remainder of this study due to the fact that although lipid content is low in Arctic shelf benthic taxa, it is variable between taxa and within the same species, and may be influenced by diet (Graeve et al., 1997).

Filters with particulate organic matter (POM) collected in 2010 from the chlorophyll maximum layer of the water column were oven-dried and acid-fumed (equivalent to acidification as outlined above) in a vacuum chamber prior to stable isotope analysis (Iken et al., 2010). One third to one half of the top layer of the POM filters was scraped off and weighed into tin capsules for stable isotope analysis.

Frozen sediment samples from CSESP 2009 and 2010 cruises were available for stable isotope analysis. Sediment samples were acidified with rinses of HCl until bubbling ceased. Samples were then frozen and freeze-dried. A 13–17 mg subsample of each was weighed into tin capsules for stable isotope analysis.

Samples were analyzed for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) tissue isotopes at the Alaska Stable Isotope Facility (ASIF), University of Alaska, Fairbanks. All analyses were performed using a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with Pee-Dee Belemnite (PDB) and atmospheric nitrogen (N_2) as standards for carbon and nitrogen isotope measurements, respectively. Sample isotope ratios are expressed in standard δ notation in parts per mil (‰) using the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N , and R is the corresponding isotopic ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Instrument error was determined by running a peptone standard every 10 samples, with three standards at the beginning of every run. Average instrument error was 0.10‰ for $\delta^{13}\text{C}$ and 0.18‰ for $\delta^{15}\text{N}$. Analysis of stable isotope data for food-web determinations relies largely on graphical presentations to document the spread of the values with respect to the expected one and three-step changes in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, respectively, for changes in trophic levels. Isotope values for primary production carbon sources entering the food web (also referred to as endmembers and including phytoplankton, deposited material on surface sediments, and ice algae), are plotted with the animal tissues. With $\delta^{13}\text{C}$ values plotted on the x-axis against $\delta^{15}\text{N}$ values on the y-axis, the expected spread of values can be expressed by a linear relationship correlated to the 1.5‰ $\delta^{13}\text{C}$ increase and 3–4‰ $\delta^{15}\text{N}$ increase that occurs from food source to the consumer and therefore the best-fit line should have a slope of 2 to 2.7 ($\Delta\delta^{13}\text{C}/\Delta\delta^{15}\text{N}$). Trophic levels were calculated using primary consumers (*Ennucula tenuis*, maldanid polychaetes) as the baseline

instead of POM due to the highly variable nature of POM and the fact that there is only one year of data for POM. Primary consumers integrate POM into their body isotope signature and represent a running average of primary production entering the food web. Trophic levels were calculated using the equation:

$$TL_{(PC)} = (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{primary consumer}})/3.4 + 2$$

where $TL_{(PC)}$ is the trophic level of the organism using primary consumers as the baseline, and 3.4‰ is the enrichment factor for one trophic step (Post, 2002).

C/N ratios are used as an indicator of food quality, with lower values representative of higher quality, more proteinaceous material and higher values indicating lower quality food sources, often terrestrial debris (Gnaiger and Bitterlich, 1984).

Statistical Methods

Density (individuals m^{-2}) and biomass ($g\ m^{-2}$) measurements were averaged from 2009–2011 and combined with trophic level calculations to determine if there were differences among trophic levels in relative proportion of density and biomass.

Analysis of variance (ANOVA) and linear regression were used to statistically evaluate the hypothesis that there are differences between food webs of the three study areas. Comparisons of POM and sediment isotope signatures were made using ANOVA. Following a significant ANOVA ($\alpha = 0.05$), the Tukey test was used for multiple comparisons. Linear regression was used to model the association between nitrogen and carbon isotopes and test the hypothesis that food webs are different among areas by determining if individual regression lines for Klondike, Burger, and Statoil were different from each other. Linear regression considered study area as a categorical variable, $\delta^{13}C$ as the quantitative predictor, and $\delta^{15}N$ as the response. A significant Area effect in the regression, and thus the food webs, would indicate a difference between areas. One assumption of linear regression is that the predictor variables are fixed values and random values, such as the $\delta^{13}C$ measured in the present study, violate the assumptions of normal regression. Linear regression methods therefore included individual analyses by area using Model II regression (ranged major axis regression: RMA) for two random variables to account for the use of measured carbon values in the regression models (Quinn and

Keough, 2002). RMA regression gives model parameter estimates and confidence intervals useful for comparisons for other studies. Determination of an Area effect is made by comparing confidence intervals from the RMA regression where lack of overlap indicates a significant difference between two study areas.

Geospatial modeling was performed using the library *geoR* in the statistical package *R*. Kriging plots were generated for Klondike, Burger, and Statoil using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from two frequently occurring primary consumers: the bivalve *Ennucula tenuis*, and polychaetes of the Maldanidae family. These animals were chosen because their isotope values reflect the average POM and sediment isotope values of the station at which they were collected due to their feeding habits and sessile nature. Isotope measurements were generated from individuals, in triplicate when possible, and then averaged by station.

RESULTS

Stable Isotope Analysis of Food Webs

Carbon isotope values ranged from -24.17‰ to -20.91‰ and nitrogen isotope values ranged from 2.03‰ to 11.78‰ (Table 4-1 and Fig. 4-2). As observed in the graph of the POM isotopes, there were significant differences among study areas ($p < 0.0001$) with POM $\delta^{13}\text{C}$ values significantly more enriched (positive) from stations in Klondike than in Burger and Statoil (Table 4-2 and Fig. 4-2). There was no significant difference between $\delta^{13}\text{C}$ values of POM from Statoil and Burger stations ($p = 0.89$). There was no significant difference among areas for POM $\delta^{15}\text{N}$ values ($p = 0.33$).

Sediment isotope values ranged from -23.54‰ to -21.33‰ for $\delta^{13}\text{C}$ and from 2.96‰ to 7.42‰ for $\delta^{15}\text{N}$ (Table 4-1 and Fig. 4-3). Sediment isotope values were also statistically different among areas ($p = 0.0001$) (Table 4-2 and Fig. 4-3). Sediment $\delta^{13}\text{C}$ was significantly more negative for Klondike as compared to Statoil (Table 4-2 and Fig. 4-3). At a higher level of significance ($\alpha = 0.10$), there is weak evidence suggesting that sediment $\delta^{13}\text{C}$ values at Burger differ from values at Klondike and Statoil (Table 4-2). Sediment $\delta^{15}\text{N}$ values were significantly lower at Klondike than at Burger, and there is weak evidence ($\alpha = 0.10$) suggesting the same is true between Klondike and Statoil (Table 4-2). POM data from stations in Klondike are relatively more enriched compared to sediments collected from the same study area, whereas

POM and sediment data have similar isotopic signatures from stations in Burger and Statoil (Table 4-1). There were no significant interannual differences within Klondike and Burger sediment data for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or C/N.

Average POM C/N ratios from Klondike, Burger, and Statoil were similar (Table 4-1) and did not differ statistically ($p = 0.15$). There was slightly more variation in the average sediment C/N ratios between study areas, ranging from 7.37 ± 0.56 to 8.50 ± 1.17 . Sediment C/N ratios differed significantly between Klondike and Statoil, with Klondike having a higher C/N ratio than Statoil (Table 4-2). Klondike sediments also had significantly higher C/N ratios than Burger sediments (Table 4-2).

The numbers of animals included in isotope food-web analyses were: 102 organisms from Klondike, 125 organisms from Burger, and 230 organisms from Statoil, for a total of 457 organisms (Figs. 4-4 to 4-6). The entire dataset is comprised of 112 taxa, representative of major fauna collected from the study areas. The stable isotope dataset from each study area contains approximately 50 taxa. The food webs from all study areas were fit to linear models (Fig. 4-7). Overall, RMA linear regression indicated no difference in tissue isotope patterns among Klondike, Burger, and Statoil (Table 4-3); however Statoil exhibits a diversion from the linear model. This can be seen in the regression plot for Statoil, where there is a clustering of suspension feeders/filter feeders that plots slightly higher than the regression line (Fig. 4-7 right-hand panel).

Table 4-1. Average POM and sediment $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C/N ratios for each study area from the Chukchi Sea 2009–2010 with standard deviations.

POM							
Study area	n	Ave. $\delta^{13}\text{C}$	SD	Ave. $\delta^{15}\text{N}$	SD	Ave. C/N	SD
Klondike	9	-21.56	0.68	5.67	2.55	6.70	0.70
Burger	10	-23.23	0.71	6.39	2.43	6.24	0.34
Statoil	11	-23.10	0.64	7.34	2.45	6.45	0.39

SEDIMENT							
Study area	n	Ave. $\delta^{13}\text{C}$	SD	Ave. $\delta^{15}\text{N}$	SD	Ave. C/N	SD
Klondike	26	-22.75	0.39	4.99	1.04	8.50	1.17
Burger	26	-22.51	0.40	5.97	0.84	7.83	0.73
Statoil	24	-22.28	0.32	5.60	0.95	7.37	0.56

Table 4-2. Summary of multiple comparisons following ANOVA for stable isotope and C/N data from the Chukchi Sea 2009–2010. Values significant at $\alpha = 0.05$ are in bold type.

Comparison	POM			SEDIMENT		
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
Klondike - Burger	<0.0001	0.802	0.127	0.0726	0.00109	0.0194
Burger - Statoil	0.891	0.659	0.612	0.0783	0.344	0.143
Klondike - Statoil	<0.0001	0.306	0.499	0.000113	0.0699	<0.0001

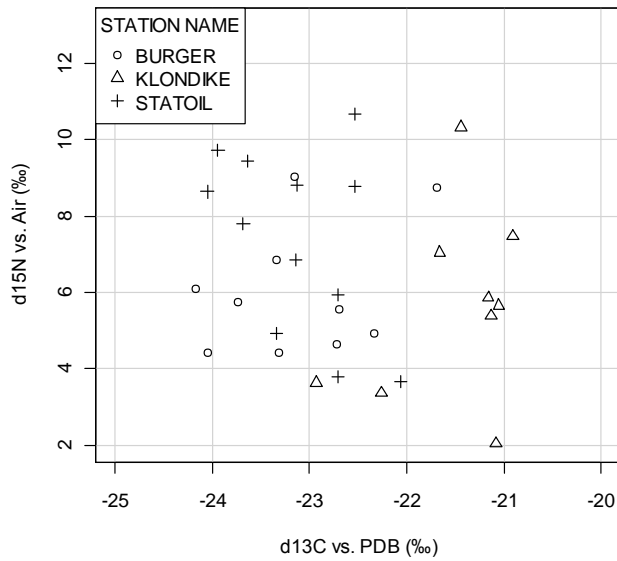


Figure 4-2. POM stable isotope data from Burger, Klondike, and Statoil study areas.

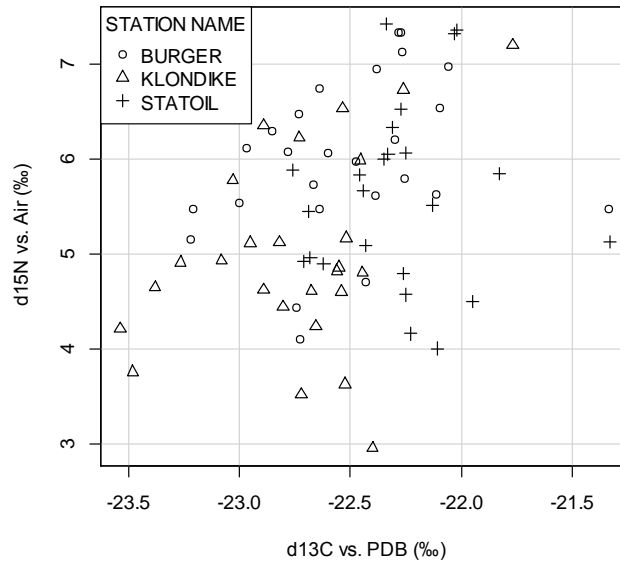


Figure 4-3. Sediment stable isotope data from the Burger, Klondike, and Statoil study areas.

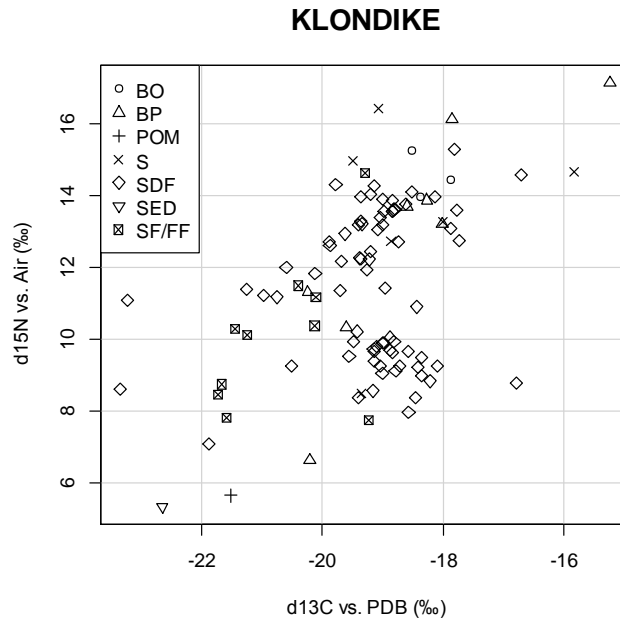


Figure 4-4. Tissue, sediment, and POM isotope data collected in the Klondike study area. Abbreviations for feeding guilds are: BO benthic omnivore, BP benthic predator, POM particulate organic matter, S scavenger, SDF sediment deposit feeder, SED sediment, SF/FF suspension feeder/filter feeder.

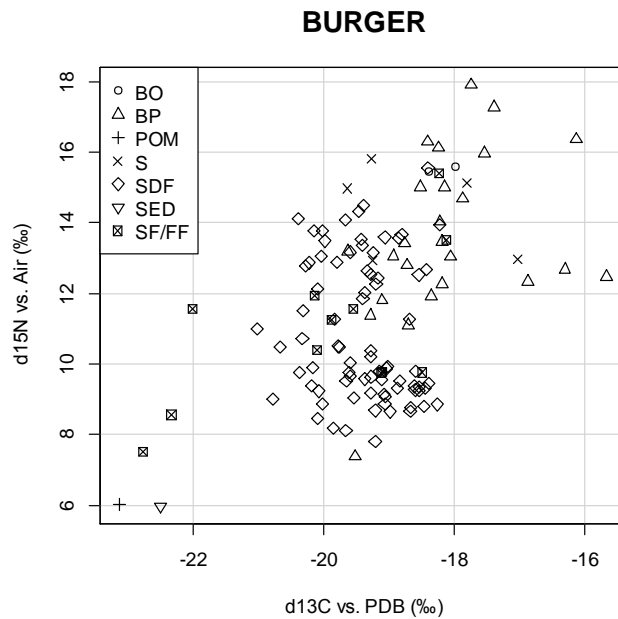


Figure 4-5. Tissue, sediment, and POM isotope data collected in the Burger study area. Abbreviations for feeding guilds are: BO benthic omnivore, BP benthic predator, POM particulate organic matter, S scavenger, SDF sediment deposit feeder, SED sediment, SF/FF suspension feeder/filter feeder.

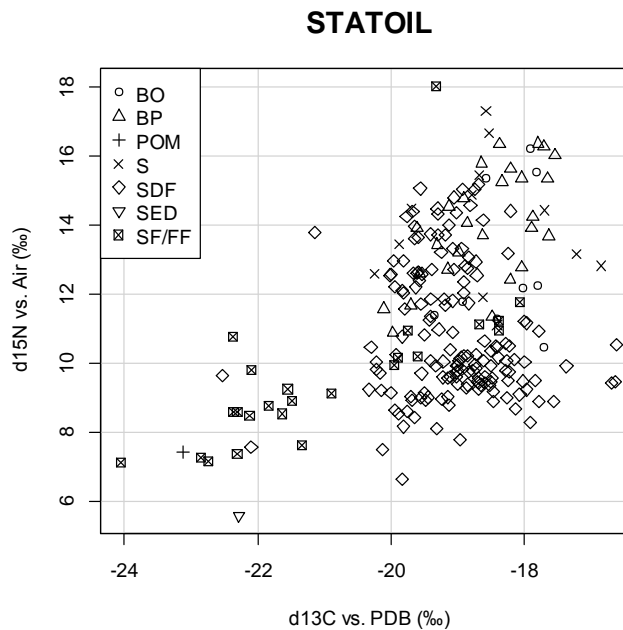


Figure 4-6. Tissue, sediment, and POM isotope data collected in the Statoil study area. Abbreviations for feeding guilds are: BO benthic omnivore, BP benthic predator, POM particulate organic matter, S scavenger, SDF sediment deposit feeder, SED sediment, SF/FF suspension feeder/filter feeder.

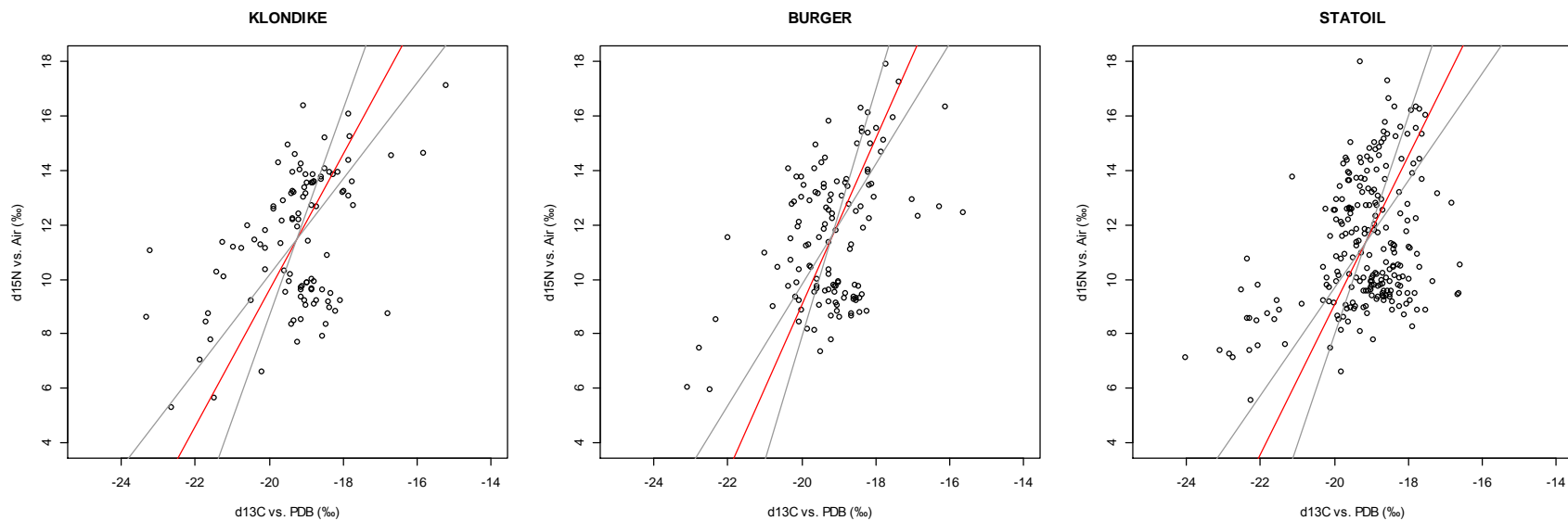


Figure 4-7. RMA regression of average POM, sediment and tissue stable isotope data from all study areas. The regression line is represented by the darker center line, with the lighter lines to either side denoting 95% confidence intervals.

Table 4-3. Summary of ranged major axis (RMA) linear regression analyses of the stable isotope data from the Chukchi Sea 2009–2011. Isotope values were averaged by taxa.

Area	Intercept	Slope	P-value	95% Confidence	
				Interval Intercept	Interval Slope
Klondike	58.97	2.42	0.01	(50.63, 70.21)	(2.02, 3.03)
Burger	70.43	3.07	0.01	(54.17, 99.18)	(2.22, 4.57)
Statoil	63.88	2.74	0.01	(49.20, 88.63)	(1.98, 4.03)
Central stratum	48.73	1.84	0.01	(36.90, 71.84)	(1.26, 2.98)
North stratum	28.35	0.83	0.02	(14.44, 46.82)	(0.15, 1.73)

The food webs span roughly 4 trophic levels from POM to higher-order benthic predators for all the study areas (Figs. 4-4 to 4-6). Biomass and density measurements averaged from 2009–2011 were combined with trophic level data to determine the relative proportion of biomass and density attributed to each trophic level. Trophic level 2 accounted for the highest proportion of density at Klondike (Fig. 4-8). In Burger, the highest proportion of density was at trophic level 3. Density at Statoil was dominated by trophic level 2. Deposit-feeders dominated density and contributed to trophic levels 1–3 from all study areas, except for trophic level 3 in Statoil, which was dominated by predators (due to high numbers of carnivorous ostracods). Klondike had approximately equal contribution of biomass to trophic levels 2 and 3 (45%), and approximately 5% of biomass accounted for by trophic level 1 (Fig. 4-9). High biomass of *Ophiura sarsi* in the Burger study area is the major contributor to trophic level 3. Trophic level 2 held the highest proportion of biomass at Statoil. Overall, deposit-feeders had the greatest presence from combined density and biomass proportions graphs.

A dataset of animals collected from the Central and North strata was also compiled. There were 32 individuals from 30 taxa analyzed from the Central stratum (Fig. 4-10), and 66 individuals from 39 taxa analyzed from the North stratum (Fig. 4-11). The food webs were fit to a linear model (Fig. 4-12). RMA linear regression indicated no difference in tissue isotope patterns between the two areas (Table 4-3). However when the North stratum was compared to the Klondike, Burger, and Statoil study areas, lack of overlap in the 95% confidence intervals for both slope and intercept indicated significant differences between food webs (Table 4-3). The progression of feeding guilds as trophic level increases appeared to be similar to those observed from the other study areas.

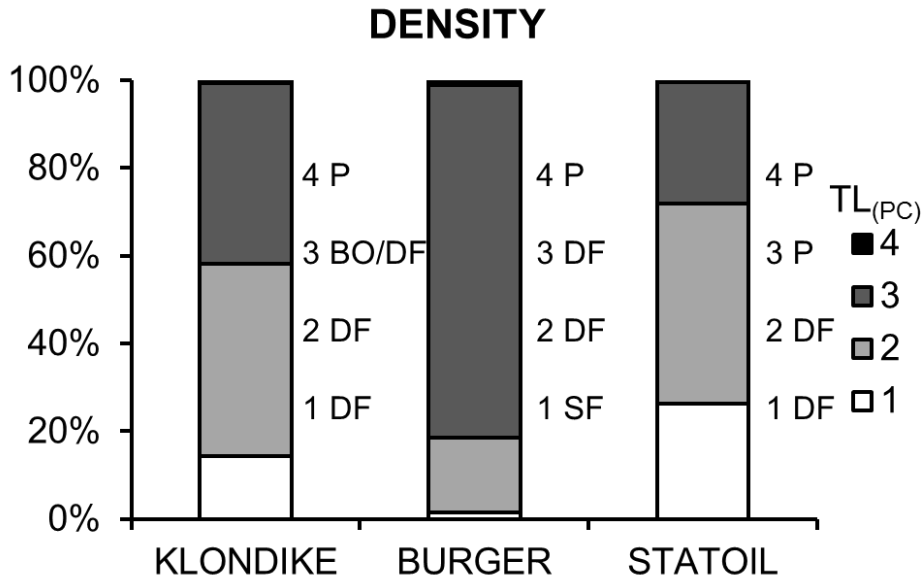


Figure 4-8. Relative proportion of density (individuals m^{-2}) contributed to trophic levels across study areas Klondike, Burger and Statoil, with the major contributing feeding guild identified at each level: BO benthic omnivore, DF deposit feeder (includes surface and subsurface), P predator, S scavenger, SF suspension feeder.

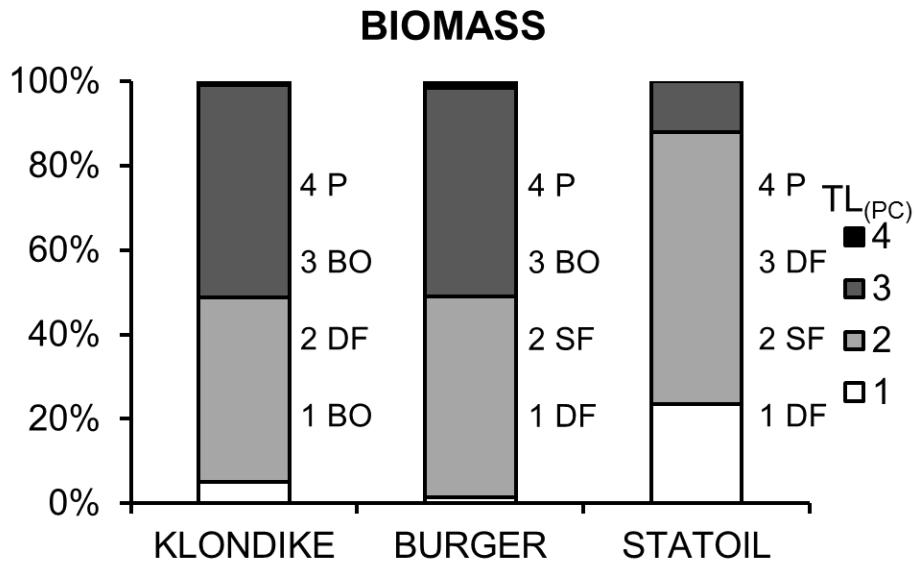


Figure 4-9. Relative proportion of biomass (g wet weight m^{-2}) contributed to trophic levels across study areas Klondike, Burger and Statoil, with the major contributing feeding guild identified at each level: BO benthic omnivore, DF deposit feeder (includes surface and subsurface), P predator, S scavenger, SF suspension feeder.

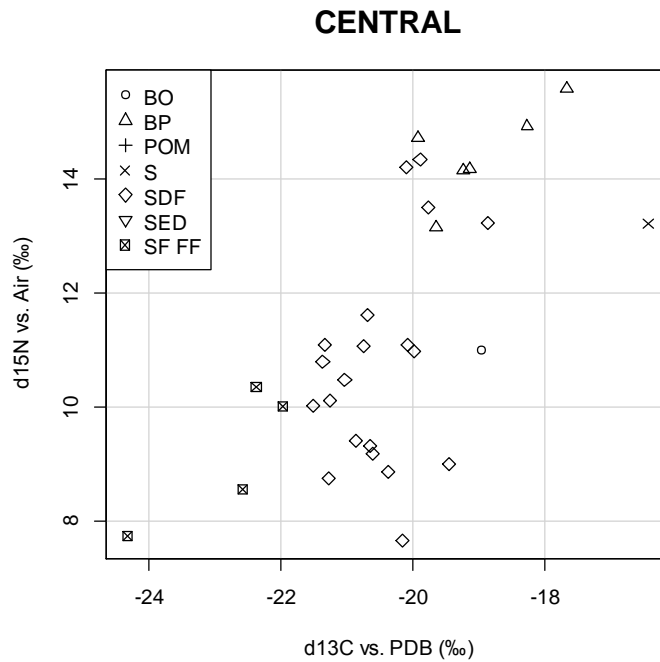


Figure 4-10. Tissue isotope data collected in the Central stratum. Abbreviations for feeding guilds are: BO benthic omnivore, BP benthic predator, POM particulate organic matter, S scavenger, SDF sediment deposit feeder, SED sediment, SF/FF suspension feeder/filter feeder.

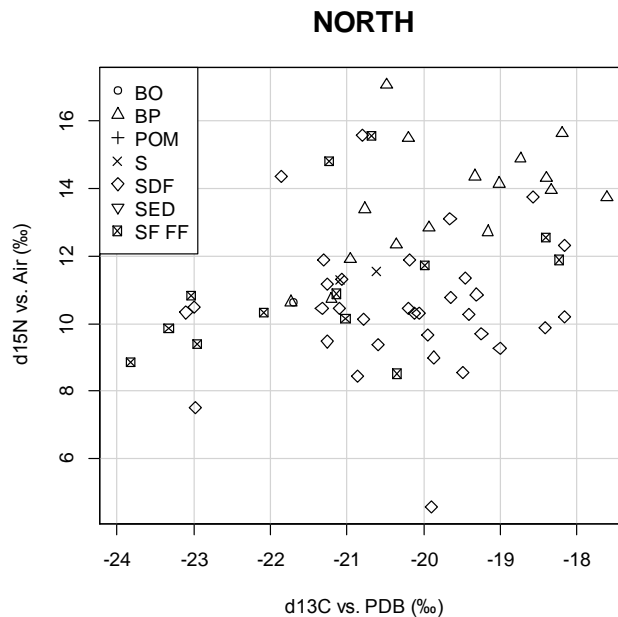


Figure 4-11. Tissue isotope data collected in the North stratum. Abbreviations for feeding guilds are: BO benthic omnivore, BP benthic predator, POM particulate organic matter, S scavenger, SDF sediment deposit feeder, SED sediment, SF/FF suspension feeder/filter feeder.

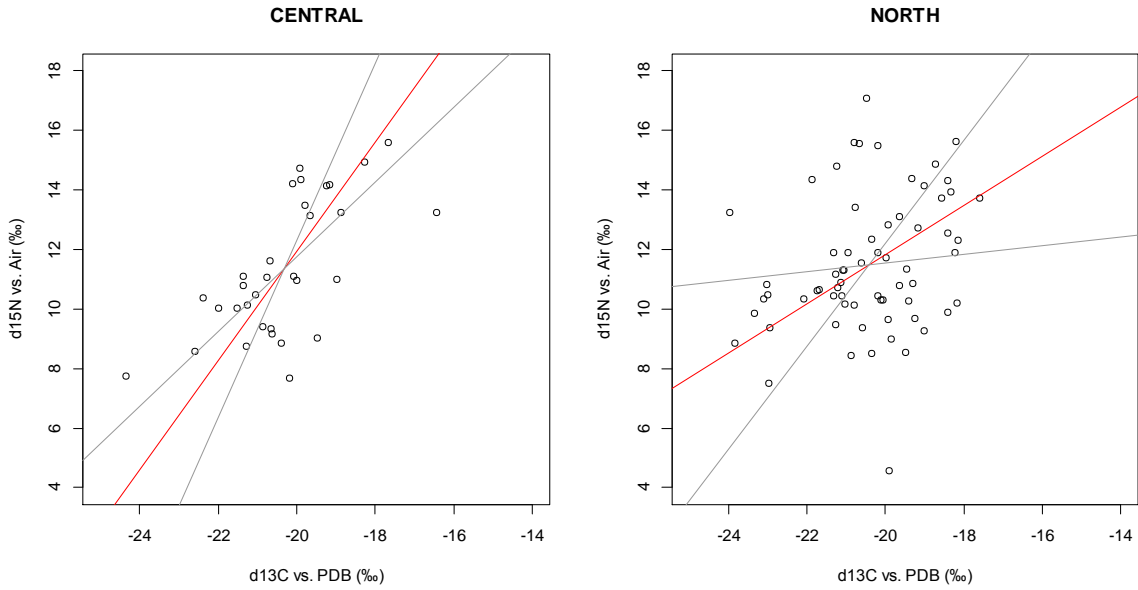


Figure 4-12. RMA regression of tissue stable isotope data from the Central and North strata. The regression line is represented by the darker center line, with the lighter lines to either side denoting 95% confidence intervals.

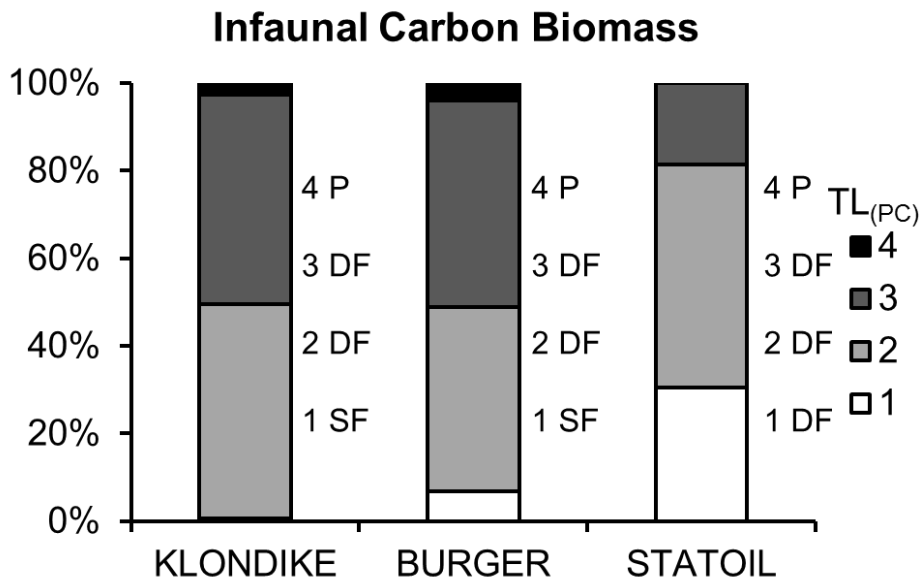


Figure 4-13. Relative proportion of infaunal carbon biomass contributed to trophic levels across study areas Klondike, Burger and Statoil. Abbreviations for feeding guilds are: DF deposit feeder (includes surface and subsurface), P predator, SF suspension feeder.

Infaunal carbon biomass proportions revealed that the majority of the biomass at Klondike and Statoil could be found in organisms at trophic level 2, while trophic level 3 held the highest carbon biomass at Burger (Fig. 4-13). As much as 50% of infaunal carbon biomass in Klondike was found at trophic level 2. Statoil showed the highest proportions of carbon biomass at lower trophic levels. Carbon biomass at trophic level 4 was low across the entire study area.

Kriging plots generated from $\delta^{13}\text{C}$ measurements showed little difference across the study areas for both *Ennucula tenuis* bivalves and Maldanidae polychaetes, most likely due to the extremely low variability in carbon isotope values from the original dataset. The kriging plot for *Ennucula tenuis* shows a range of predicted $\delta^{13}\text{C}$ from -18.9‰ to -18.7‰ and most stations plotted out individually, and the plot for Maldanidae shows a $\delta^{13}\text{C}$ range of -20.2‰ to -19.2‰ (Figs. 4-14 and 4-15). The same was true for $\delta^{15}\text{N}$ plots generated from *Ennucula tenuis* data. The plot of predicted $\delta^{15}\text{N}$ from *Ennucula tenuis* reflects individual station with values ranging from 9.37‰ to 9.54‰ (Fig. 4-16). There was an observable gradient in the Maldanidae $\delta^{15}\text{N}$ plots across the study site that began with lower $\delta^{15}\text{N}$ values on the eastern side of Klondike and ended with higher $\delta^{15}\text{N}$ values in the northeastern corners of Burger and Statoil, near Barrow Canyon for a total predicted $\delta^{15}\text{N}$ range of 11.9‰ to 13.6‰ (Fig. 4-17). This gradient represents approximately a 1.7‰ nitrogen isotope enrichment of Maldanidae from Klondike to Burger and Statoil indicating a change in food source equivalent in magnitude to a ½ step increase in trophic level.

Comparisons of isotope values for a group of taxa sampled from all three study areas indicate minor differences in average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among study areas (Table 4-4). Overall, $\delta^{15}\text{N}$ differences between all study areas were less than 1.1‰. The differences in $\delta^{13}\text{C}$ ranged from 0.54‰ to 0.69‰.

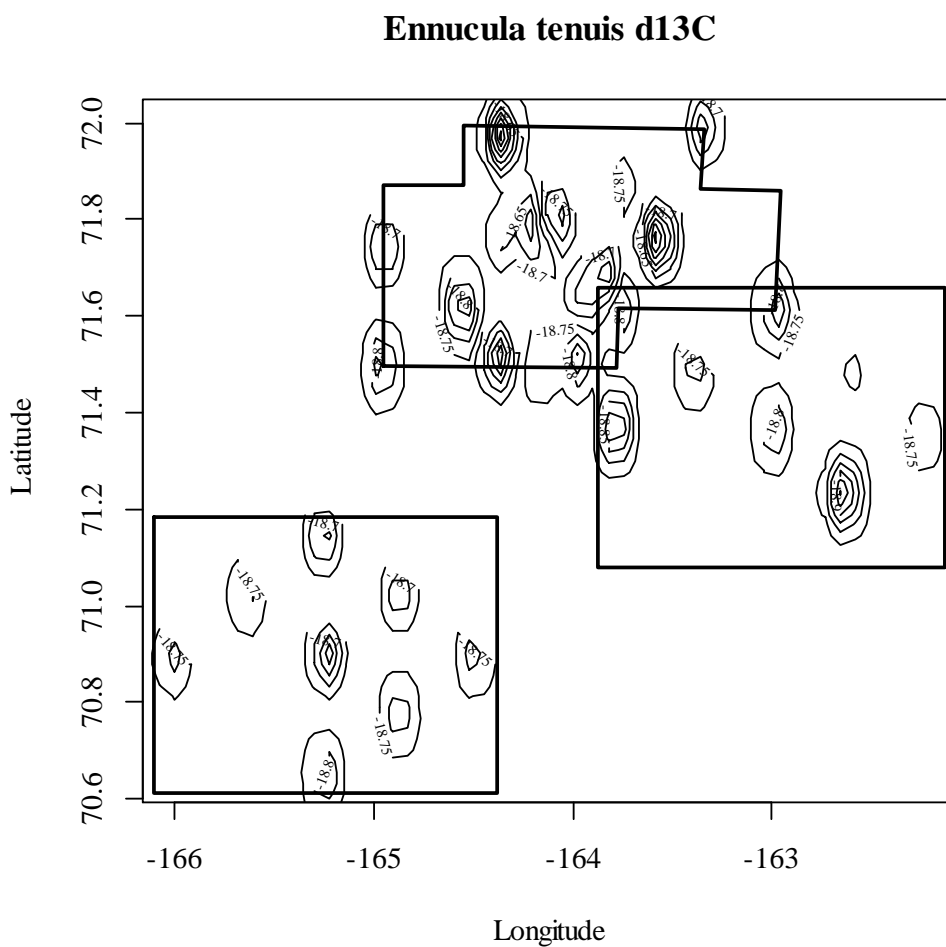


Figure 4-14. Kriging plot of $\delta^{13}\text{C}$ measurements from *Ennucula tenuis* across the study areas. $\delta^{13}\text{C}$ values were averaged by station, and then analyzed using the library geoR in the statistical package R.

Maldanidae d13C

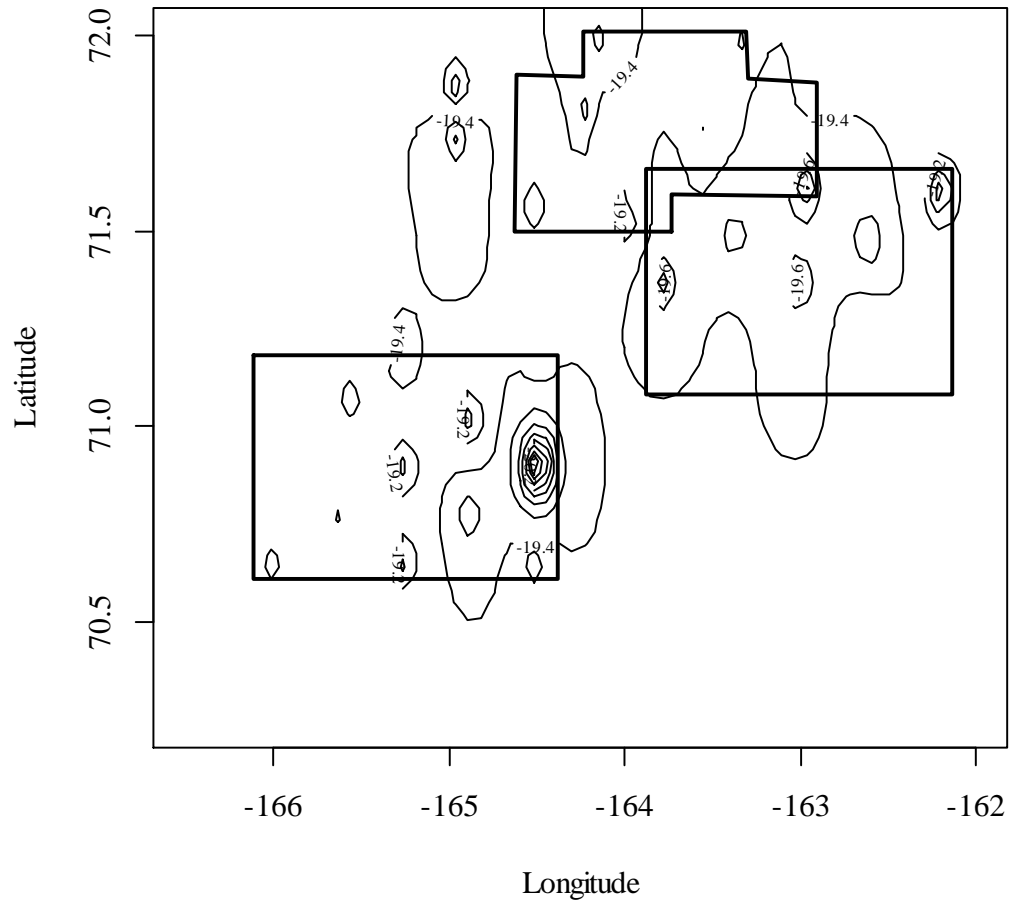


Figure 4-15. Kriging plot of $\delta^{13}\text{C}$ measurements from Maldanidae across the study areas. $\delta^{13}\text{C}$ values were averaged by station, and then analyzed using the library geoR in the statistical package R.

Ennucula tenuis d15N

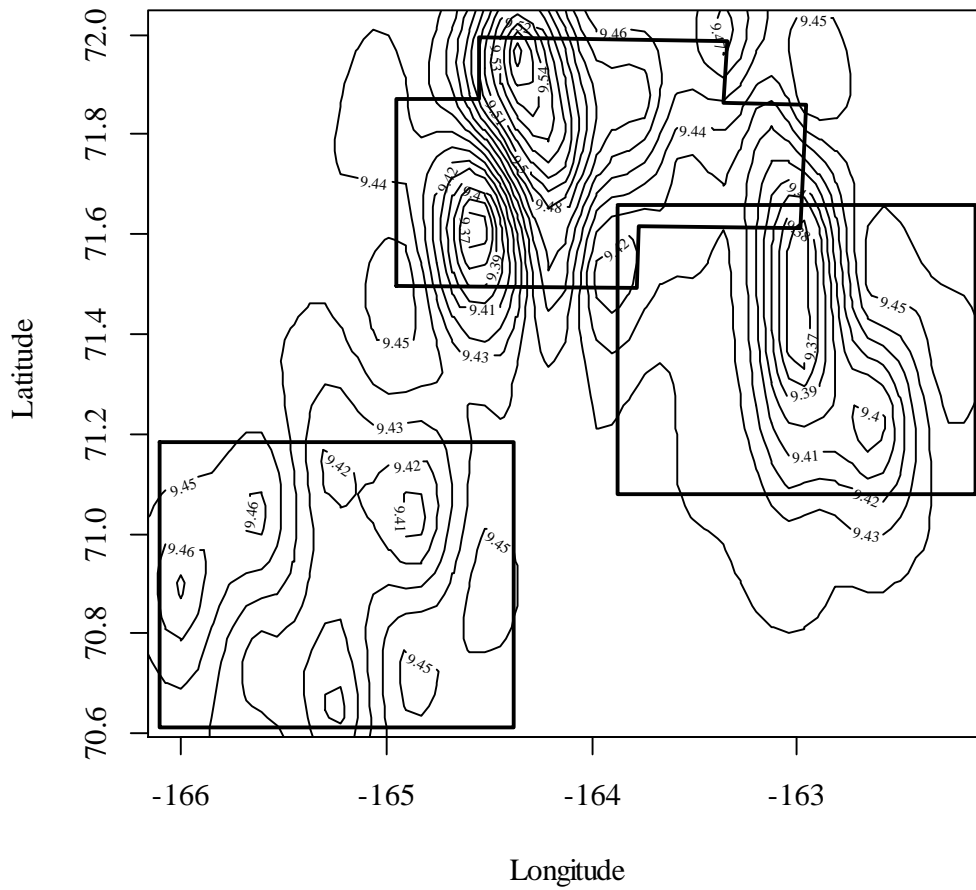


Figure 4-16. Kriging plot of $\delta^{15}\text{N}$ measurements from *Ennucula tenuis* across the study areas. $\delta^{15}\text{N}$ values were averaged by station, and then analyzed using the library geoR in the statistical package R.

Maldanidae d15N

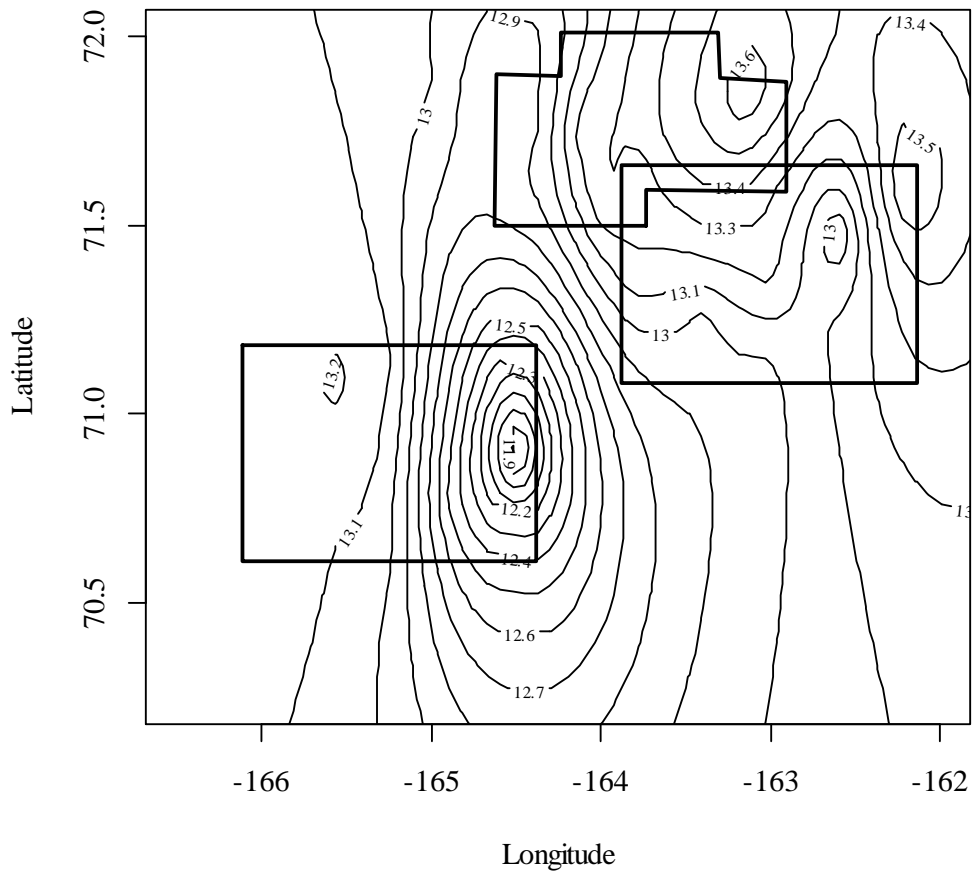


Figure 4-17. Kriging plot of $\delta^{15}\text{N}$ measurements from Maldanidae across the study areas. $\delta^{15}\text{N}$ values were averaged by station, and then analyzed using the library geoR in the statistical package R.

Table 4-4. Mean carbon and nitrogen stable isotope values, and trophic level for a select group of organisms from all study areas. Columns to the far right calculate the difference between mean values for the respective isotope. Taxa are ordered by trophic level. Trophic steps are separated by dashed lines.

Taxon	Ave. TL _(PC)	Klondike		Burger		Statoil		Difference Klondike - Burger		Difference Burger - Statoil		Difference Klondike - Statoil	
		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Ampelisca sp.</i>	1.49	-21.44	10.29	-22.77	7.51	-22.39	8.20	1.33	2.78	0.38	0.69	0.95	2.10
<i>Macoma sp.</i>	1.65	-19.41	8.37	-19.89	9.71	-19.57	8.79	0.47	1.34	0.32	0.92	0.15	0.42
<i>Nuculana sp.</i>	1.68	-18.57	7.95	-19.77	10.49	-20.22	10.05	1.20	2.54	0.45	0.43	1.65	2.10
<i>Ennucula tenuis</i>	1.77	-18.73	9.37	-19.06	9.19	-18.57	9.66	0.33	0.18	0.49	0.47	0.16	0.29
<i>Ampelisca eschrichti</i>	1.82	-21.48	9.29	-22.33	8.56	-22.10	9.78	0.85	0.73	0.23	1.22	0.62	0.49
Ampharetidae	2.31	-20.76	11.16	-21.01	10.99	-18.73	12.95	0.25	0.17	2.28	1.96	2.03	1.79
<i>Golfingia margaritacea</i>	2.31	-19.34	11.38	-18.68	11.27	-19.28	10.99	0.66	0.11	0.60	0.28	0.06	0.39
Terebellidae	2.67	-20.12	12.46	-19.17	12.42	-19.95	12.21	0.95	0.04	0.78	0.22	0.17	0.25
Maldanidae	2.73	-19.56	12.56	-19.73	12.70	-19.39	13.00	0.18	0.14	0.34	0.31	0.16	0.45
Polynoidae	2.81	-18.27	13.85	-19.00	12.08	-19.52	12.70	0.73	1.77	0.52	0.62	1.25	1.15
<i>Maldane sarsi</i>	2.95	-18.97	13.28	-19.54	14.06	-19.36	13.55	0.57	0.78	0.18	0.51	0.39	0.27
<i>Ophiura sarsi</i>	3.06	-15.83	14.66	-17.03	12.97	-17.46	13.79	1.20	1.69	0.43	0.82	1.63	0.87
<i>Nephtys sp.</i>	3.55	-17.85	16.11	-17.74	17.91	-18.15	15.36	0.11	1.80	0.41	2.55	0.30	0.75
<i>Anonyx sp.</i>	3.57	-19.29	15.68	-19.26	14.37	-18.64	16.07	0.03	1.31	0.62	1.70	0.65	0.39
<i>Priapulius caudatus</i>	3.48	-17.88	14.41	-18.18	15.52	-18.10	15.71	0.30	1.11	0.08	0.19	0.22	1.30
Ave. difference								0.61	1.10	0.54	0.86	0.69	0.87

DISCUSSION

POM and Sediments as Food-web Carbon Sources

The composition of benthic assemblages reflects the availability of carbon (as particulate organic matter: POM), its quality, and the processes that deliver nutrients and the POM on which benthic consumers feed. In the northeastern Chukchi Sea, water masses of southern origin transport heat, nutrients, carbon, and animals through the Chukchi Sea to the Arctic Ocean, and are vitally important for maintenance of the ecological structure of the region (Weingartner et al., 2005; Grebmeier et al., 2006; Hopcroft et al., 2010). The northward current flow, derived from sea level differences between the Pacific and Arctic oceans (Weingartner et al., 2005), also transports POM, enhancing communities in some locations (Feder et al., 2011). The northward currents in the Chukchi Sea can be substantial influences on faunal community structure as community structure and trophic modes (i.e., feeding types) will reflect the processes delivering carbon to the system (Feder et al., 1994a; Grebmeier et al., 2006). In areas with high currents and scouring, sediments will tend towards rock with filter-feeding organisms settled on the hard substrate. Where currents are slower and sediments are deposited, the benthic communities will shift towards deposit-feeding organisms. Thus, the trophic modes of animals within a food web can provide insights into the communities not observed in other ways (Iken et al., 2010).

Sources of carbon in benthic marine systems include water column, benthic, and ice-edge and sea-ice production in arctic regions, as well as export from terrestrial and nearshore sources to offshore benthos. These particulate organic matter (POM) carbon sources to the benthos are heterogeneous materials that can be highly variable spatially and temporally (Gradinger, 2009, Iken et al., 2010). The general isotopic signatures for POM and sediments in the northeastern Chukchi Sea suggest mainly marine carbon sources, as indicated by Naidu et al. (1993 and 2000) and Iken et al. (2010). Bering Sea phytoplankton have a $\delta^{13}\text{C}$ value of $-21.2 \pm 1\text{‰}$, and terrestrial material in the southern Chukchi Sea has been estimated to have a $\delta^{13}\text{C}$ signature of -27‰ (Naidu et al., 1993). The carbon values of POM from the study areas fall between these signatures, indicating a food source composed of largely marine carbon, possibly supplemented with degraded material at Burger and Statoil (Naidu et al., 1993 and 2000). The average Klondike POM value more closely reflected solely marine phytoplankton, whereas average Burger and Statoil POM isotope values reflected marine carbon and influence from depleted

sources. Low C/N ratios and high $\delta^{15}\text{N}$ values are typical of marine POM, as shown here (Naidu et al., 2000).

Several explanations exist for the difference in POM values between Klondike and the remaining study areas. All three areas are subject to different delivery processes; Klondike is exposed to higher current flow whereas Burger and Statoil are more depositional in nature. Burger and Statoil POM isotopic signatures were similar to their respective sediment isotopic signatures, presumably reflecting slower-moving currents that allow settling-out of material from the water column (Spall, 2007). Conversely, differences between POM and surface sediment carbon isotope signatures in Klondike suggest the POM at Klondike is not settling there, likely reflecting the faster water movement through the area, as suggested by coarser sediments and indicated by oceanographic modeling (Spall, 2007). The proximity of the site to the currents of the Central Channel may prevent POM from settling before it is transported out of the area. Preferential grazing of marine material and microbial degradation earlier on in the lifetime of the water mass (over Klondike) leaves carbon depleted sources at sites further downstream (Burger and Statoil), thereby depleting the POM signal; lighter material remains suspended in the water column as it is transported downstream and is subject to microbial degradation for a longer period of time (Altabet & McCarthy, 1985). The presence of isotopically depleted bacterial lipids would deplete the POM isotope signature (Eadie & Jeffrey, 1973). Phytoplankton size and composition can also affect POM isotope signatures because larger, fast growing cells in early stages of a bloom are typically more enriched in ^{13}C than smaller, slower growing cells at late stages of a bloom (Fry & Wainwright, 1991, Korb et al., 1996, Burkhardt et al., 1999, Tamelander et al., 2009). Phytoplankton assemblages were not analyzed, but analysis of chlorophyll-*a* and nutrient concentrations indicate that Klondike POM was sampled post-bloom, and Burger/Statoil POM were sampled at its final stages (Questel et al., 2012). This does not explain the enriched carbon isotope signature in Klondike POM, but may apply to the relatively depleted POM sampled at the remaining two areas. The different bloom stages may be a result of delayed flushing of winter water over Burger and Statoil, and ultimately could be the mechanism behind the different POM signatures.

Missing endmembers not taken into consideration in this study are benthic and sea ice algae. The importance of sea ice algae to benthic food webs of this area has not yet been fully investigated; however substantial amounts of material are released from ice melt in the Chukchi

Sea and are likely an important food source to the benthos and pelagic organisms (Gradinger, 2009). Ice algae tend to aggregate and sink quickly out of the water column (Mincks et al. 2008); therefore it is unlikely that they were captured by the CTD cast for POM sampling. Benthic microalgae are also major contributors of primary production to communities in shallow seas (McMinn et al., 2005). Dense filamentous microalgal mats have been observed in the nearshore Chukchi Sea after ice melt (Matheke and Horner, 1974), but have not been extensively studied. Benthic diatoms from bay and offshore areas in southern Korea had average carbon and nitrogen isotope measurements of -14.1‰ and 11.0‰, respectively (Kang et al., 2003), and presumably the signature of benthic microalgae from the Chukchi Sea would be similar (enriched in carbon, similar to any marine source of primary production). Sediment signatures from the study areas are too depleted to suggest large amounts of benthic microalgae during the time of collection.

Stable Isotope Food-web Structures

Food webs indicated in the isotope scatterplots for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were similar to the patterns demonstrated by prior studies in the southern Chukchi Sea (Iken et al., 2010; Feder et al., 2011). The smooth, linear movement of the food web from POM to higher level trophic organisms is indicative of classic benthic food webs in Klondike and Burger starting with primary consumers feeding on POM and ranging to predatory organisms feeding on lower trophic levels. A linear food web is indicative of one primary carbon source, or multiple carbon sources with overlapping isotopic signatures, while a nonlinear food web, such as the food web for Statoil, suggests multiple carbon sources with differing $\delta^{13}\text{C}$ signatures (Feder et al., 2011). Infaunal feeding guilds are commonly represented by ranges in isotope values rather than distinct levels due to the wide range of food sources and feeding habits as animals switch between feeding modes depending on how carbon is delivered to the sediments (Iken et al., 2010; Feder et al., 2011). Thus, the general pattern of enrichment (i.e., increase) in isotope values in the present study indicates links between different levels in food webs similar to those observed in prior studies (Dunton et al., 1989; Iken et al., 2010; Feder et al., 2011).

Feeding guild ranges overlapped among Klondike, Burger, and Statoil indicating no difference in food-web structure. Animals classified as suspension feeders and sediment deposit-feeders appeared to have the most variable isotope signatures from Klondike, Burger and Statoil. The higher variability for these groups (i.e., the clustering of suspension feeders in Statoil's

RMA regression plot that fall out above the regression line) likely reflects variability of available material in the water column, selective feeding habits, and feeding at multiple levels. The food webs were tightly linked to the POM and sediments as $\delta^{13}\text{C}$ values increase consistently through the trophic levels, ranging from approximately -25‰ to -15‰ (Figs. 4-4 to 4-6), with similar values found in prior studies (Iken et al., 2010; Feder et al., 2011).

Food web lengths as shown by nitrogen were similar among study areas with all food webs spanning trophic levels 1–4. The quantitative representations of trophic levels (density, biomass) in conjunction with feeding mode information reflect the nature of primary production delivered to an area and currents. In cases where food-web length and proportions of trophic levels are similar, such quantitative data are useful in understanding energy transfer in a food web (Iken et al., 2010). Iken et al. (2010) found that communities in the southern Chukchi Sea under influence from Anadyr Water were dominated by lower trophic levels, emphasizing the abundant supply of fresh material, while communities under Alaskan Coastal Water were dominated by higher trophic levels that utilized refractory material. A similar pattern was observed in this study, with communities at Klondike and Statoil showing more dominance of density and biomass by trophic level 2 consumers (*Ennucula tenuis*, *Astarte borealis*, *Golfingia margaritacea*), and Burger being dominated by trophic level 3 consumers (the nonselective deposit-feeder *Maldane sarsi*, *Ophiura sarsi*). In this study, the differences are not attributed to differences in water mass, but rather to indirect effects of topographic control of water movement on biological communities. The decreased water circulation in Burger (resulting indirectly from the presence of Hanna Shoal) causes increased deposition of POM, which is then utilized by benthic organisms. Dominance by a nonselective deposit-feeder at Burger is further evidence that it is a depositional area with large amounts of refractory material delivered to the sediments.

The difference in trophic level between maldanidae and *E. tenuis* reflects the differences in feeding modes for subsurface deposit-feeders (Fauchald and Jumars, 1979, Spies and Davis, 1979, Feder et al., 1994a and 1994b, Holte, 1998, Holte & Gulliksen, 1998, Oug, 2000, Wlodarska-Kowalczyk and Pearson, 2004). As nonselective deposit-feeders, polychaetes of the family Maldanidae may have access to older enriched material and the smaller organisms feeding on the buried carbon, as they are tube dwelling organisms feeding at depth. *Ennucula tenuis* are selective subsurface deposit feeders, presumably feeding on fresh carbon. Iken et al.

(2005) also found the same pattern of selective deposit-feeders at trophic level 2 and nonselective deposit-feeders at trophic level 3 in taxa collected from the Arctic deep Canada Basin. A combination of difference in feeding mode and access to different layers of sediment is proposed as the cause for the separation of trophic levels between the two taxa.

CONCLUSIONS

Many similarities between areas were evident in the small scale qualitative comparisons made in the present study. All food webs consisted of 4 main trophic levels, consistent with previous findings that marine food webs are generally comprised of 3–5 trophic levels (Vander Zanden and Fetzer, 2007), and RMA regressions indicated no differences in general structure between the three main areas. Nitrogen patterns, including average $\delta^{15}\text{N}$ differences between tissue isotopes and proportion of taxa contributing to trophic levels, were also similar between areas. High proportions of density, biomass, and infaunal carbon biomass at low trophic levels indicate that most of the available carbon for marine mammal predators is at the level of primary and secondary consumers. This is also indicative of tight benthic-pelagic coupling, and effective transformation of primary production into high biomass (Iken et al., 2010).

Despite the many similarities, some quantitative comparisons revealed differences that corresponded with the environmental gradient encompassed by all three study areas. Density and biomass proportions at Burger (the deepest study area with muddy sediments) show a strong dominance of trophic level 3, driven by high numbers of maldanid polychaetes and brittle stars. The dominance of the system by these deposit-feeding consumers in Burger indicates a food web driven by depositional processes (Blanchard et al., 2011).

Differences in POM as a food-web source to the study areas reflect oceanographic characteristics at each site. The higher POM $\delta^{13}\text{C}$ values in Klondike, an area exposed to stronger currents, indicate seasonal delivery of a more marine carbon source than for the other areas. Carbon isotope values at Burger and Statoil were more depleted in comparison, possibly due to greater degradation of food in the water column. The difference in the POM carbon isotope signatures for Klondike did not appear to translate to sediments or the food web as there were negligible $\delta^{13}\text{C}$ differences among sediment and tissue isotopes compared to the other study areas. The $\delta^{15}\text{N}$ signatures of POM from Burger and Statoil correspond with more decomposed

material (manifested through their enriched nitrogen isotope values) deposited on the seafloor. The changes in food sources are also seen in the nitrogen isotope signatures of maldivid polychaetes across the study areas with a progressive enrichment from Klondike to Burger and Statoil equivalent in magnitude to a ½ step increase in trophic level, a change of magnitude with ecological significance.

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CHAPTER 5

BENTHIC ECOLOGY 2011:

Caloric Analysis of Marine Mammal Prey Items in the Northeastern Chukchi Sea

By Kelley Tu and Arny L. Blanchard

INTRODUCTION

The robust benthic community in the northeastern Chukchi Sea supports high densities of upper trophic level predators such as bearded seals and walrus. Both of these marine mammals rely heavily on the benthos as prey items (Lowry et al., 1980; Fay, 1982; Dehn et al., 2007; Sheffield and Grebmeier, 2009). The Arctic favors large-bodied, energy-rich prey, making it possible to sustain the large predator populations found in this area (Weslawski et al., 2006). Understanding energetics of the benthic community is important in the study area because this arctic shelf region is characterized by a tight benthic-pelagic coupling, and changes to the benthos will have a direct effect on higher trophic levels (Grebmeier et al., 2006). As a result, climatic variation and environmental changes in the Arctic have effects on distribution and biomass of benthic prey (Grebmeier et al., 2006; Bluhm and Gradinger, 2008), which may impact marine mammal predators that are important to subsistence hunters and balancing marine food webs.

Caloric data provide important information about prey items that can be combined with diet studies to determine metabolic requirements for predators and energy flow through an ecosystem. Caloric information makes it possible to estimate the potential value of a particular area as foraging ground, as well as the capacity of predators it can support. Tracking changes to the benthic community can give insight into changes in predatory marine mammal populations, as prey density may have an effect on the predator density (Darling et al., 1998). Thus, feeding areas with high energy densities may be of interest to resource managers who will want to ensure that appropriate monitoring plans are put into place.

The Chukchi Sea Environmental Studies Program (CSESP) is a multi-disciplinary research project with the aim of understanding the ecology of the northeastern Chukchi Sea. The CSESP includes nine disciplines encompassing bird and mammal distributions, oceanographic characteristics, and benthic ecology. Sampling has occurred over a four-year period at the

Klondike, Burger, and Statoil sites (2010 and 2011 only), and across the Chukchi regional study area encompassing Hanna Shoal (2011 only). Ecological information from the CSESP research in the northeastern Chukchi Sea will be used to provide a baseline prior to gas and oil exploration activities in the area. The CSESP will provide insights on scales appropriate for understanding the ecology of benthic organisms and their interactions with the physical characteristics of the study area. The 2008–2011 CSESP provides an important opportunity to examine spatial variability of caloric content of major benthic prey items of the northeastern Chukchi Sea in detail. The 2008–2011 CSESP included sampling of infauna (smaller invertebrates living within the sediments) and epifauna (larger invertebrates living on the sediment surface) for determination of community structure and the factors associated with spatial and temporal variations. The present study fills gaps in the CSESP benthic ecology studies by providing detailed energetics information from the study areas to document the spatial variability in benthic prey items available for predator consumption within the region, in terms of energy (kilocalories).

One objective of this component of the CSESP was to obtain caloric values for prey items that marine mammal predators forage on in this area. A second objective was to combine caloric value data with biomass data from stations in the study areas Klondike, Burger, and Statoil, to examine spatial variability of areas with high caloric densities of prey items. The relative proportional contribution of energy to each trophic level was also of interest to examine energy flow through the food web. The overarching goal was to better understand the importance of the study area to larger marine predators by attempting to identify potential energy-rich foraging areas. Ecologically-significant community-level differences were observed in the benthic ecology component of the CSESP related to physical qualities of the study area (spatial variability) and annual differences in oceanographic characteristics (temporal variability) (Blanchard et al., 2011; Chapter 2). We hypothesized that differing species composition, as a result of environmental characteristics, may result in areas of high caloric densities of prey items. These “hotspots” may be foraging areas targeted by marine mammal predators.

METHODS

Sampling and Laboratory Methods

Epifauna for this study were collected by plumb staff beam trawls during sampling cruises in 2009 and 2010 in each study area. Epifauna were sorted, identified to the lowest taxonomic level possible, placed into labeled Whirlpak bags, and frozen for transport to the lab. Infauna were collected by van Veen grab (0.1 m²) in 2009–2011. Grab samples were rinsed through 1.0-mm mesh, collected into jars, and frozen for transport to the lab. A total of 47 taxa were selected for bomb calorimetry analysis, on the basis that they were prey items for marine mammal predators due to the fact that they have been found in stomach content analyses (Fay, 1982; Sheffield et al., 2001; Dehn et al., 2007; Sheffield and Grebmeier, 2009). Samples were thawed in the laboratory, and shells were removed from gastropods and bivalves. Animals that had inorganic structures that were difficult to separate from tissue (echinoderms, decapods) were analyzed whole. When one animal did not provide sufficient tissue for caloric analysis, multiple animals were composited for the sample. Composited samples consisted of individuals that were collected from the same trawl or van Veen grab (i.e., the same station). Average caloric content of a species may include species from multiple study areas. Wet weights were measured, and samples were frozen before being freeze-dried for a minimum of 48 h. Freeze-drying was used instead of oven-drying to reduce the loss of lipids from melting (Lucas, 1996). Dry weights were measured and samples were homogenized with a mortar and pestle. Homogenized dried samples were formed into pellets and analyzed on a Parr model 6300 oxygen bomb calorimeter for caloric content per gram of sample. Samples that would not hold their form in a pellet were instead analyzed in gelatin capsules. Five empty gelatin capsules were weighed and then analyzed to determine their average weight and average added caloric value. Three benzoic acid standards were analyzed at the beginning of every batch of samples run on the calorimeter to determine instrument error (average instrument error was 0.135 kcal g⁻¹). Replicates were run for as many times as the amount of available sample would allow. Occasionally subsampling of species occurred where the same species was analyzed from multiple study areas. Caloric values of samples analyzed in pills were calculated using the following formula:

$$(Wt_{\text{Capsule}} \times Cal_{\text{Capsule}}) + (Wt_{\text{Sample}} \times Cal_{\text{Sample}}) = (Wt_{\text{Total}} \times Cal_{\text{Total}})$$

where $W_{t_{\text{Capsule}}}$ is the weight of the empty gelatin capsule in grams, Cal_{Capsule} is the average caloric content of an empty gelatin capsule in cal g^{-1} DW (calories per gram dry weight), $W_{t_{\text{Sample}}}$ is the weight of the sample contained within the pill in grams, Cal_{Sample} is the unknown caloric value of that sample in cal g^{-1} DW, $W_{t_{\text{Total}}}$ is the combined weight of the capsule and the contained sample in grams, and Cal_{Total} is the gross heat generated by the entire sample in cal g^{-1} DW. Final caloric values are reported in kcal g^{-1} DW (kilocalories per gram dry weight).

Density and biomass data were averaged for all years (2009–2011 for infauna, 2009–2010 for epifauna) by station and taxon. Trophic levels were calculated based on primary consumer $\delta^{15}\text{N}$ values from stable isotope data using the following formula:

$$TL_{(\text{PC})} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{primary consumer}})/3.4 + 2$$

with 3.4‰ being the enrichment between trophic levels (Post, 2002; Chapter 4). Trophic level calculations were based on primary consumers rather than POM measurements due to the fact that only one year of POM stable isotope data was collected with no replicates, and POM is temporally and spatially variable due to its heterogeneous composition. Sessile primary consumers provide a running average of primary production entering the food web in the area from which they are collected. Energy content data for major prey items were multiplied by a weight conversion factor and then by biomass values to determine total kcal m^{-2} , using the following formula:

$$\text{Kcal m}^{-2} = \text{Kcal}_{\text{prey}} \times \text{DW}/\text{WW} \times \text{Biomass}_{\text{prey}}$$

where $\text{Kcal}_{\text{prey}}$ is the energy content of the prey item in kcal g^{-1} DW, DW/WW (dry weight/wet weight) is the ratio of the weight of the prey item after to the weight before freeze drying in grams, and $\text{Biomass}_{\text{prey}}$ is the averaged wet biomass of the prey item in g m^{-2} (grams per square meter). Energy data were combined with averaged biomass data and were then binned by the trophic level of the prey item to generate a graph of relative energy proportions by trophic level for each study area.

Statistical Methods

Differences in caloric content by study area and by phylum were analyzed using analysis of variance (ANOVA), followed by a Tukey test for multiple comparisons with a significance level of $\alpha = 0.05$.

Geospatial modeling was performed using the library *geoR* in the statistical package R (www.r-project.org). Kriging plots were generated for Klondike, Burger, and Statoil using caloric values of prey items.

When combining caloric data with biomass data, some weight conversion factors were required due to the fact that wet weight/dry weight differences for mollusks in this study were calculated without shells, and biomass data took into account the whole wet weight of the organism with the shell. Literature values for tissue dry weight percent total wet weight conversions from previous studies (Stoker, 1978; Ricciardi and Bourget, 1998) were used as weight conversion factors in order to produce accurate energy estimates for mollusks.

Where infaunal and epifaunal biomass data were combined, only stations where both infaunal and epifaunal data were available were used.

RESULTS

Analysis of Prey Item Energy Content

Mean caloric value across the 47 individual taxa analyzed ranged from as low as 0.782 kcal g⁻¹ DW to as high as 6.719 kcal g⁻¹ DW (Table 5-1). Ophiuroids had the two lowest caloric values, and amphipods had the two highest caloric values. There were differences in the mean caloric value between phyla as indicated by the significant ANOVA ($p < 0.0001$). Multiple comparisons using the Tukey comparisons showed that the phylum Echinodermata had a significantly lower median caloric value than phyla Annelida and Mollusca (Tables 5-2 and 5-3).

There appears to be a general trend of increasing energy density from west to east across Burger and Statoil, ending in an area of peak energy density at the northeast corners of these areas (Fig. 5-1). Projected energy density ranges from 155 kcal m⁻² to 180 kcal m⁻² in Burger, and from 125 kcal m⁻² to 175 kcal m⁻² in Statoil. Klondike energy density is relatively constant across the study area, ranging from approximately 120 kcal m⁻² at the western edge to approximately 130 kcal m⁻² at the eastern edge of the study area.

The average energy densities by study area were 114 kcal m⁻², 178 kcal m⁻², and 142 kcal m⁻² for Klondike, Burger, and Statoil respectively. Energy density by station ranged from values as low as 34 kcal m⁻² (KF021) to as high as 307 kcal m⁻² (SF018). The highest proportions of energy density occurred at trophic level 2 at all study areas (Fig. 5-2). Approximately 80% of total energy density was attributed to trophic level 2 in Klondike, and approximately 70% of total infaunal and epifaunal energy density was attributed to trophic level 2 in Statoil. Trophic level 2 at Burger held roughly 70% of the energy density. Proportion of energy density attributed to trophic level 1 was low overall except at Statoil. Energy density at trophic levels 3 and 4 was low across all areas, and absent at Statoil (for trophic level 4) with the current data set. Energy density proportions were dominated by predators at higher trophic levels, and deposit-feeders at lower trophic levels (due to presence of *Golfingia margaritacea*, Maldanidae, and bivalves).

There were significant differences in energy density by study area as shown by the significant analysis of variance ($p = 0.01$). The Tukey test for multiple comparisons showed that Burger had significantly higher energy density than Klondike ($p = 0.01$, Table 5-4). There were also highly significant differences in caloric content by phylum, shown by a significant analysis of variance ($p < 0.0001$). Phylum Echinodermata had significantly lower caloric content than the three phyla with the highest caloric content: Mollusca, Annelida, and Arthropoda ($p < 0.0001$, Table 5-3).

Table 5-1. Energy content of 47 benthic taxa from the northeastern Chukchi Sea, ranked by highest to lowest mean kcal g⁻¹ DW within Class. -- = not calculated.

Species/Taxon	n	Ave.	SD	Species/Taxon	n	Ave.	SD
CNIDARIA				<i>Macoma</i> sp.	4	4.80	0.38
Actinaria				<i>Astarte montagui</i>	2	4.39	0.04
<i>Stomphia</i> sp.	2	3.91	0.57	<i>Cyclocardia crebricostata</i>	2	4.05	0.09
SIPUNCULA				<i>Nuculana radiata</i>	2	4.00	0.98
Sipunculid	4	3.13	0.33	<i>Yoldia hyperborea</i>	1	3.90	--
<i>Golfingia margaritacea</i>	2	2.49	0.73	CRUSTACEA			
PRIAPULA				Amphipoda			
<i>Priapulus caudatus</i>	3	3.86	0.072	<i>Ampelisca</i> sp.	1	6.72	--
POLYCHAETA				Amphipoda	1	5.78	--
<i>Paradiopatra</i> sp.	1	5.58	--	<i>Anonyx</i> sp.	2	4.32	0.04
Flabelligeridae	2	5.13	0.22	<i>Stegocephalus</i> sp.	3	4.17	0.13
<i>Paradiopatra parva</i>	1	4.64	--	Decapoda			
<i>Lumbrineris</i> sp.	4	4.47	0.06	Pandalidae	2	4.60	0.19
Polynoidae	3	4.41	0.03	<i>Argis lar</i>	5	4.54	0.23
<i>Nephtys</i> sp.	2	4.06	0.23	<i>Pagurus</i> sp.	5	3.73	0.20
Terebellidae	4	3.28	0.08	Hippolytidae	6	3.64	0.22
Maldanidae	4	2.95	0.89	<i>Chionoecetes opilio</i>	3	3.26	0.19
MOLLUSCA				<i>Hyas coarctatus</i>	2	1.94	0.04
Polyplacophora				ECHINODERMATA			
<i>Ishnochiton albus</i>	7	1.89	0.23	Asteroidea			
Gastropoda				<i>Leptasterias</i> sp.	3	3.17	0.37
<i>Euspira pallida</i>	2	5.22	0.09	<i>Pteraster obscurus</i>	2	2.78	0.75
<i>Neptunea</i> sp.	2	5.08	0.10	<i>Leptasterias groenlandica</i>	3	2.30	0.97
<i>Buccinum scalariforme</i>	10	4.98	0.37	<i>Ctenodiscus crispatus</i>	3	1.63	0.09
<i>Cryptonatica affinis</i>	3	4.97	0.27	Ophiuroidea			
<i>Buccinum polare</i>	4	4.86	0.08	<i>Gorgonocephalus</i> sp.	2	1.29	0.08
<i>Plicifusus</i> sp.	3	4.46	0.08	<i>Ophiopholis aculeata</i>	1	1.03	--
<i>Margarites</i> sp.	3	4.25	0.89	<i>Ophiura sarsi</i>	2	0.78	0.14
Bivalvia				Holothuroidea			
<i>Astarte borealis</i>	1	5.22	--	<i>Ocnus</i> sp.	4	1.98	0.24
<i>Astarte</i> sp.	2	5.05	0.01	<i>Psolus</i> sp.	2	1.46	0.30
<i>Ennucula tenuis</i>	2	4.83	0.48				

Table 5-2. Summary of energy content (kcal g⁻¹ DW) of 47 benthic taxa by phylum. -- = not calculated.

Phylum	Ave.	SD
Annelida	4.315	0.88
Arthropoda	4.268	1.32
Cnidaria	3.910	--
Echinodermata	1.823	0.80
Mollusca	4.497	0.82
Priapulida	3.856	--
Sipuncula	2.808	0.45

Table 5-3. Tukey test results of multiple comparisons of average caloric content of species by phylum following a significant analysis of variance ($p < 0.0001$).

Phylum Comparison	p-value
Echinodermata - Annelida	< 0.0001
Echinodermata - Arthropoda	< 0.0001
Echinodermata - Mollusca	< 0.0001

Table 5-4. Tukey test results of multiple comparisons of average energy density between study areas following a significant analysis of variance ($p = 0.01$). Values significant at $\alpha = 0.05$ are bolded.

Comparison	p-value
Klondike - Burger	0.01
Burger - Statoil	0.22
Klondike - Statoil	0.40

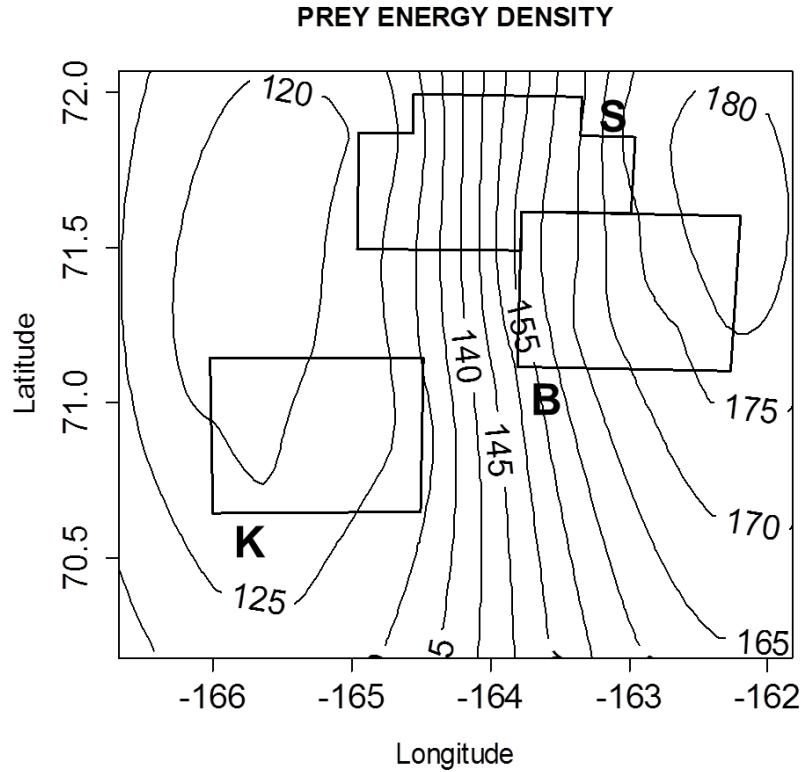


Figure 5-1. Spatial variability of prey item energy density among study areas Klondike, Burger, and Statoil. Energy values are expressed in kcal m⁻².

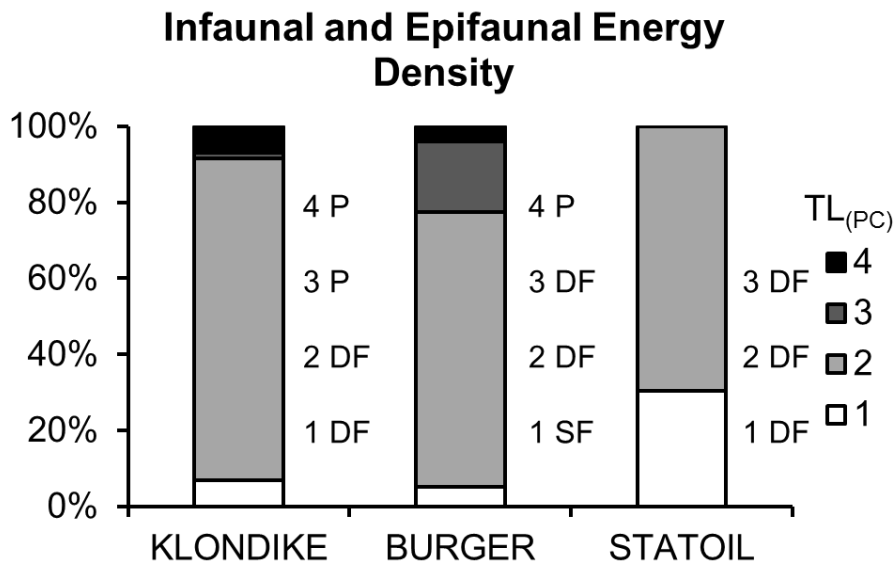


Figure 5-2. Proportional contribution of average energy density (kcal m⁻²) of infaunal and epifaunal major prey items to each trophic level in study areas Klondike, Burger and Statoil with the major contributing feeding guild identified at each level: DF deposit feeder (includes surface and subsurface), P predator, SF suspension feeder. Energy densities were averaged for each prey item by study area, and then binned into their respective trophic level at that study area.

DISCUSSION

Energetics of Prey Items of the Klondike, Burger, and Statoil Study Areas

Caloric values obtained in this study were comparable to those found in previous studies (Brawn et al., 1968; Wacasey and Atkinson, 1987; Hondolero et al., 2012). The caloric information provided here was obtained using dry weight, as opposed to ash-free dry weight (AFDW). Dry weights were used for purposes of combining caloric data with wet weight biomass data from the taxonomic analysis from this project, which were measured in g m^{-2} . Dry weight is often calculated in benthic studies, making results from this study applicable to benthic work done by others. It should also be noted that the caloric content of benthic invertebrates can be variable depending on different factors. Lawson et al. (1998) found that northern shrimp (*Pandalus borealis*) exhibited sex differences when it came to energy content, with males having a higher caloric value than females. Differences in lipid content have been shown in freshwater macroinvertebrates and mollusks with strong seasonal variations (Gardner et al., 1985; Bagatini et al., 2007), possibly due to changes in food composition and temperature (Tessier and Goulden, 1982; Bagatini et al., 2007). Animal size and reproduction 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 potentially consisted of a mixture of size classes, sex, and body condition. Season was consistent for all samples, as sampling occurred in late summer/early fall every year.

The highest average energy density by study area occurred in Burger at 178 kcal m^{-2} , reflecting the environmental and biological differences among the study areas. For comparison, Brawn et al. (1968) found that the mean caloric content of the standing crop of invertebrates in St. Margaret's Bay, Nova Scotia was 76 kcal m^{-2} . The highest value found by Brawn et al. (1968) was 174 kcal m^{-2} , while the highest station energy density in this study was found to be 307 kcal m^{-2} (at SF018). The difference between the energy density values in these two studies emphasizes the high productivity of the arctic shelf area in comparison to other areas.

Sediment characteristics such as grain size, OC/N, and water content, have been shown to be closely associated with the major drivers in benthic community structure (Feder et al., 1994b). Current divergences, resulting from topographic variations may drive a greater availability of particulate organic carbon in Burger (Chapter 2). The complexity of circulation patterns is still

under investigation. High biomass of bivalves and maldanid polychaetes contribute to the higher energy density in the Burger area, as mollusks were found to have the highest caloric content of all the phyla analyzed in this study (Blanchard et al., 2011; Chapter 2). Density and biomass were found to be significantly higher in Burger as compared to Klondike for both infauna and epifauna (Blanchard et al., 2011), which also accounts for the higher energy densities seen there. Marine mammal observations from 2008–2010 indicate that benthic-feeding walruses and bearded seals were more common in Burger and Statoil (Aerts et al., 2011; Delarue et al., 2011) in agreement with the location of the highest concentration of caloric content shown.

The proportion of energy in prey items contributing to each trophic level highlights an overall importance of taxa identified as trophic level 2 consumers. Trophic level 2 contained the highest proportion of prey energy density in all study areas and was primarily composed of sediment deposit feeding taxa such as mollusks and sipunculids. Traditional food-web views estimate that only 10% of energy is transferred from prey to predator, with much of the available energy being used in metabolism or lost as heat. It is the inefficiency of energy transfer that limits the number of trophic steps that can exist within an ecosystem. The majority of prey items consumed by marine mammal predators taken into account in this study were shown to feed at trophic levels 1 or 2, with less than 15% of prey energy density attributed to trophic level 3 and higher. Taking into account the marine mammal predators, the trophic level information models a food web that ends at trophic level 5. This is consistent with other studies that employed stable isotopes to determine trophic level and found that marine ecosystems generally have 3-5 trophic levels (Vander Zanden and Fetzer, 2007; Iken et al., 2010). High proportions at low trophic levels make it possible to sustain large predator populations.

Infaunal biomass was the main driving factor in the energy density kriging plots generated from this study. Predicted infaunal energy densities were two to three orders of magnitude larger than predicted epifaunal energy densities. Infaunal energy density in Burger was uniformly high, while Statoil showed a low-to-high gradient, and Klondike was uniformly low. The high infaunal biomass in Burger, including high mollusk biomass, makes it a good foraging area with dense patches of high energy prey items available for consumption. Feeding at areas of high energy density, such as in Burger and Statoil, also maximizes the amount of prey that could be captured during a single dive.

CONCLUSIONS

All study areas exhibit the highest proportions of energy densities at low trophic levels (1 and 2), indicating the assimilation of primary production and subsequent conversion to high levels of biomass. Burger and Statoil have similar environmental conditions and support higher biomass of infaunal and epifaunal prey items. The depositional characteristics of the Burger study area make it an ideal habitat for sediment deposit feeders, thereby supporting high numbers of bivalves and sediment deposit feeding polychaetes. These animals were high in energy, and have often been found in stomach content analyses of large marine mammal predators. The highest energy densities in the study area were found in Burger and Statoil, coinciding with marine mammal observation data that showed walruses and bearded seals were found more commonly in these areas. Presumably these areas were being targeted for their areas of high infaunal energy density. Data from this study provide further supporting evidence that the Burger survey is an important foraging area for these higher trophic level animals.

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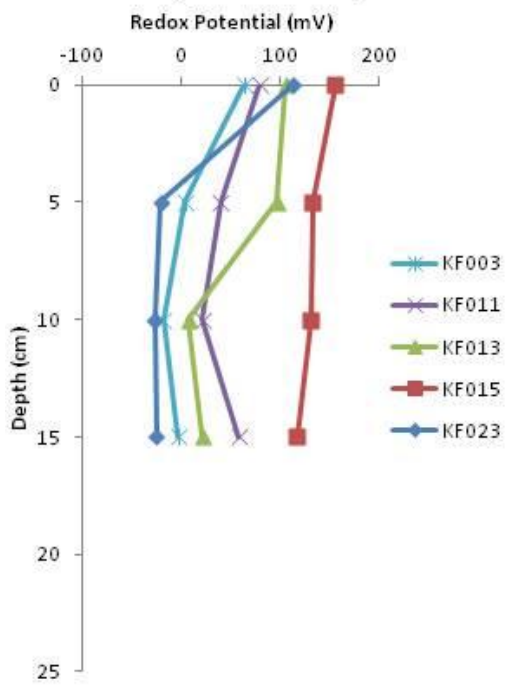
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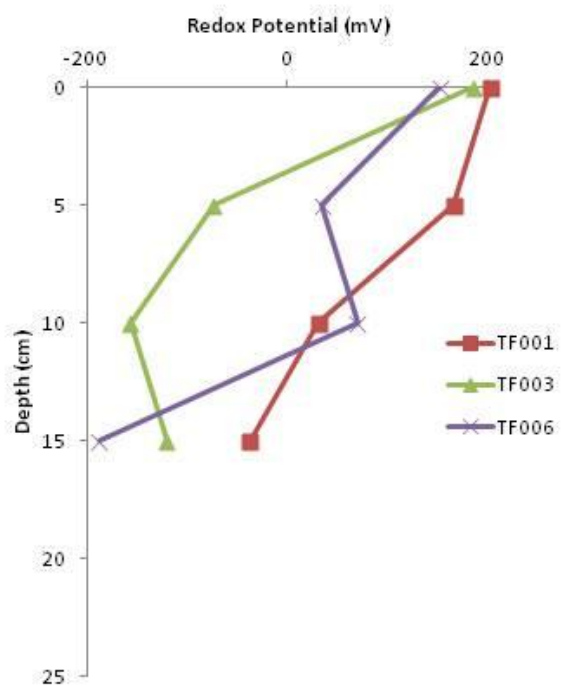
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APPENDIX I:
REDOX DEPTH PROFILES 2011

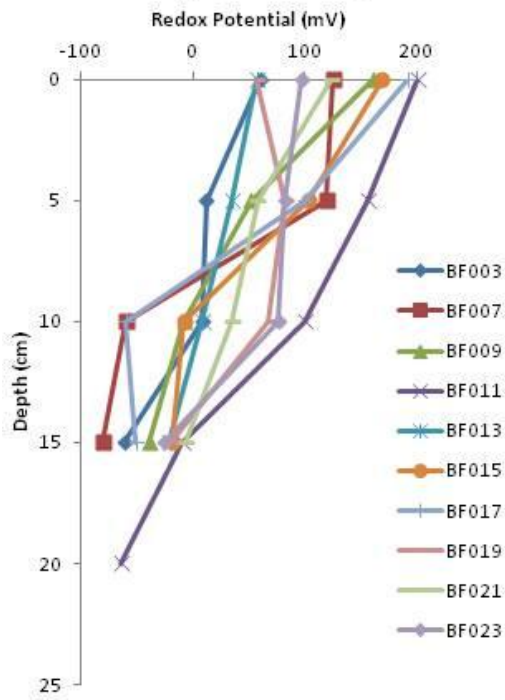
Klondike (HAPS PVC)



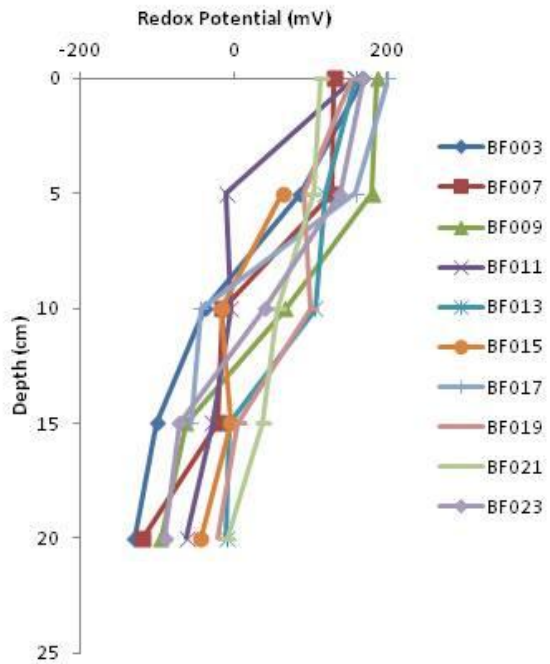
Transitional (DVVN)



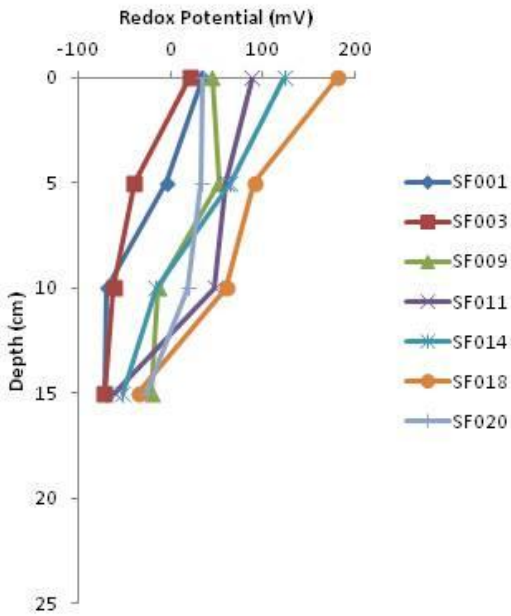
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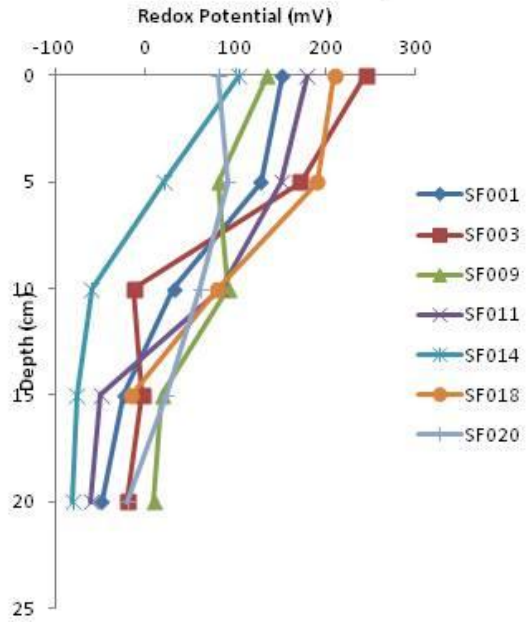
Burger (HAPS WHOLE)

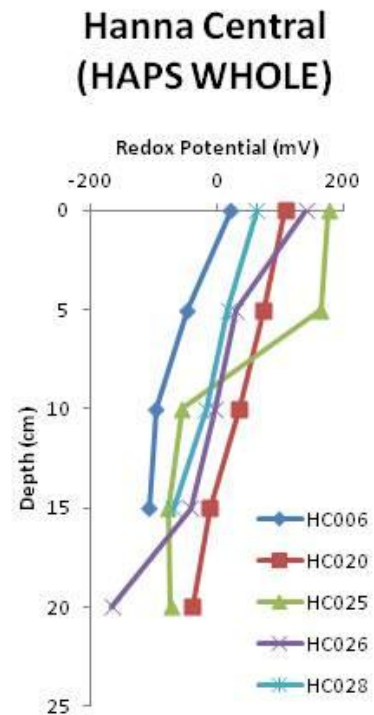
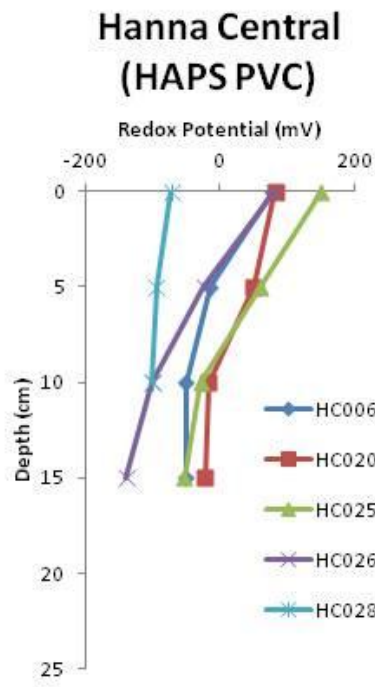
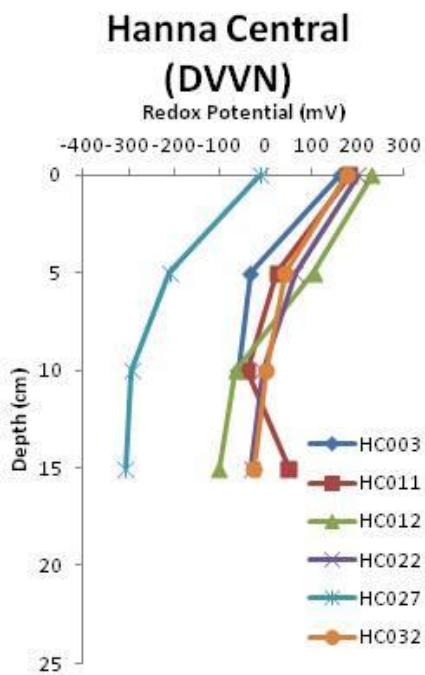
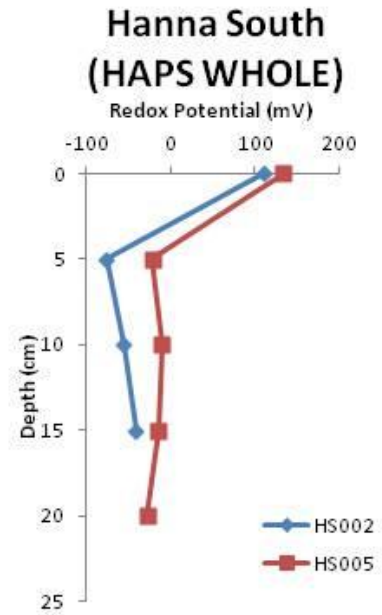
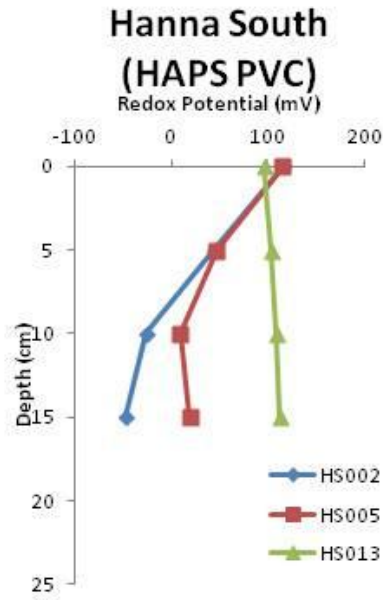
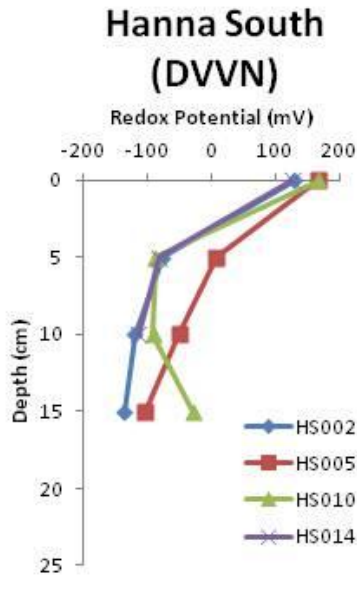


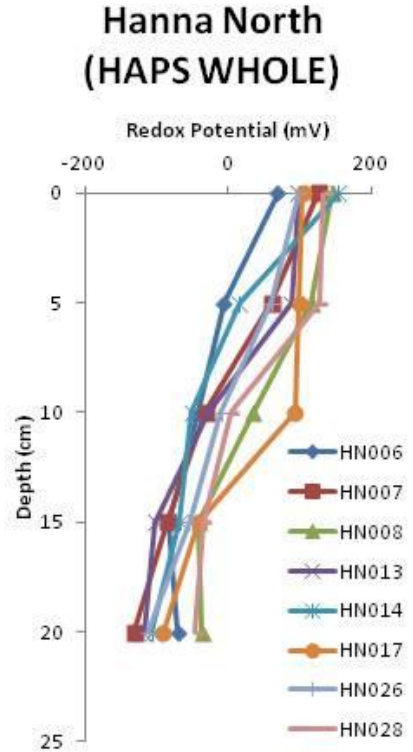
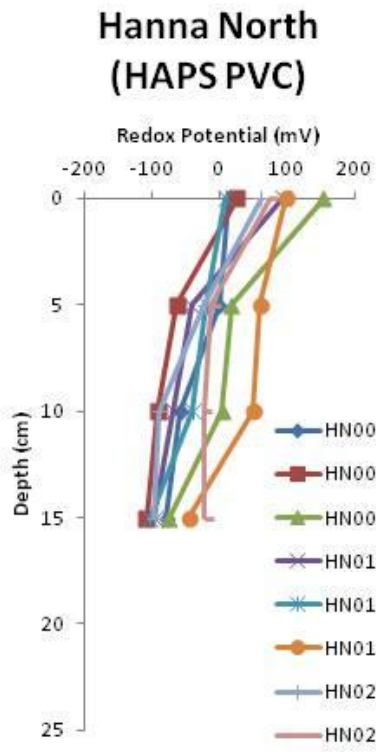
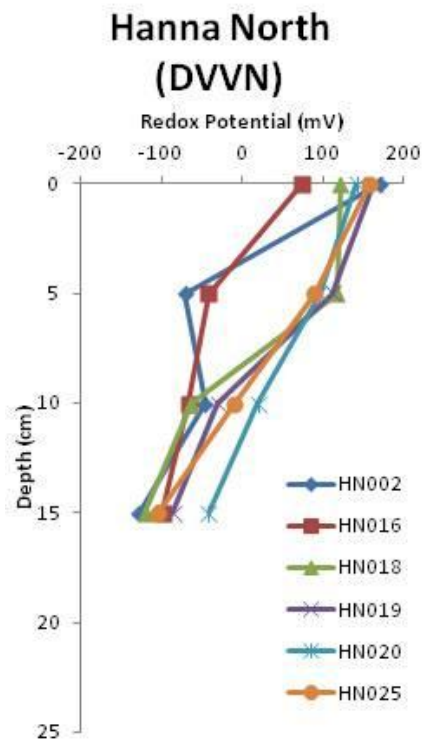
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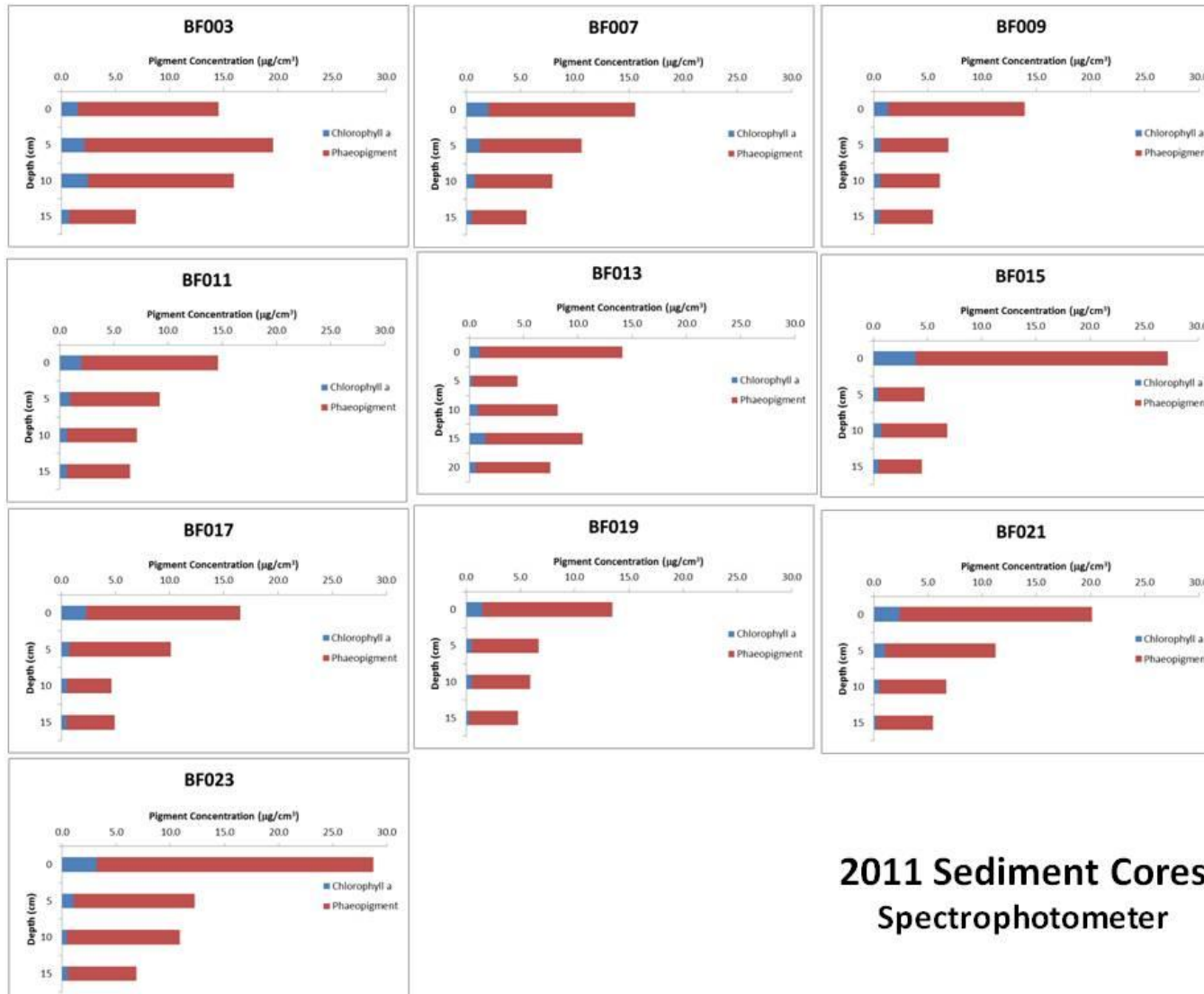
Statoil (HAPS WHOLE)





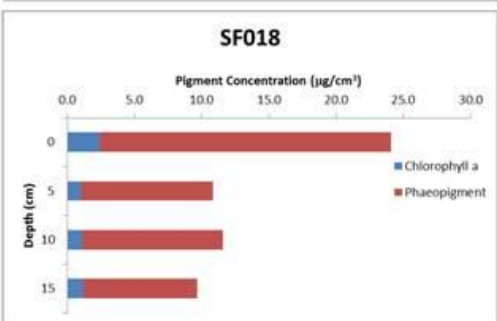
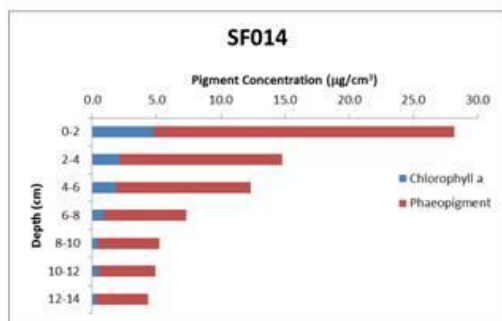
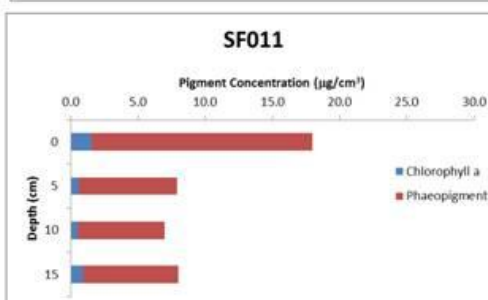
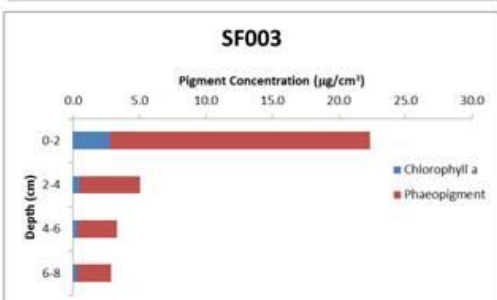
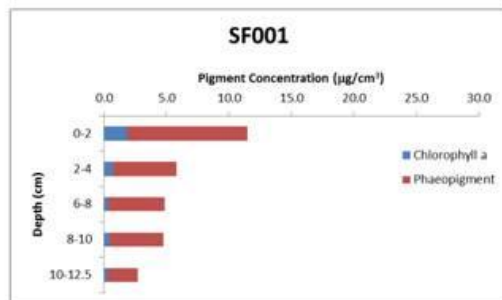
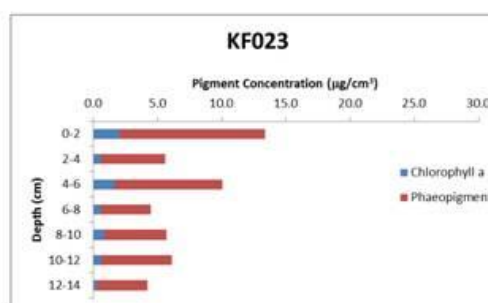
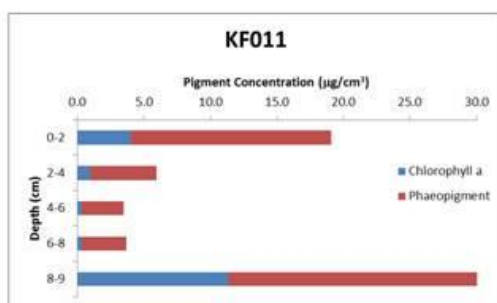
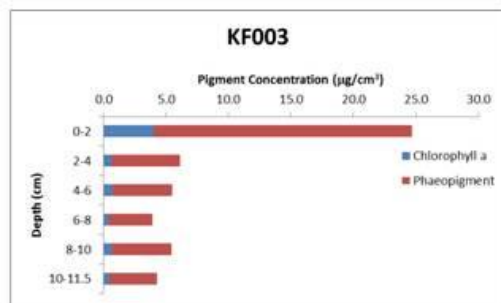


APPENDIX II:
CHLOROPHYLL CONCENTRATION DEPTH PROFILES 2011

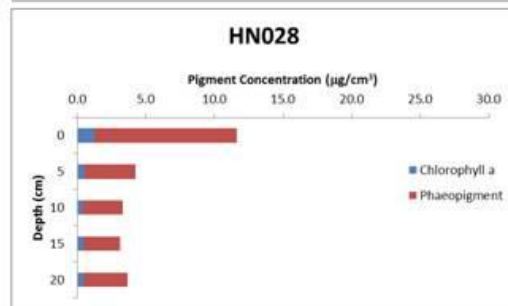
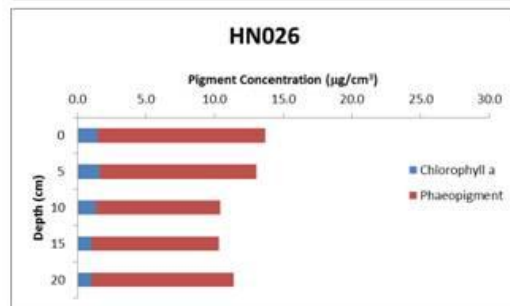
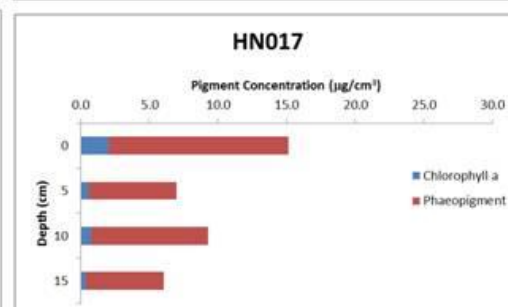
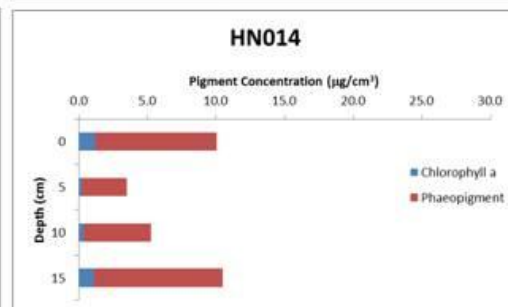
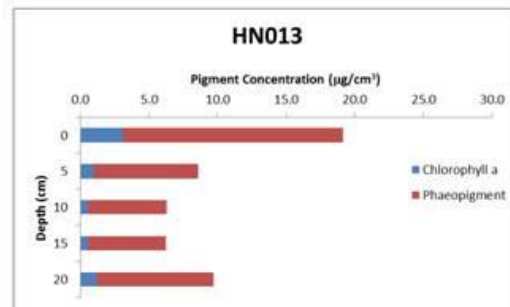
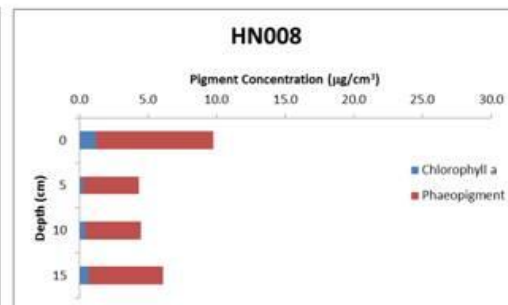
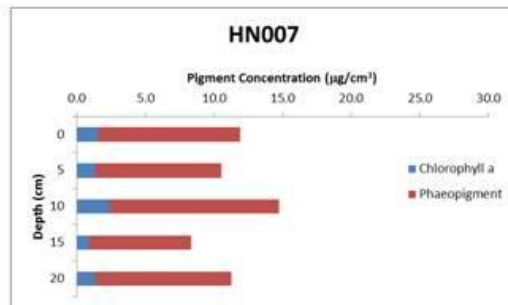
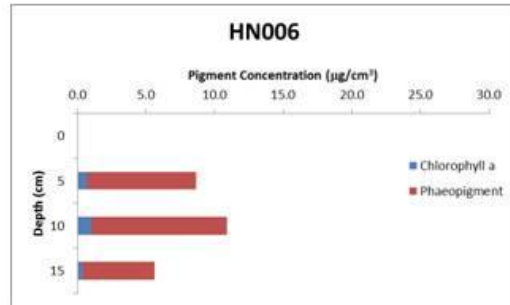


2011 Sediment Cores Spectrophotometer

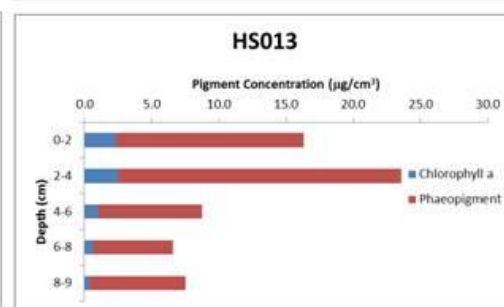
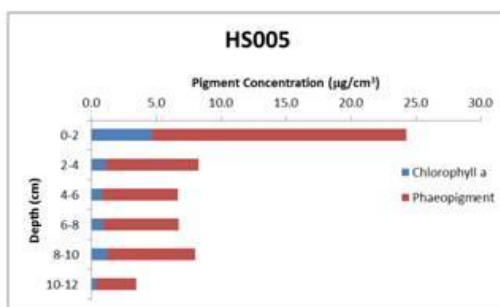
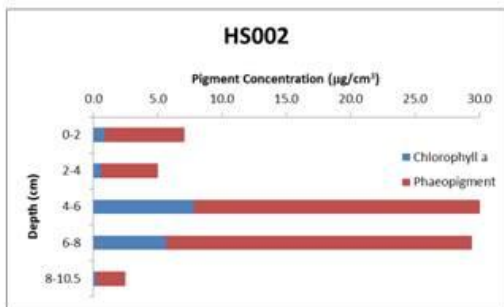
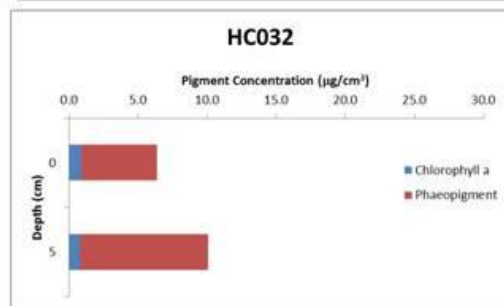
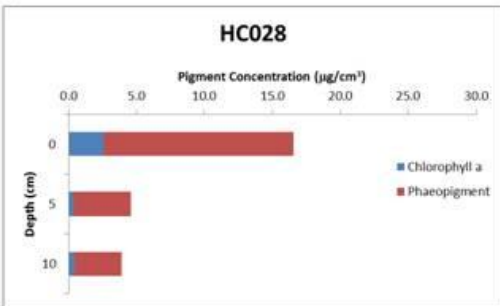
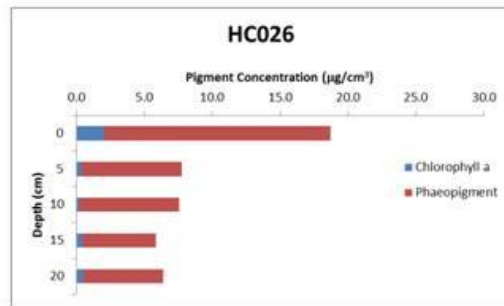
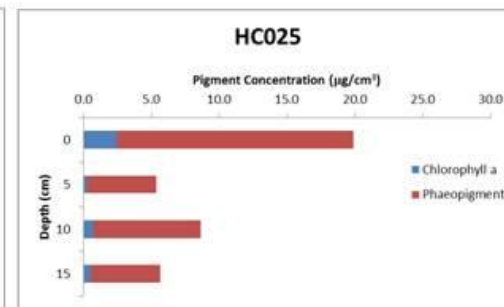
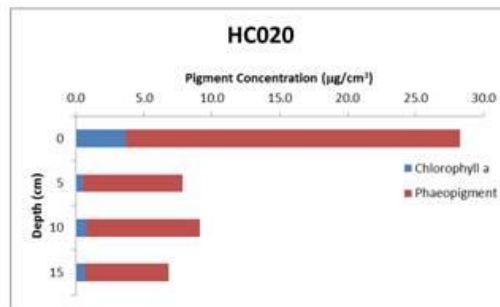
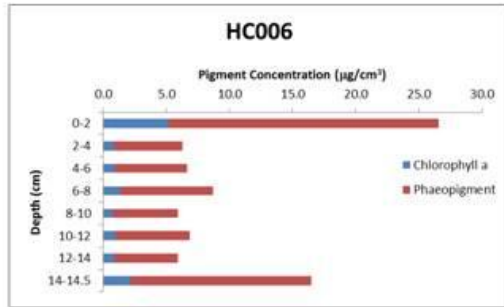
2011 Sediment Cores Spectrophotometer



2011 Sediment Cores Spectrophotometer



2011 Sediment Cores Spectrophotometer



APPENDIX III:

LIST OF INFAUNAL TAXA COLLECTED DURING THE 2008–2011 CSESP

PORIFERA

CNIDARIA

Hydrozoa

Anthozoa

Actiniidae

Edwardsiidae

Edwardsia sp.

Nephtheidae

Eunephtya rubiformis

Halcampoididae

Haloclavidae

Halcampidae

Halcampa crypta

Platyhelminthes

Turbellaria

Trematoda

NEMERTEA

ANNELIDA

POLYCHAETA

Polynoidae

Bylgides sarsi

Bylgides promamme

Arcteobia anticostiensis

Eunoe sp.

Eunoe depressa

Eunoe nodosa

Eunoe oerstedii

Eunoe clarki

Gattyana sp.

Gattyana amondseni

Gattyana cirrhosa

Harmothoe sp.

Harmothoe beringiana

Harmothoe extenuata

Harmothoe imbricata

Polynoe canadensis

Polynoe gracilis

Hesperonoe sp.

Hesperonoe Adventor

Enipo torelli

Pholoidae/Sigalionidae

Pholoe minuta

Phyllodocidae

Anaitides groenlandica

Eteone sp.

Eteone pacifica

Eteone longa
Hesionidae
Syllidae
Autolytus sp.
Syllis sp.
Syllis elongata
Typosyllis sp.
Typosyllis pigmentata
Exogone sp.
Nephtyidae
Nephtys sp.
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 sp.
Paradiopatra parva
Eunicidae
Lumbrineridae
Lumbrineris sp.
Scoletoma fragilis
Arabellidae
Drilonereis sp.
Dorvilleidae
Orbiniidae
Scoloplos armiger
Leitoscoloplos pugettensis
Paraonidae
Aricidea sp.
Levinsenia gracilis
Aapistobranchidae
Aapistobranchus ornatus
Spionidae
Polydora sp.
Prionospio steenstrupi
Spio cirrifera

Spiophanes bombyx
Pygospio elegans
Marenzelleria wireni
Magelonidae
Magelona sp.
Magelona longicornis
Trochochaetidae
Trochochaeta sp.
Trochochaeta carica
Trochochaeta multisetosa
Chaetopteridae
Phyllochaetopterus sp.
Cirratulidae
Cirratulus cirratus
Chaetozone setosa
Cossuridae
Cossura sp.
Flabelligeridae
Brada sp.
Brada granulata
Brada villosa
Brada nuda
Flabelligera sp.
Flabelligera affinis
Flabelligera mastigophora
Diplocirrus longisetosus
Scalibregmatidae
Scalibregma californicum
Opheliidae
Travisia forbesi
Travisia pupa
Ophelina breviata
Ophelina acuminata
Sternaspidae
Sternaspis scutata
Capitellidae
Capitella capitata
Heteromastus filiformis
Notomastus sp.
Mediomastus sp.
Decamastus gracilis
Barantolla americana
Maldanidae
Maldane sarsi
Nicomache sp.
Nicomache lumbricalis

Nicomache personata
Petaloproctus sp.
Petaloproctus Tenuis
Petaloproctus tenuis borealis
Petaloproctus tenuis tenuis
Axiothella sp.
Axiothella catenata
Praxillella gracilis
Praxillella praetermissa
Rhodine bitorquata

Oweniidae

Owenia fusiformis
Myriochele heeri
Galathowenia oculata

Sabellariidae

Idanthyrus saxicavus

Pectinariidae

Pectinaria granulata

Ampharetidae

Amage sp.
Ampharete sp.
Ampharete goesi goesi
Ampharete acutifrons
Ampharete finmarchica
Lysippe labiata
Asabellides sibirica

Terebellidae

Neoamphitrite groenlandica
Nicolea zostericola
Thelepus sp.
Thelepus setosus
Artacama sp.
Artacama proboscidea
Lanassa nordenskioldi
Lanassa venusta venusta
Axionice maculata
Laphania boeckii
Proclea sp.
Proclea emmi
Proclea graffii

Trichobranchidae

Terebellides kobei
Terebellides reishi
Trichobranchus glacialis

Sabellidae

Chone sp.

Chone infundibuliformes

Chone duneri

Chone mollis

Euchone sp.

Euchone analis

Euchone incolor

Bispira crassicornis

Laonome kroeyeri

Jasmineira pacifica

Serpulidae

Spirorbis sp.

OLIGOCHAETA

MOLLUSCA

GASTROPODA

Lepetidae

Lepeta caeca

Trochidae

Margarites sp.

Margarites giganteus

Margarites costalis

Solariella sp.

Solariella obscura

Solariella varicosa

Turbinidae

Moelleria costulata

Rissoidae

Alvania sp.

Cingula sp.

Turritellidae

Tachyrhynchus sp.

Tachyrhynchus erosus

Tachyrhynchus reticulatis

Trichotropidae

Trichotropis sp.

Trichotropis borealis

Trichotropis kroeyeri

Iphinoe coronata

Velutinidae

Velutina undata

Naticidae

Cryptonatica affinis

Euspira pallida

Muricidae

Boreotrophon sp.

Boreotrophon clathratus

Boreotrophon truncatus

Boreotrophon muriciformis

Buccinidae

Buccinum sp.

Buccinum polare

Colus sp.

Colus spitzbergensis

Colus roseus

Liomesus sp.

Neptunea sp.

Neptunea ventricosa

Neptunea communis

Neptunea borealis

Neptunea heros

Plicifusus sp.

Plicifusus kroyeri

Pyrulofusus deformis

Volutopsius sp.

Cancellariidae

Admete sp.

Admete regina

Admete viridula

Conidae

Oenopota sp.

Oenopota elegans

Oenopota excurvatus

Oenopota impressa

Obesotoma simplex

Propebela sp.

Propebela turricula

Propebela arctica

Propebela nobilis

Curtitoma incisula

Curtitoma novajasemljensis

Pyramidellidae

Odostomia sp.

Cylichnidae

Cylichna sp.

Cylichna occulta

Cylichna alba

Diaphanidae

Diaphana minuta

Haminoeidae

Haminoea virescens

Retusidae

Retusa obtusa

NUDIBRANCHIA

OPISTHOBRANCHIA

POLYPLACOPHORA

Leptochitonidae

Leptochiton sp.

Ischnochitonidae

Ischnochiton albus

Mopaliidae

Amicula vestita

BIVALVIA

Nuculidae

Ennucula tenuis

Nuculana sp.

Nuculana pernula

Nuculana minuta

Yoldiidae

Yoldia sp.

Yoldia hyperborea

Yoldia myalis

Yoldia scissurata

Mytilidae

Crenella decussata

Musculus sp.

Musculus niger

Musculus discors

Musculus glacialis

Pectinidae

Chlamys behringiana

Lucinidae

Parvilucina tenuisculpta

Thyasiridae

Adontorhina cyclia

Axinopsida serricata

Thyasira flexuosa

Lasaeidae

Neaeromya compressa

Mysella sp.

Mysella planata

Rochefortia tumida

Carditidae

Cyclocardia sp.

Cyclocardia crebricostata

Cyclocardia crassidens

Cyclocardia ovata

Astartidae

Astarte sp.

Astarte montagui

Astarte borealis

Cardiidae

Clinocardium sp.

Clinocardium ciliatum

Serripes sp.

Serripes groenlandicus

Serripes laperousii

Tellinidae

Macoma sp.

Macoma calcarea

Macoma brota

Macoma moesta

Veneridae

Liocyma fluctuosa

Nutricula lordi

Myidae

Mya sp.

Mya arenaria

Hiatellidae

Hiatella arctica

Pandoridae

Pandora glacialis

Lyonsiidae

Lyonsia arenosa

Periplomatidae

Periploma aleuticum

Thraciidae

Thracia sp.

Lampeia adamsi

PYCNOGONIDA

CRUSTACEA

OSTRACODA

CIRRIPEDIA

Balanidae

Balanus sp.

Balanus crenatus

Balanus rostratus

CUMACEA

Lampropidae

Lamprops krasheninnikovi

Leuconidae

Leucon sp.

Eudorella sp.

Eudorella emarginata

Eudorella groenlandica

Eudorellopsis sp.

Eudorellopsis integra
Eudorellopsis biplicata
 Diastylidae
Diastylis sp.
Diastylis bidentata
Diastylis paraspinulosa
Ektondiastylis robusta
 Nannastacidae
Campylaspis sp.
Campylaspis rubicunda
Campylaspis papillata
Cumella sp.
 TANAIIDACEA
 ISOPODA
 Antarcturidae
Pleuroprion murdochi
 Idoteidae
Synidotea sp.
Synidotea bicuspidata
Synidotea muricata
 Munnidae
Munna sp.
 AMPHIPODA
 Odiidae
Odius sp.
 Ampeliscidae
Ampelisca sp.
Ampelisca macrocephala
Ampelisca birulai
Ampelisca eschrichti
Byblis sp.
Byblis gaimardi
Byblis robusta
Byblis frigidis
Byblis pearcyi
Byblis breviramus
Haploops laevis
 Argissidae
Argissa hamatipes
 Corophiidae
Corophium sp.
 Ischyroceridae
Erichthonius sp.
 Dexaminidae
Guernea nordenskioldi
 Eusiridae

Eusirus cuspidatus
Pontogeneia sp.
Rhachotropis sp.

Gammaridae
Maera sp.
Maera loveni
Melita sp.
Melita dentate

Haustoriidae
Eohaustorius eous

Pontoporeiidae
Pontoporeia sp.
Pontoporeia femorata
Priscillina armata

Isaeidae
Photis sp.
Photis vinogradovi
Protomedeia sp.

Ischyroceridae
Ischyrocerus sp.

Lysianassidae
Anonyx sp.
Hippomedon sp.
Lepidepecreum sp.
Orchomene sp.

Uristidae
Centromedon sp.

Melphidippidae

Oedicerotidae
Aceroides latipes
Bathymedon sp.
Monoculodes sp.
Paroediceros sp.
Westwoodilla caecula

Epimeriidae
Paramphithoe polyacantha

Phoxocephalidae
Harpinia sp.
Harpinia kobjakovae
Harpinia gurjanovae
Paraphoxus sp.
Grandifoxus sp.
Grandifoxus acanthinus
Grandifoxus vulpinus
Grandifoxus nasuta

Pleustidae

Pleustes panoplus
Podoceridae
Dyopedos arcticus
Stenothoidae
Synopiidae
Syrrhoë longifrons
Tiron biocellata
Caprellidea
BRACHYURA
Pinnotheridae
Pinnixa sp.
SIPUNCULA
SIPUNCULIDAE
Golfingiidae
Golfingia margaritacea
Phascoliidae
Phascolion strombus
ECHIURA
Echiuridae
Echiurus echiurus alaskanus
CEPHALORHYNCHA
PRIAPULIDAE
Priapulus caudatus
BRACHIOPODA

APPENDIX IV:

LIST OF MEIOFAUNAL TAXA COLLECTED DURING THE 2011 CSESP

PROTOZOA

FORAMINIFERA

CNIDARIA

HYDROZOA

BRYOZOA

NEMERTEA

KINORHYNCHA

NEMATODA

ANNELIDA

POLYCHAETA

Polynoidae

Gattyana amondseni

Pholoidae/Sigalionidae

Pholoe minuta

Phyllodocidae

Eteone sp.

Eteone pacifica

Eteone longa

Hesionidae

Syllidae

Nephtyidae

Nephtys sp.

Nephtys punctata

Sphaerodoridae

Sphaerodoropsis minuta

Sphaerodoropsis sphaerulifer

Glyceridae

Glycera capitata

Goniadidae

Onuphidae

Paradiopatra sp.

Paradiopatra parva

Lumbrineridae

Lumbrineris sp.

Orbiniidae

Scoloplos armiger

Leitoscoloplos pugettensis

Paraonidae

Aricidea sp.

Apistobranchidae

Apistobranchus ornatus

Spionidae

Polydora sp.

Prionospio steenstrupi

Spio cirrifera

Magelonidae
 Magelona sp.
Cirratulidae
Cossuridae
 Cossura sp.
Flabelligeridae
 Diplocirrus longisetosus
Scalibregmidae
Opheliidae
 Travisia forbesi
 Ophelina acuminata
Capitellidae
Maldanidae
 Maldane sarsi
 Praxillella praetermissa
Pectinariidae
 Cistenides granulata
Ampharetidae
 Ampharete sp.
Terebellidae
Trichobranchidae
 Terebellides stroemi
Sabellidae
c.f. Nerillidae
 Nerilla sp.

OLIGOCHAETA

MOLLUSCA

GASTROPODA

Trochidae
 Solariella varicosa
Turritellidae
 Tachyrynchus reticulatis
Trichotropidae
Naticidae
 Cryptonatica affinis
Cancellariidae
 Admete viridula
Cylichnidae
 Cylichna sp.
 Cylichna occulta
Retusidae
 Retusa obtusa

BIVALVIA

Nuculidae
 Ennucula tenuis
 Nuculana sp.

Nuculana pernula
Yoldiidae
Yoldia sp.
Yoldiella nana
Mytilidae
Musculus sp.
Thyasiridae
Thyasira flexuosa
Carditidae
Astartidae
Astarte sp.
Astarte montagui
Astarte borealis
Cardiidae
Serripes sp.
Tellinidae
Macoma sp.
Veneridae
Liocyma fluctuosa
Lasaeidae
Lyonsiidae
Lyonsia arenosa

PYCNOGONIDA

CRUSTACEA

OSTRACODA

COPEPODA

Harpacticoida

CIRRIPEDIA

Balanidae

Balanus sp.

Balanus sp. cyprid

CUMACEA

Leuconidae

Leucon sp.

Leucon nasica

Eudorella sp.

Eudorellopsis sp.

Eudorellopsis biplicata

Diastylidae

Ektondiastylis robusta

Nannastacidae

Campylaspis sp.

Campylaspis rubicunda

TANAIDACEA

ISOPODA

Munnidae

Munna sp.

AMPHIPODA

Ampeliscidae

Ampelisca macrocephala

Ampelisca eschrichti

Byblis sp.

Byblis frigidis

Byblis pearcyi

Pontoporeiidae

Pontoporeia femorata

Priscillina armata

Isaeidae

Photis sp.

Protomedeia sp.

Lysianassidae

Anonyx sp.

Hippomedon sp.

Oedicerotidae

Aceroides latipes

Bathymedon sp.

Paroediceros sp.

Phoxocephalidae

Harpinia sp.

Harpinia kobjakovae

Paraphoxus sp.

Grandifoxus sp.

Podoceridae

Dyopedos arcticus

Stenothoidae

SIPUNCULA

SIPUNCULIDAE

Golfingiidae

Golfingia margaritacea

ECHIURA

Echiuridae

Echiurus echiurus

CEPHALORHYNCHA

PRIAPULIDAE

Priapulus caudatus

ECHINODERMATA

ASTEROIDEA

Echinoida

Strongylocentrotidae

Strongylocentrotus droebachiensis

HOLOTHUROIDEA

OPHIUROIDEA

OPHIURIDEA

ARTHROPODA

ACARINA

CHORDATA

Ascidiacea

APPENDIX V:

LIST OF BENTHIC TAXA COLLECTED DURING THE 2011 CSESP VIDEO SURVEYS

PORIFERA

Demospongiae

Semisuberites cribrosa

CNIDARIA

Anthozoa

Nephtheidae

Gersemia rubiformis

Actinaria

Actiniidae

Hydrozoa

Hydrozoa/Bryozoa complex 1 – feathery/fluffy

Hydrozoa/Bryozoa complex 2 – stick-like

BRYOZOA

Bryozoa 1 – *Flustrella*-like

Bryozoa 2 – leaf-like

Bryozoa 3 – staghorn-like

Alcyonidiidae

Alcyonidium disciforme

Alcyonidium pedunculatum

NEMERTEA

ANNELIDA

Polychaeta

Sabellidae

Serpulidae

Terebellidae

MOLLUSCA

Bivalvia

Cardiidae

Clinocardium sp.

Yoldiidae

Yoldia hyperborea

Polyplacophora

Gastropoda

Naticidae

Trochidae

PYCNOGONIDA

CRUSTACEA

Amphipoda

Ampeliscidae

Isopoda
Balanomorpha (as “intact barnacle tests”)
Decapoda
 Anomura
 Oregoniidae
 Chionoecetes opilio
 Hyas coarctatus
 Paguroidea
 Paguridae
 Caridea (all shrimps)
 Brachyura

ECHINODERMATA

 Asteroidea
 Solasteridae
 Crossaster papposus
 Echinoida
 Strongylocentrotidae
 Strongylocentrotus cf. droebachiensis
 Holothuroidea
 Psolidae
 Psolus fabricii
 Cucumariidae
 Ocnus glacialis
 Ophiuroidea
 Gorgonocephalidae
 Gorgonocephalus sp.

CHORDATA

 Ascidiacea
 Pyuridae
 Boltenia sp.
 Halocynthia aurantium

Unidentified Organisms

 Unidentified Animals – discrete individuals
 Unidentified Animal Epifauna
 Unidentified Animal Infauna
 Unidentified Colonies – colonial organisms
 Unidentified Colony Epifauna
 Unidentified Colony Infauna
 Unidentified – indeterminate between individual or colony
 Unidentified Epifauna
 Unidentified Infauna

APPENDIX VI:

VIDEO TRANSECT SUMMARIES 2011

Table VI-1. Summary of transect-specific environmental and biological characteristics from photographic sampling of benthos during the 2011 CSESP survey. Values in parentheses are standard deviations. "--" = no video sampling was conducted; "na" = data not available, "--" = not calculated.

South	Distance Along Transect					
	0 m	50 m	100 m	250 m	500 m	1000 m
KF015						
Usable Frames	6	3	2	2	4	3
Depth (m)	36.1	36.2	36.2	36.1	36.5	36.4
% Frequency Sediment Types						
Mud	50	100	0	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	33	0	0	0	0	0
Rock/Mud	17	0	100	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	36.7 (16.0)	13.6 (13.5)	68.0 (2.7)	38.3 (21.9)	18.3 (11.0)	73.4 (33.7)
# Taxa	21	4	17	3	5	5
TF001						
Usable Frames	6	2	1	1	2	3
Depth (m)	40.0	40.0	40.1	40.0	40.1	40.2
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	282.9 (34.3)	267.6 (14.7)	208.9 (--)	196.3 (--)	339.0 (7.1)	287.1 (12.1)
# Taxa	10	6	3	5	5	6

Table VI-1. Continued.

Central A	Distance Along Transect					
	0 m	50 m	100 m	250 m	500 m	1000 m
BF013						
Usable Frames	1	-	2	2	3	1
Depth (m)	na	-	na	na	na	na
% Frequency Sediment Types						
Mud	100	-	100	100	100	100
Sand	0	-	0	0	0	0
Gravel	0	-	0	0	0	0
Sand/Mud	0	-	0	0	0	0
Gravel/Mud	0	-	0	0	0	0
Rock/Mud	0	-	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	288.4 (--)	-	275.3 (6.6)	385.7 (13.5)	333.3 (25.8)	305.5 (--)
# Taxa	3	-	6	5	6	3
TF003						
Usable Frames	6	3	2	2	2	2
Depth (m)	43.4	43.4	43.4	43.4	43.4	43.4
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	215.1 (75.4)	250.5 (224.7)	216.2 (38.8)	331.3 (37.4)	173.8 (42.5)	249.5 (5.5)
# Taxa	6	3	3	6	3	4

Table VI-1. Continued.

Central B	Distance Along Transect					
	0 m	50 m	100 m	250 m	500 m	1000 m
HC012						
Usable Frames	4	2	3	2	2	4
Depth (m)	40.7	40.7	40.7	40.8	40.6	40.5
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	0.0 (0.0)	3.3 (4.6)	6.4 (0.3)	3.1 (4.4)	0.0 (0.0)	1.5 (3.1)
# Taxa	0	1	2	1	0	1
HC020						
Usable Frames	2	1	2	2	2	2
Depth (m)	47.3	47.4	47.4	47.5	47.5	47.6
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	16.9 (5.7)	13.7 (--)	56.3 (8.7)	63.1 (6.3)	39.0 (18.7)	31.1 (6.6)
# Taxa	3	1	7	3	3	3

Table VI-1. Continued.

Central B (cont.)	Distance Along Transect					
	0 m	50 m	100 m	250 m	500 m	1000 m
HC025						
Usable Frames	4	5	3	4	4	3
Depth (m)	40.0	40.0	40.1	39.8	39.9	39.9
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	16.4 (14.1)	35.4 (19.2)	19.2 (6.9)	25.6 (11.6)	19.3 (12.0)	24.6 (3.4)
# Taxa	6	12	6	8	4	5
HC032						
Usable Frames	5	4	6	5	5	6
Depth (m)	36.8	36.6	36.5	36.5	36.6	36.9
% Frequency Sediment Types						
Mud	0	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	100	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	67.1 (24.6)	38.7 (19.4)	52.0 (9.5)	37.1 (15.7)	42.9 (14.1)	46.4 (26.6)
# Taxa	12	9	11	10	9	14

Table VI-1. Continued.

Central B (cont.)	Distance Along Transect					
	0 m	50 m	100 m	250 m	500 m	1000 m
SF007						
Usable Frames	7	2	3	2	2	2
Depth (m)	38.0	38.1	38.1	38.0	38.0	38.2
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	11.1 (6.4)	12.4 (8.7)	6.3 (6.4)	3.5 (4.9)	6.3 (0.3)	6.7 (9.5)
# Taxa	7	3	3	2	2	2
SF020						
Usable Frames	4	1	4	5	4	4
Depth (m)	37.2	37.2	37.2	37.2	37.2	37.1
% Frequency Sediment Types						
Mud	100	100	100	100	100	100
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	0
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	3.1 (3.6)	12.7 (--)	8.1 (3.4)	16.4 (12.3)	11.4 (11.4)	11.2 (3.0)
# Taxa	3	2	5	8	6	6

Table VI-1. Continued.

North	Distance Along Transect					
	0 m	50 m	100 m	250 m	500 m	1000 m
HN005						
Usable Frames	8	5	4	5	4	5
Depth (m)	27.4	27.7	27.7	27.5	25.6	27.7
% Frequency Sediment Types						
Mud	0	0	0	0	0	0
Sand	88	100	0	20	100	60
Gravel	0	0	25	0	0	0
Sand/Mud	0	0	0	20	0	40
Gravel/Mud	12	0	75	60	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	32.2 (14.8)	21.0 (12.0)	25.0 (13.6)	13.0 (10.9)	20.6 (6.5)	19.7 (11.4)
# Taxa	8	7	6	7	2	6
HN013						
Usable Frames	3	5	3	4	4	3
Depth (m)	42.2	42.0	42.5	42.6	42.6	41.9
% Frequency Sediment Types						
Mud	100	100	100	100	100	67
Sand	0	0	0	0	0	0
Gravel	0	0	0	0	0	0
Sand/Mud	0	0	0	0	0	33
Gravel/Mud	0	0	0	0	0	0
Rock/Mud	0	0	0	0	0	0
Benthic Fauna						
Ave. Density (ind. m ⁻²)	34.4 (30.6)	27.4 (16.6)	22.1 (7.7)	10.0 (9.4)	15.3 (13.9)	16.9 (19.7)
# Taxa	4	11	5	4	5	7