

Sediment Characteristics and Infauna of Deltaic Mudflats Along the Alaskan Beaufort Sea



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Authors

Abby N. Powell, Roy T. Churchwell, Kenneth H. Dunton, Jeffrey G. Baguley, Anthony D. Kamikawa, Colleen T. E. Kellogg, Byron C. Crump, Philip Bucolo

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Abby Powell

U.S. Geological Survey Alaska Cooperative Fish and Wildlife Research Unit

University of Alaska Fairbanks

Fairbanks, Alaska 99775-7020

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US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
3801 Centerpoint Drive, Suite 500
Anchorage, AK 99503-5820
Phone: 907-334-5200
Fax: 907-334-5202

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Abbreviations and Acronyms

ANWR	Arctic National Wildlife Refuge
C	carbon
chl <i>a</i>	chlorophyll <i>a</i>
DOC	dissolved organic carbon
HPLC	high pressure liquid chromatography
JOHC	Jago, Okpilak/Hulahula, and Canning River deltas
MDS	multidimensional scaling
N	nitrogen
NH ₄	ammonium
NWR	National Wildlife Refuge
OCS	Outer Continental Shelf
OTUs	Operational Taxonomic Units
PCR	polymerase chain reaction
POM	particulate organic matter
rRNA	ribosomal ribonucleic acid
TOC	total organic carbon
USFWS	US Fish and Wildlife Service

1. Executive Summary

Nearshore shelf areas of the Beaufort Sea are defined by biological and physical gradients that have influence on the Arctic ecosystem including trophic structure, productivity, and the species that inhabit the area. The coast's biologically productive habitats support diverse biota during the summer that could be affected by oils spills or other physical disturbances resulting from offshore oil exploration in the Beaufort Sea. A greater understanding of benthic community structure and function is necessary to better understand the importance of these systems as food resources for migratory shorebirds. The primary objectives of this study were to (1) quantify the spatial and temporal distribution of bacterial assemblages, meiofauna, and macrofauna at coastal lagoons and river deltas along the Beaufort Sea coast, and (2) characterize the sediment pore water chemistry for salinity, ammonium, organic carbon, chlorophyll *a*, stable carbon isotopic signature, and sediment grain size at sample locations representative of each site. We describe the underlying characteristics of sediments and their influence on lower trophic levels to better understand the food webs that ultimately support shorebirds on their migration out from their arctic breeding grounds.

Single-celled organisms in sediments are the principal diet for the meiobenthos and macrobenthos that sustain shorebird communities, but little is known about the species composition of these microbenthic communities or their sensitivity to oil exposure. We investigated taxonomic composition of prokaryotic and eukaryotic communities in deltaic mudflats of the Jago, Okpilak/Hulahula, and Canning river deltas (JOHC) using DNA sequencing. Bacterial communities were highly diverse in all samples, and variability was explained by salinity, ammonium concentrations, total organic carbon content, and organic carbon and nitrogen stable isotope ratios. Bacterial communities showed minimal interannual variability and only slight geographic variability, suggesting a broadly distributed and persistent community that may serve as a sensitive indicator of shifts in detrital organic matter including oil-associated hydrocarbons. One genera of bacteria that includes known hydrocarbon-degrading species (*Marinobacter*) was detected in high proportions in the Okpilak and Canning deltas, suggesting prior or ongoing exposure to hydrocarbons associated with oil. Microeukaryotic communities showed greater interannual variability than prokaryotic communities suggesting

that microeukaryotic community composition is less predictable and thus less useful as an indicator of environmental change.

Metazoan meiofauna are abundant and diverse benthic invertebrates that reside in marine, estuarine, and freshwater soft-sediment habitats. With rapid growth rates and short generation times, their biomass and production are a vital component of benthic food webs. We found abundances of meiofauna comparable to other estuarine habitats studied in the Arctic. Meiofauna diversity was relatively low. There were only minor spatiotemporal differences in abundance and diversity. Based on their high abundance, meiofauna presumably contribute significantly to the annual biomass bloom and provide a vital carbon source that is transferred up the food web.

On shallow tidal flats, benthic microalgae are among the most prolific primary producers of labile carbon, but there is little quantitative data to assess their overall importance. We determined the nutritional quality of deltaic sediments at JOHC based on analyses of sediment chlorophyll, stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures, total organic carbon, C:N ratios, and sediment porewater ammonium (NH_4^+) and salinity. Our analyses revealed the presence of a healthy microphytobenthos based on chlorophyll *a* concentrations ranging from 3.6 – 203.9 mg m^{-2} with consistent presence of fucoxanthin reaching 93 mg m^{-2} , indicating that the microphytobenthos consisted primarily of diatoms. The chlorophyll *a* compound is degraded into pheopigments by bacterial and metazoan foraging. Pigment analysis revealed that chlorophyll *a*:total pheopigments ratios were < 1 , providing clear evidence for the importance of the microphytobenthos to primary consumers. Sediment porewaters were clearly estuarine, and sediment geochemical parameters clearly reveal strong contributions of terrestrial organic matter based on low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and high C:N ratios.

Shorebirds are dependent on benthic invertebrates as energy and nutrient sources to fuel migration, and the JOHC river deltas are used by thousands of shorebirds as migratory stopover sites. We found that the fauna of JOHC were depauperate compared to river deltas at more boreal latitudes, reflecting a highly stressed environment for macroinvertebrates in the Arctic. Only six taxa regularly occurred in our samples: Oligochaeta, Chironomidae, Tipulidae, Amphipoda, Chaetiliidae, and Spionidae; however, these taxa were not found at every river

delta. The Jago and Okpilak/Hulahula deltas had similar sediment environmental characteristics, but the Canning Delta had four times higher salinity and carbon values and tended to be cooler and drier on average than the other two sites. These differences resulted in variable abundances and distributions of macroinvertebrates among deltas. In addition, despite nine-month periods of frozen sediments, JOHC deltas were populated by a range of taxa represented by both marine and freshwater assemblages. Freshwater taxa such as Diptera and Oligochaeta survived extreme freezing events, and marine organisms such as Amphipoda and Polychaeta rapidly recolonized deltas following ice ablation. Stable isotopic analyses revealed that both marine and freshwater assemblages of macroinvertebrates assimilated both marine and terrestrial sources of organic carbon. Sediment accretion in river deltas of the Beaufort Sea may be greater now than in the past due to increased melting of glaciers in the Brooks Range and sediment transport will likely decline in the next 50-75 years when glacial ice disappears. Changes in sedimentation rates will likely transform sediment structure by increasing grain size, a change that could further affect some invertebrates, especially those associated with more fine-grain sediments (e.g. Chironomidae). Although the deltaic mudflats of JOHC river deltas had different characteristics in terms of sediments and associated infauna, they each provide critical food resources for shorebirds as they leave their arctic breeding grounds on fall migration.

2. Introduction

Nearshore shelf areas of the Beaufort Sea are defined by specific biological and physical gradients that have influence on the Arctic ecosystem including trophic structure, productivity, and the species that inhabit there. Massive freshwater discharges from the Mackenzie River along with numerous smaller rivers including the Jago, Okpilak/Hulahula, and Canning River delta systems (JOHC) produce an environment that is estuarine in characteristic (Figure 2.1). The features of these estuarine ecosystems vary in trophic structure and productivity. The role of terrestrial carbon in these estuarine food webs is especially important in view of current warming trends in the Arctic and from Outer Continental Shelf (OCS) post-lease exploration and development (Dunton et al. 2006; 2012). Shorebirds depend on invertebrates for food for pre-migratory fattening along the delta mudflats that are at the river face (Connors et al. 1979; Taylor et al. 2011, Churchwell 2015). Smaller organisms that supply food sources for these organisms also make important contributions to estuarine food webs (Crump et al. 2013). However, there is little information on species composition, abundance, or distribution of the microfauna and meiofauna living within the intertidal habitats of the littoral zones along the Beaufort Sea coast (Churchwell et al. 2015). In addition, the distribution of these microfauna and meiofauna may be linked to sediment grain size characteristics, as has been shown elsewhere along the Beaufort Sea coast (Dunton and Schonberg 1980).

The Beaufort Sea coast includes a variety of biologically productive habitats in lagoons, barrier islands, river deltas, and adjacent tundra areas. These habitats support diverse biota and could be affected by oils spills or other physical disturbances resulting from offshore oil exploration in the Beaufort Sea. Oil spills, disruption of tundra surfaces, impoundments, and human activities, among other changes could potentially impact the benthic invertebrate community including important shorebird prey (Truett 2000). These ecosystems are particularly vulnerable to predicted climate-change effects, such as inundation and increased erosion caused by rising sea levels, glacial melt, and longer periods of open water (Churchwell et al. 2015). Recent studies, focused on the trophic linkages among estuarine and lagoon fauna and the assimilation of various carbon sources have provided valuable insights into the sensitivity and resilience of these systems to anthropogenic changes (Dunton et al. 2012), but have not addressed the intimate

linkages with higher trophic level species, including shorebirds, that are summer residents of arctic nearshore systems.

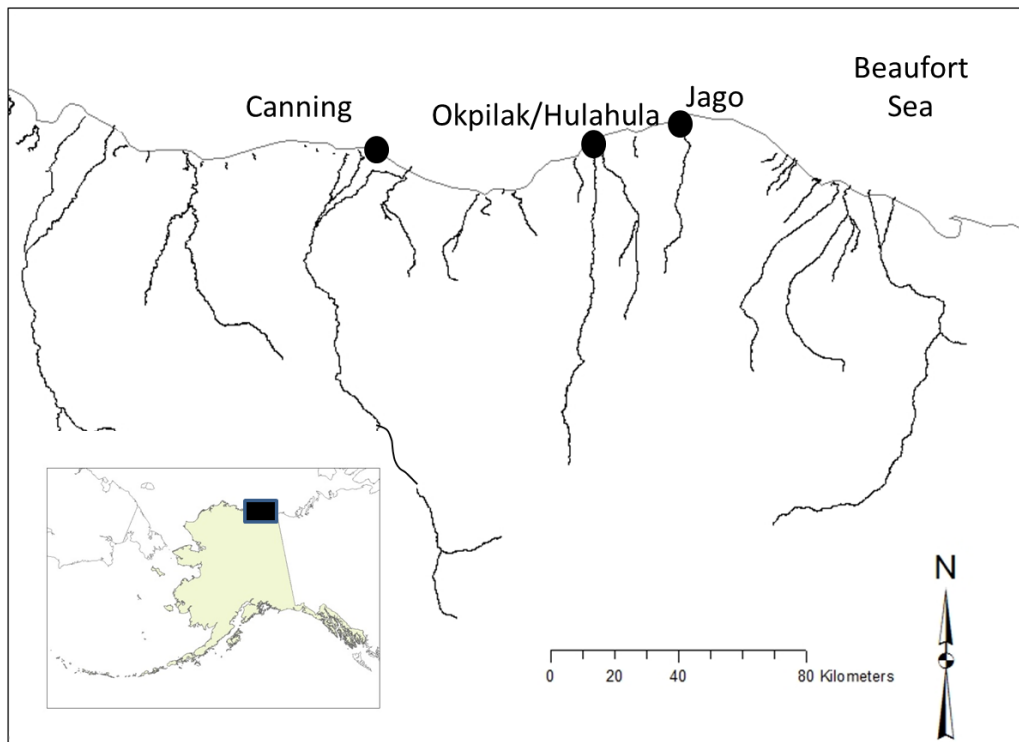


Figure 2.1. Location of the three river deltas (JOHC) in the eastern Beaufort Sea in northern Alaska.

It is known that oils spills adversely affect invertebrate communities, including microfauna (e.g. bacterial, fungal, or protozoan populations), and meiofauna (nematodes, gastrotriches, and other eukaryotic organisms) living within the interstitial spaces of sediments on the seabed (for review see Churchwell et al. 2015). Baseline information pertaining to the biogeochemistry of these benthic environments (e.g. sediment characteristics, porewater nutrients, organic matter) would allow scientists to identify river and coastal ecosystem processes that may result from anthropogenic or regional climate change along the Beaufort Sea coast. A secondary component of the estuarine chemistry is the degree of the water-borne constituents (i.e. sediment, nutrients, and organic matter) from the JOHC rivers coming from glacier melt (Nolan et al. 2011). To date

it is unclear how inputs from these rivers affect the coastal ocean ecosystem, and how this likely to change as the glaciers disappear. Biogeochemical studies of arctic coastal estuarine environments may provide more insights into the function of these systems.

2.1 Objectives

The specific objectives of this study were to:

1. Quantify the spatial and temporal distribution of bacterial assemblages, meiofauna, and macrofauna at coastal lagoons and river deltas along the Beaufort Sea coast within the US Fish and Wildlife Service (USFWS) Arctic National Wildlife Refuge at three sites associated with the coastal lagoons and deltas of the JOHC rivers.
2. Characterize the sediment pore water chemistry for salinity, ammonium, organic carbon, chlorophyll *a*, stable carbon isotopic signature, and sediment grain size at sample locations representative of each site.

2.2 Tasks

There were seven tasks within the scope of work:

1. Quantify the spatial and temporal distribution of macrofaunal benthic invertebrates at three coastal lagoons and river deltas along the Beaufort Sea coast within the USFWS Arctic National Wildlife Refuge.
2. Examine the role of meiofaunal populations as food resources through quantitative analysis of benthic cores taken at all three sites.
3. Conduct a census of the microbial populations (bacteria archaea, and eukarya) in the sediments of the three research sites using DNA sequencing.
4. Quantify sediment chlorophyll and describe the predominant sediment microalgae.
5. Describe the associated sediment characteristics at the three sites. Include salinity, organic carbon, ammonium, and sediment grain size at each sample location.
6. Relate the organic composition of the sediments to river sources of organic matter based on stable carbon isotopic measurements of sediments to identify the relative importance of allochthonous and autochthonous carbon sources.

7. Provide a synthesis that links shorebirds and their macro-invertebrate prey within mudflat habitats to broader and multiple trophic food web levels (include meio- and macrofauna population assemblages) and the nature of their carbon footprints.

The results of these tasks are presented herein in the following manner. Tasks 2, 3, and 4 are presented as separate chapters of this report (Chapters 3, 4, and 5). Task 5 is incorporated into several sections. Finally, we present Tasks 1 and 7 as a cohesive section (Chapter 6; Churchwell et al. 2015).

2.3 References

- Churchwell RT. 2015. Stopover ecology of semipalmated sandpipers (*Calidris pusilla*) at coastal deltas of the Beaufort Sea, Alaska. PhD Dissertation, University of Alaska, Fairbanks. 149 pp.
- Churchwell RT, Kendall SJ, Blanchard AL, Dunton KH, Powell AN. 2015. Natural disturbance shapes benthic intertidal macroinvertebrate communities of high latitude river deltas. *Estuaries and Coasts*. DOI 10.1007/s12237-015-0028-2
- Connors PG, Myers JP, Pitelka FA. 1979. Seasonal habitat use by arctic Alaskan shorebirds. *Studies in Avian Biology*. 2:101–111.
- Crump BC, Ducklow HW, Hobbie JE. 2013. Estuarine Microbial Food Webs. Day JH et al., editors. *Estuarine Ecology*. Second Edition. John Wiley and Sons, Inc. p. 263-284.
- Dunton KH, Schonberg SV. 2000. The benthic faunal assemblage of the Boulder Patch kelp community. Truett JC, Johnson SR, editors. *The Natural History of an Arctic Oil Field*. Academic Press. p. 371-397.
- Dunton KH, Schonberg SV, Cooper LW. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. *Estuaries and Coasts*. 35:416-435.
- Dunton KH, Weingartner T, Carmack EC. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. *Progress in Oceanography*. 71:362-378. DOI:10.1016/j.pocean.2006.09.011.
- Taylor AR, Lanctot RB, Powell AN, Kendall SJ, Nigro DA. 2011. Residence time and movements of postbreeding shorebirds on the northern coast of Alaska. *Condor*. 113:779–794.

- Nolan, MR, Churchwell R, Adams J, McClelland J, Tape KD, Kendall S, Powell AN, Dunton K, Payer D, Martin P. 2011. Predicting the Impact of Glacier Loss on Fish, Birds, Floodplains, and Estuaries in the Arctic National Wildlife Refuge. US Geological Survey Scientific Investigations Report 2011-5169, Reston, Virginia.
- Truett JC. 2000. Introduction. Truett JC, Johnson SR, editors. The Natural History of an Arctic Oil Field. Academic Press. p. 3-13.

3. Sediment Meiofaunal Populations

Jeffrey G. Baguley and Anthony D. Kamikawa, Marine Ecosystems Analysis Laboratory, University of Nevada-Reno

3.1 Introduction

Meiofauna are small benthic invertebrates ranging in size from 0.063–0.500 mm, and include members of 22 of 35 known animal phyla (mostly marine). Metazoan meiofauna are ubiquitous in marine, estuarine, and freshwater soft-sediments with high abundance, biomass, and diversity (Coull and Bell 1979; Baguley et al. 2006a; Giere 2009). Meiofauna live on smaller spatial and temporal scales (Bell 1980; Schwinghamer 1981) and have shorter generation times and higher metabolic rates (Mahaut et al. 1995) compared to the larger macrobenthos, and lack planktonic larval dispersal (Giere 2009). These life-history characteristics make meiobenthos useful for studying ecological and evolutionary mechanisms (Thistle 2003), but also aid in assessing environmental or ecotoxicological effects (Montagna and Harper 1996; Bejarano et al. 2006).

Meiofauna have been unequivocally identified as food for higher trophic levels (Coull 1990 and references therein). Macrobenthos and zooplankton also feed on meiofauna, providing additional mechanisms for transfer of carbon to higher trophic levels (Coull 1990). Predator exclusion/inclusion experiments report reductions in meiofauna biomass during inclusions (e.g., Gee et al. 1985; Smith and Coull 1987). Based on our understanding of meiofauna as food for higher trophic levels, it is expected that this group of microscopic metazoan and protistan organisms serves as sources of secondary production and fuels higher trophic levels in benthic estuarine food webs of the high Arctic. A detailed study of meiofauna community structure and function is necessary to understand potential trophic linkages that may fill important knowledge gaps.

Here, the first report of metazoan meiofauna community structure is presented for high Arctic estuarine habitats within the Arctic National Wildlife Refuge (ANWR). The objectives of this study were to quantify the spatial and temporal distribution of meiofauna assemblages at three coastal lagoons along the Beaufort Sea coastline within ANWR.

3.2 Methods

Sampling occurred during field seasons in 2011 and 2012. During the first field season (July/August 2011), meiobenthic samples were randomly collected from three JOHC coastal lagoon sites. Approximately 100 core samples from separate sampling stations were collected from the Jago and Okpilak/Hulahula deltas, while approximately 50 core samples from separate sampling stations were collected from the Canning Delta (Figure 3.1). During the second field season (July/August 2012), core samples were collected from the same three deltas. Approximately 50 core samples from separate sampling stations were collected from the Jago and Okpilak/Hulahula deltas, while 30 core samples were collected from the Canning Delta. During both 2011 and 2012 field seasons temporal replication occurred between the two months, July and August.



Figure 3.1. Sediment core sampling at the Jago River delta.

Metazoan meiofauna (0.5 mm to 45 μ m) were collected using a modified 50-cc syringe as a coring device (2.9 cm i.d.). The cores were then sectioned into three vertical depth profiles: 0-1, 1-3, and 3-5 cm. Each section was collected and stored in separate 100-ml plastic sample jars. Within each sample jar, animals were narcotized with 20 ml of a 7% magnesium chloride solution for 10 min before being preserved in an equal volume of 10% buffered formalin (resulting in a final 5% formalin concentration) mixed with a small amount of Rose Bengal dye. Buffered formalin was made from estuarine water filtered through a 0.042 mm sieve to exclude pelagic and contaminant organisms. Sample jars were then closed tightly and lids were wrapped in electrical tape to prevent leakage during shipping. No sieving or sorting of meiofauna occurred in the field. Intact sediment samples were shipped to the University of Nevada-Reno for analysis in the Marine Ecosystems Analysis Laboratory.

In the laboratory, samples were rinsed over 0.500-mm and 0.045-mm mesh sieves. Macrofauna were removed from the meiofauna sample by the 0.500-mm mesh sieve, and meiofauna were retained on the 0.045-mm mesh sieve. Fine sediments (silt and clay) pass through the 0.045-mm sieve, but the coarser fraction remains. Meiofauna were separated from coarse sediments using isopycnic centrifugation in Ludox HS-40 (Burgess 2001). Meiofaunal specimens were counted and identified to the major taxonomic level, which will yield estimates of total abundance as well as major taxonomic diversity. The methods are consistent with those used in previous Minerals Management Service-funded studies by members of the project team (e.g., Baguley et al. 2006b).

Meiofauna community structure was analyzed using univariate and multivariate statistical procedures to test the following null hypotheses:

H₀₁: There is no difference in community structure between the three estuarine basins (“sites”).

H₀₂: There is no difference in community structure between sampling years (“years”).

H₀₃: There is no difference in community structure between sampling months (“sessions”).

Two-way analysis of variance (ANOVA) was used to test for differences in community metrics of total abundance (N) and diversity (Hill’s N1) across the main effects of site, year, and session and also the interactions of site by year, site by session, and year by session. Within the randomized design, each sample was considered a multivariate replicate; therefore, there were 10

replicate samples per basin, per month, for a total of 20 spatial replicates per year. Tukey's Studentized Range test was used for post-hoc analysis of group means across the main effects. Abundance was $\log(x+1)$ transformed prior to analysis to conform to the assumptions of the general linear model. N1 is already a log transformation and therefore did not require additional transformation prior to analysis. Descriptive statistics and ANOVA were carried out using PROC MEANS and PROC GLM in SAS Statistical Software, version 9.3 (SAS Institute Inc.). Community structure was analyzed with non-parametric multivariate statistical routines. Non-metric Multidimensional Scaling (MDS) was used to ordinate samples based on similarity and multivariate community structure differences were tested using analysis of similarity (ANOSIM). Similarity percentages were calculated to explain differences in community structure. Community structure data was fourth root transformed prior to calculation of sample similarity using the Bray Curtis index. All multivariate routines were carried out in PRIMER, version 6.1.2. Diversity indices were also calculated in PRIMER.

3.3 Results

A total of 120 samples were processed from the 2011 (60 samples) and 2012 (60 samples) field seasons (Table 3.1). We processed samples from the 2011/2012 field seasons for a balanced design as follows: 10 samples per month, per year, and per delta, with the only exception being that 8 samples were taken during the July 2012 field season at the Canning Delta due to excessive inundation of the delta. In order to balance the sampling design between years, 12 samples were analyzed from the August 2012 field season at the Canning Delta.

Of the 120 samples processed in the study, a total of 1.57×10^5 individuals were enumerated from 21 major meiofaunal taxa. Mean core abundance extrapolated to N m^{-2} was 1.98×10^6 with a standard deviation of 1.58×10^6 . The maximum abundance collected at each lagoon was found in 2012. Nematoda, Harpacticoida, nauplii, and Tardigrada were the three dominant groups accounting for 99.3%. The remaining 0.7% of the meiofaunal community was comprised of Kinorhyncha, Ostracoda, Gastrotricha, Rotifera, Nemertinea, Cyclopoida, Bivalvia, Gastropoda, Acari, Oligochaeta, Sipuncula, Amphipoda, Aplacophora, Chironomidea, and unknowns. Unknown or unidentifiable individuals contributed less than 0.02% to the overall abundance. These unknowns are most likely soft-bodied taxa (such as Turbellaria, Bryozoans, and protists),

which often become morphologically distorted during fixation with formalin and are therefore unrecognizable.

Table 3.1. Total number of core samples processed from each site [Canning (CRD), Jago, Okpilak/Hulahula (OKP)], month, and year. All completed samples include 3 depth profiles (0-1, 1-3, and 3-5 cm). *Only 8 samples were taken due to inundation of the mudflat at time of sampling.

YEAR	BASIN	SESSION	SAMPLES COMPLETED	ANNUAL TOTAL SAMPLES COMPLETED
2011	CRD	July	10	20
2011	CRD	August	10	
2011	JAGO	July	10	20
2011	JAGO	August	10	
2011	OKP	July	10	20
2011	OKP	August	10	
2012	CRD	July	8*	20
2012	CRD	August	12	
2012	JAGO	July	10	20
2012	JAGO	August	10	
2012	OKP	July	10	20
2012	OKP	August	10	

Meiofauna abundance patterns differed across sites in both 2011 (Figure 3.2) and 2012 (Figure 3.3). In 2011, abundance showed an increasing trend between July and August at the Canning and Okilpilak/Hulahula deltas, but not at the Jago Delta. In 2012, there was no apparent trend of abundance changes across sessions or sites. At the Canning Delta, abundance increased between July and August, but did not vary at the Jago Delta, and showed the opposite trend at Okilpilak/Hulahula Delta.

Meiofauna abundance was not significantly different between years ($P = 0.3781$) or sessions ($P = 0.4419$), but was significantly different among sites ($P = 0.0120$) (Table 3.2). There were no significant interactions (Table 3.3). Tukey post-hoc comparison revealed significant differences between Canning and Jago deltas, but the Okpilak/Hulahula Delta was not significantly different than either the Canning or Jago deltas. Across both years, average abundance was highest at the Canning Delta and lowest at the Jago Delta. At the Canning Delta, meiofauna abundance averaged 1152.8 individuals per core, or 1.74×10^6

individual per m^{-2} . At the Okpilak/Hulahula Delta, meiofauna abundance averaged 994.1 individuals per core, or 1.50×10^6 individual m^{-2} . At the Jago Delta, meiofauna abundance averaged 592.3 individuals per core, or 8.96×10^5 individual m^{-2} .

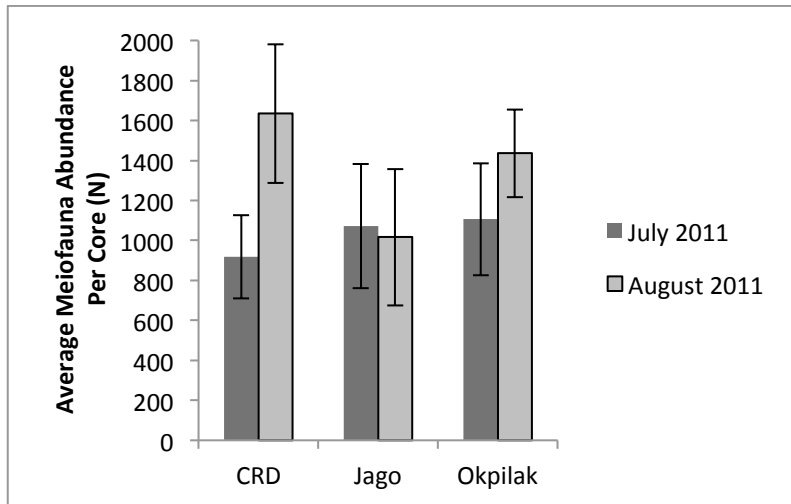


Figure 3.2. Average meiofaunal abundance from each site [Canning (CRD), Jago, Okpilak/Hulahula (OKP)] in 2011, broken down by sampling session (July/August) with standard error (δ/\sqrt{n}).

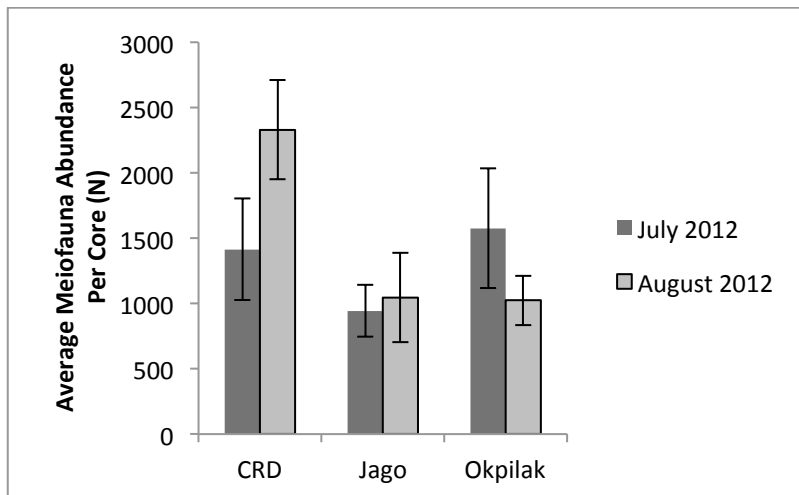


Figure 3.3. Average meiofaunal abundance from each site [Canning (CRD), Jago, Okpilak/Hulahula (OKP)] 2012, broken down by sampling session (July/August) with standard error (δ/\sqrt{n}).

Table 3.2. Two-way ANOVA results for the test of total meiofauna abundance (N) differences across year, site (Canning, Jago, Okpilak/Hulahula), and session, including the interactions.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Year	1	0.51280128	0.51280128	2.15	0.1453
Site	2	0.96663345	0.48331672	2.02	0.1365
Session	1	2.55883306	2.55883306	10.73	0.0014
Year*Site	2	0.07531043	0.03765522	0.16	0.8541
Year*Session	1	0.05821690	0.05821690	0.24	0.6221
Site*Session	2	0.00778965	0.00389483	0.02	0.9838

Table 3.3. Two-way ANOVA results for the test of total meiofauna diversity (Hill's N1) differences across year, site (Canning, Jago, Okpilak/Hulahula), and session, including the interactions.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Year	1	0.15031662	0.15031662	0.78	0.3781
Site	2	1.76829870	0.88414935	4.61	0.0120
Session	1	0.11432323	0.11432323	0.60	0.4419
Year*Site	2	0.28895165	0.14447583	0.75	0.4735
Year*Session	1	0.38462033	0.38462033	2.00	0.1597
Site*Session	2	0.66812140	0.33406070	1.74	0.1802

Meiofauna diversity patterns were more consistent across sites, years, and sessions. Diversity increased between July and August at all sites in both 2011 (Figure 3.4) and 2012 (Figure 3.5). Diversity trends were generally similar across sites.

Meiofauna diversity was not different between years ($P = 0.1453$) or sites ($P = 0.1365$), but was different between sessions ($P = 0.0014$) (Table 3). There were no significant interactions (Table 3). Diversity increased significantly in August compared to July. Hill's N1 is a measure of the effective number of dominant species (in this case taxa). The average number of dominant taxa was 1.22 in July, compared to 1.55 in August.

Multivariate analysis of meiofauna community structure was carried out to test differences between years and also test differences within years. In the one-way ANOSIM to test for year differences, community structure was significantly different ($P = 0.001$) from a multivariate perspective. The SIMPER routine revealed that the average community dissimilarity between

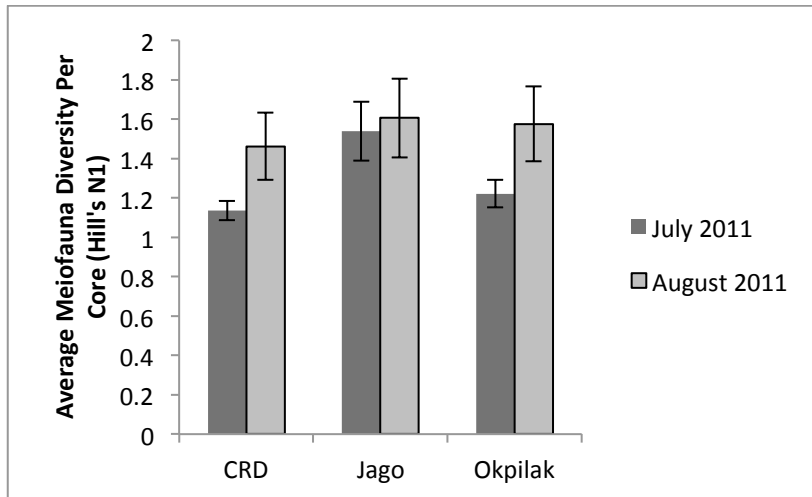


Figure 3.4. Average meiofaunal diversity (Hill's N1) from each site [Canning (CRD), Jago, Okpilak/Hulahula (OKP)] 2011, broken down by sampling session (July/August) with standard error (δ/\sqrt{n}).

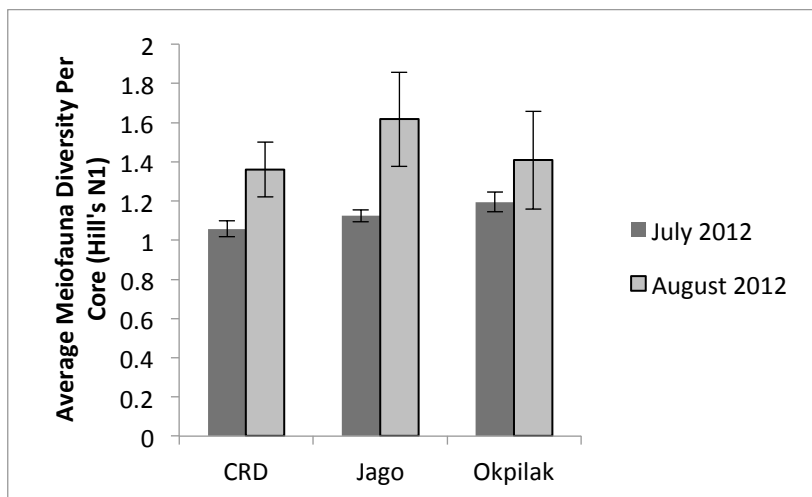


Figure 3.5. Average meiofaunal diversity (Hill's N1) from each site [Canning (CRD), Jago, Okpilak/Hulahula (OKP)] 2012, broken down by sampling session (July/August) with standard error (δ/\sqrt{n}).

years was 47.9%, and nematodes contributed to 84% of the overall community dissimilarity, while harpacticoid copepods and tardigrades contributed to 4.97% and 4.96% of the community dissimilarity across years, respectively. In 2011, nematodes accounted for 96.8% of total community structure across all years, sites, and sessions, but in 2012 nematodes accounted for 99.0% of community structure.

MDS ordination of samples from 2011 suggested that sites were clustering differently (Figure 3.6). The Canning and Jago delta samples clustered farther apart, while Okpilak/Hulahula samples overlapped with both Canning and Jago. Community structure differences were independently tested within years using two-way ANOSIM to test for differences between sites and sessions. In 2011, two-way ANOSIM revealed a significant difference between sites across all session groups ($P = 0.021$), but no significant difference between session groups across all sites ($P = 0.074$). Although, it should be noted that the lack of session significance was marginal. So, while community structure differed spatially in 2011, it did not vary temporally. Pairwise test of site groups revealed significant differences in community structure between the Canning and Jago delta samples ($P = 0.001$), but no difference between the Canning and Okpilak/Hulahula delta samples ($P = 0.199$) or the Jago and Okpilak/Hulahula delta samples ($P = 0.212$). The SIMPER routine found an average dissimilarity of 39.6%

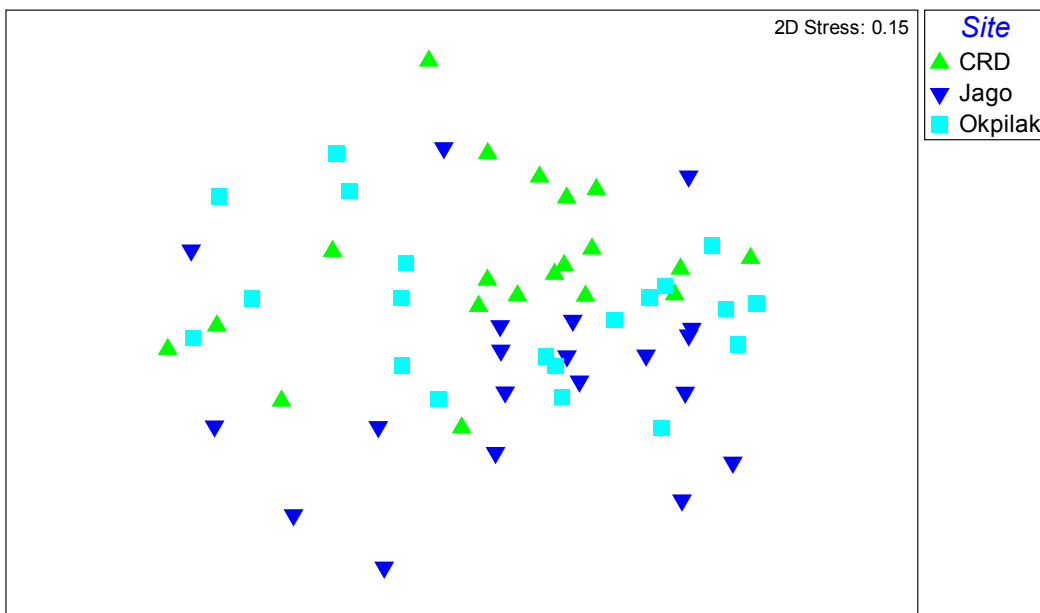


Figure 3.6. MDS ordination of meiofauna community structure across all sites [Canning (CRD), Jago, Okpilak/Hulahula (OKP)] 2011. Data were fourth root transformed prior to Bray Curtis similarity analysis. Ordination of stations reveals lower similarity between Canning and Jago, with Okpilak/Hulahula having overlapping similarity with both Canning and Jago.

between the Canning and Jago deltas. Nine different taxa accounted for 91% of the community dissimilarity between these two sites in 2011. Four taxa accounted for 71.5% of the dissimilarity,

and were nematodes (20.15%), tardigrades (18.95%), harpacticoids (16.6%), and nauplii (15.85%).

In 2012, the MDS ordination of samples was similar to 2011 with samples from the Canning and Jago deltas clustering farthest from one another and Okpilak/Hulahula samples overlapping with both the Canning and Jago delta samples (Figure 3.7). However, two-way ANOSIM revealed significant differences between site groups across all session groups ($P = 0.001$) and significant session differences across all site groups ($P = 0.007$). So, in 2012 community structure differed both temporally and spatially. Pairwise differences of site groups suggested that all sites differed from each other as follows: Canning/Jago ($P = 0.006$); Canning /Okpilak ($P = 0.002$); and Jago/Okpilak ($P = 0.048$). Community structure differences between the Canning and Jago deltas

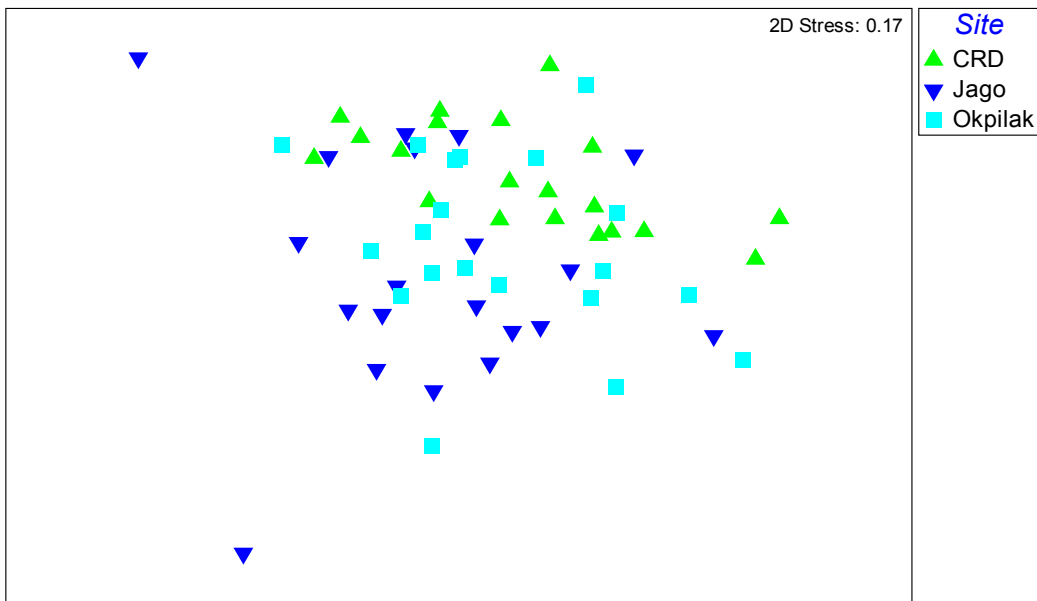


Figure 3.7. MDS ordination of meiofauna community structure across all sites [Canning (CRD), Jago, Okpilak/Hulahula (OKP)] 2012. Data were fourth root transformed prior to Bray Curtis similarity analysis. Ordination of stations reveals lower similarity between Canning and Jago, with Okpilak/Hulahula having overlapping similarity with both Canning and Jago.

were due to nematodes, tardigrades, nauplii, harpacticoids, and rotifers that together accounted for a total of 77.8% of total between-site dissimilarity. Community structure differences between Canning and Okpilak/Hulahula were due to nematodes, harpacticoids, tardigrades, nauplii, and turbellarians that together accounted for 73.8% of the between-site dissimilarity. Community

structure differences between the Jago and Okpilak/Hulahula deltas were due to nematodes, nauplii, tardigrades, rotifers, and harpacticoids that together accounted for 74.7% of the between-site dissimilarity. Between July and August 2012, nematode abundance dropped from 80% of total community structure to 74% of total community structure, which explains this within-year temporal difference in community structure.

3.4 Discussion

The meiofauna community is ubiquitous in marine, estuarine, and freshwater soft-sediment habitats (Coull and Bell 1979) and is a crucial component of associated benthic food webs (Coull 1990; Montagna 1995). Meiofauna feed on bacteria, benthic microalgae, detritus, and prey upon other meio- or microfauna (Weiser 1960; Montagna 1995). Macrobenthos are known to feed on meiofauna, thus providing a mechanism for transfer of meiofauna secondary production to higher trophic levels (Coull 1990). With high abundance, biomass, and short generation times, meiofauna respond quickly to spring bloom conditions, allowing for rapid transfer of primary produced carbon up the food web. With abundances on the order of $10^5 - 10^6$ individuals m^{-2} (Figures 3.2 & 3.3), estuarine sediments within the Jago, Canning, and Okpilak/Hulahula deltas have densely populated meiofauna communities that are comparable to other estuarine habitats at lower latitudes (Geire 2009).

When pooling samples across both sampling years, meiofauna abundance varied spatially suggesting that environmental conditions across the three sampling sites were not similar, with Canning having highest meiofauna abundance year over year (Figures 3.2 & 3.3). Seasonally, meiofauna abundance increased from July to August consistently at the Canning Delta, while the Jago Delta did not see consistent seasonal changes in abundances in either year (Figures 3.2 & 3.3). At the Okpilak/Hulahula Delta, the pattern of abundance change from July to August differed in 2011 and 2012 (Figures 3.2 & 3.3). When independently analyzing 2011 and 2012 data, it was clear that community structure varied spatially in both years. Further, community structure patterns were similar between years, with the Canning and Okpilak/Hulahula deltas being least similar to each other. The Jago Delta had overlapping community similarity with the Canning and Okpilak/Hulahula deltas in 2011, but became less similar to both sites in 2012 (Figures 3.6 & 3.7).

Patterns of abundance are subject to biotic and abiotic factors that can stimulate or disturb community structure. For example, increased freshwater inundation can disturb estuarine and marine communities that favor higher salinities. Fully understanding the dynamics of meiobenthic community structure and function in Arctic communities will require detailed analyses of sediment characteristics, water quality, thermal variation, as well as potential physical and biological sources of disturbance. Unfortunately, an environmental variable dataset was not collected that allowed for direct comparison to meiobenthic community structure in order to understand how environmental conditions help structure biotic patterns.

Diversity patterns were similar across sites and exhibited consistent seasonal changes within sites from July to August (Figures 3.4 & 3.5). At all sites, in both years, diversity increased from July to August. Meiofauna community diversity was clearly dominated by nematode worms in all samples, which is consistent with our understanding of meiofauna communities in general (Coull and Bell 1979; Giere 2009). Nematodes are likely competitively superior to other meiofauna, and respond quickly to increases in food supply, and may be more tolerant to disturbance (Giere 2009). Here, nematode dominance was always greatest in July, perhaps due to faster responses by nematodes to relative to other taxa after the onset of the spring bloom. Between July and August, other minor taxa, principally harpacticoid copepods, rotifers, and tardigrades increased in proportional abundance, but their relative contributions to community abundance and diversity differed by year, site, and session as presented above. The short annual period without ice cover likely favors the highly tolerant nematodes, only allowing brief windows in the late summer for less competitive taxa to flourish.

3.5 References

- Baguley JG, Montagna PA, Lee W, Hyde LJ, Rowe GT. 2006a. Spatial and bathymetric trends in Harpacticoida (Copepoda) community structure in the Northern Gulf of Mexico deep-sea. *Journal of Experimental Marine Biology and Ecology*. 330:327-341.
- Baguley JG, Montagna PA, Hyde LJ, Kalke RD, Rowe GT. 2006b. Metazoan meiofauna abundance in relation to environmental variables in the northern Gulf of Mexico deep sea. *Deep-Sea Research I*. 53:1344-1362.

- Bejarano AC, Chandler GT, Lijian H, Coull BC. 2006. Individual to population level effects of South Louisiana crude oil water accommodated hydrocarbon fraction (WAF) on a marine meiobenthic copepod. *Journal of Experimental Marine Biology and Ecology*. 332:49-59
- Bell SS. 1980. Meiofauna–macrofauna interactions in a high saltmarsh habitat. *Ecological Monographs*. 50:487-505.
- Burgess R. 2001. An improved protocol for separating meiofauna from sediments using colloidal silica sols. *Marine Ecology Progress Series*. 214: 161-165.
- Coull BC. 1990. Are members of the meiofauna food for higher trophic levels? *Transactions of the American Microscopical Society*. 109: 233-246.
- Coull BC, Bell SS. 1979. Perspectives of marine meiofauna ecology. In: Livingston RJ, editor. *Ecological processes in coastal and marine systems*. New York (NY): Plenum Publishing Corp. p. 189-216.
- Gee MJ, Warwick RM, Schaanning M, Berge JA, Ambrose WG. 1985. Effects of organic enrichment on meiofaunal abundance and community structure in sublittoral soft sediments. *Journal of Experimental Marine Biology and Ecology*. 91:247-262.
- Giere O. 2009. *Meiobenthology: the microscopic motile fauna of aquatic sediments*. Heidelberg: Springer-Verlag Berlin.
- Mahaut ML, Sibuet M, Shirayama Y. 1995. Weight-dependent respiration rates in deep-sea organisms. *Deep-Sea Research* 42:1575-1582.
- Montagna PA. 1995. Rates of metazoan meiofauna microbivory: a review. *Vie et Milieu*. 45:1-9.
- Montagna P, Harper Jr DE. 1996. Benthic infaunal long-term response to offshore production platforms in the Gulf of Mexico. *Canadian Journal of Fisheries and Aquatic Sciences*. 53:2567-2588.
- Schwinghamer P. 1981. Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Sciences*. 38:1255-1263.
- Smith LD, Coull BC. 1987. Juvenile spot (Pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrata. *Journal of Experimental Marine Biology and Ecology*. 105(2): 123-136.
- Thistle D. 2003. The deep-sea floor: An overview. In: Tyler PA, editor. *Ecosystems of the deep*. Amsterdam (the Netherlands): Elsevier Science B.V. Chapter 2, p. 5-38.

Weiser W. 1960. Benthic studies in Buzzards Bay. II. The meiofauna. *Limnology and Oceanography*. 5:121-137.

4. Sediment Microbial Populations

Colleen T. E. Kellogg, University of British Columbia, Vancouver, BC, Canada
Byron C. Crump, Oregon State University, Corvallis, OR

4.1 Introduction

Single-celled organisms in sediments (i.e., microbenthos) are the principle diet for the meiobenthos and macrobenthos that sustain shorebird communities (Gerlach 1978, Tsuchiya and Kurihara 1979, Andresen and Kristensen 2002, van Oevelen et al. 2006a), but little is known about the species composition of these communities in the nearshore shelf areas of the Beaufort Sea. Microbenthos, including Bacteria, Archaea, heterotrophic protists (e.g., ciliates, flagellates), and microphytobenthos (e.g., diatoms) form a complex, species-rich microbial food web in estuaries that consume detrital organic matter from terrestrial and planktonic environments (Carlsson et al. 1993, Hamels et al. 2004, McCallister et al. 2004, van Oevelen et al. 2006b). The species composition of these communities is highly variable and has been found to be driven by temporal and spatial variability in environmental conditions (e.g., organic matter source) and the physical constraints of sediment environments (e.g., interstitial space size/shape and hydrodynamic disturbances) (Tankere et al. 2002, Crump et al. 2003, Hamels et al. 2004, Judd 2004, Judd et al. 2006, Crump et al. 2009, Feng et al. 2009, Auguet et al. 2010).

Recent research also demonstrated that the diversity of sediment microbial communities is sensitive to oil exposure, and suggested that several genera of bacteria may serve as useful indicators of oil contamination in coastal sediments (dos Santos et al. 2011). Similarly, shifts in microbial community composition were observed over winter months in sea ice experimentally contaminated with crude oil (Brakstad et al. 2008), suggesting that only a subset of the polar microbial community possesses the capacity to use hydrocarbon sources for growth. Enrichment cultures and bacterial isolates from polar waters and sea ice were found to effectively degrade hydrocarbons at cold temperatures ($<5^{\circ}\text{C}$; Deppe et al. 2005, Lin et al. 2009).

We hypothesized that the composition of microbial communities in sediments of the Beaufort Sea coastal lagoons will correlate with seasonal and site-specific variation in organic matter source and character. Microbial communities are more diverse and dynamic than meiobenthos communities and can change in composition in a matter of days to weeks. Thus, the composition

of these communities may serve as a sensitive indicator of environmental shifts, including shifts in the character of organic matter and the introduction of oil contamination in the Beaufort Sea coastal lagoons.

4.2 Materials and Methods

4.2.1 Microbial community composition

The taxonomic composition of prokaryotic and microeukaryotic communities was investigated in deltaic mudflats of the Canning, Jago, and Okpilak/Hulahula rivers using PCR amplicon Illumina DNA sequencing of 16S and 18S rRNA genes in summer 2011 and 2013. Microbial community composition was determined for a subset of samples collected in 2011 (n=20) and 2013 (n=33). DNA extracted from ~0.5 g of sediment using the MoBio PowerSoil DNA extraction kit was PCR-amplified with primers targeting the V4 region (515F, GTGCCAGCMGCCGCGGTAA and 806R, GGACTACHVGGGTWTCTAAT) of the 16S rRNA gene for prokaryotic composition and the V9 region (1391F, GTACACACCGCCCGTC and EukBr, TGATCCTTCTGCAGGTTACCTAC) of the 18S rRNA gene for microeukaryotic composition for sequencing on the Illumina MiSeq platform using Earth Microbiome Project (Gilbert et al. 2014) protocols, but with only 30 total cycles. Amplicons from each sample were pooled in equimolar concentrations and sent either to Argonne National Lab (2011 16S amplicons) or to Oregon State University Center for Genome Research and Biocomputing (all 18S amplicons and 2013 16S amplicons) for sequencing at 2x150 bp read lengths. Sequences were paired using fastq-join (Aronesty 2013), quality controlled and clustered using USEARCH (Edgar 2013), and assigned taxonomy using the RDP classifier in QIIME (Caporaso et al. 2010). Chloroplast, mitochondria, and Archaea were removed from the prokaryote sequences prior to analysis. Microeukaryote analysis focused only on protist and fungal sequences by removing sequences assigned to multicellular organisms (metazoan, unassigned eukaryotes, unassigned holozoans, and multicellular Archaeplastida). Note that quantitative assessment of microeukaryotic communities using rRNA gene sequencing is less reliable than for prokaryotes due to large variation in gene copy number per cell, which is not well understood but ranges from <30 to >30,000 (Prokopowich et al. 2002).

4.3 Results and Discussion

4.3.1 Bacterial Community

Bacterial community composition showed minimal interannual variation across the three river deltas sampled (ANOSIM $R = 0.1208$, $P = 0.015$) and was consistently dominated by Proteobacteria (Figure 4.1). Slight geographic differences in community composition were observed (Figure 4.2; ANOSIM $R = 0.2816$, $P = 0.001$) and were mainly driven by 2013 samples. The Canning River delta had higher proportions of *gammaproteobacteria* (average = 15%) while the Jago and Okpilak/Hulahula mudflats had lower proportions (6% and 9% on average) in favor of higher average proportions of *betaproteobacteria* (13% and 11%, respectively, Figure 4.1). These differences likely result from the longer residence time of freshwater in the Jago and Okpilak/Hulahula River deltas compared to the Canning Delta, due to the presence of barrier islands in the Jago and Okpilak/Hulahula delta regions.

Availability of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TOC, ammonium, and salinity measurements for 2013 samples allowed for direct comparison between prokaryotic community composition and sediment characteristics. These data explained approximately 41% of the variation in 2013 bacterial community structure. Salinity accounted for 20% of the total variation explained, which is consistent with several studies that show salinity is an important control on estuarine microbial communities (Crump et al. 2004, Fortunato and Crump 2011, Herlemann et al. 2011). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ accounted for 12% and 8% of the total variation explained, respectively, supporting the hypothesis that microbial community composition correlates with seasonal and site-specific variation in organic matter source and character (Bowen et al. 2009).

Given the development of oil fields in nearshore arctic environments, we were also interested in detecting known hydrocarbon degraders (e.g., *Marinobacter* sp., *Alcanivorax* sp., *Colwellia* sp., *Oleiphilaceae* sp., etc.) (dos Santos et al. 2011, Beazley et al. 2012). One genera of bacteria that includes known hydrocarbon-degrading species (*Marinobacter*; Gauthier et al. 1992) was observed at concentrations between 0.5-10% in Okpilak/Hulahula and Canning deltas, suggesting prior or ongoing exposure to hydrocarbons associated with oil (Yakimov et al. 2005, Al-Mailem et al. 2010, Kostka et al. 2011, Jurelevicius et al. 2013, Lamendella et al. 2014). This species was more rare in Jago mudflats. *Alcanivorix*, *Colwellia* and *Oleiphilaceaea* spp. were

present in low proportions throughout the dataset. Thus, the broadly distributed and persistent bacterial community detected in Beaufort lagoons may serve as a sensitive indicator of shifts in detrital organic matter including oil-associated hydrocarbons. Future work on this topic will allow us to begin to address the degree to which mudflat microbiota are poised to remediate hydrocarbon spills in this region.

4.3.2 Microeukaryotic Community

Based on 18S gene abundance, microeukaryotic communities were dominated by diatoms and other Stramenopiles, and by dinoflagellates and other Alveolates. Interannual differences were more apparent in the Protistan and Fungal communities than Bacterial communities in these mudflats (Figure 4.2; ANOSIM $R = 0.2231$, $P = 0.001$), but among-lagoon variation was not as strong (ANOSIM $R = 0.22$, $P = 0.001$). In general, 2011 microeukaryotic communities had a higher proportion of diatom sequences, particularly Bacillariophytes, while 2013 communities had a higher proportion of Alveolate sequences (Figure 4.3). As was done for the bacterial community, we compared microeukaryotic community composition with mudflat chemical characteristics measured in 2013. These data explained nearly 34% of the variation in 2013 microeukaryotic community structure, with salinity (10%) and $\delta^{15}\text{N}$ (8%) explaining the largest amount of variation, followed by $\delta^{13}\text{C}$ (6%). When chemical data from 2011 becomes available we will examine temporal variability in the sediment environment that gave rise to the shift from a diatom to an alveolate-dominated microeukaryotic community. These findings suggest the importance of salinity and organic matter source as important determinants of microeukaryotic community composition. Future shifts in these environmental variables could have dramatic impacts on the microeukaryotic communities in these mudflats and have far-reaching implications for higher trophic levels that use this habitat as breeding and feeding grounds.

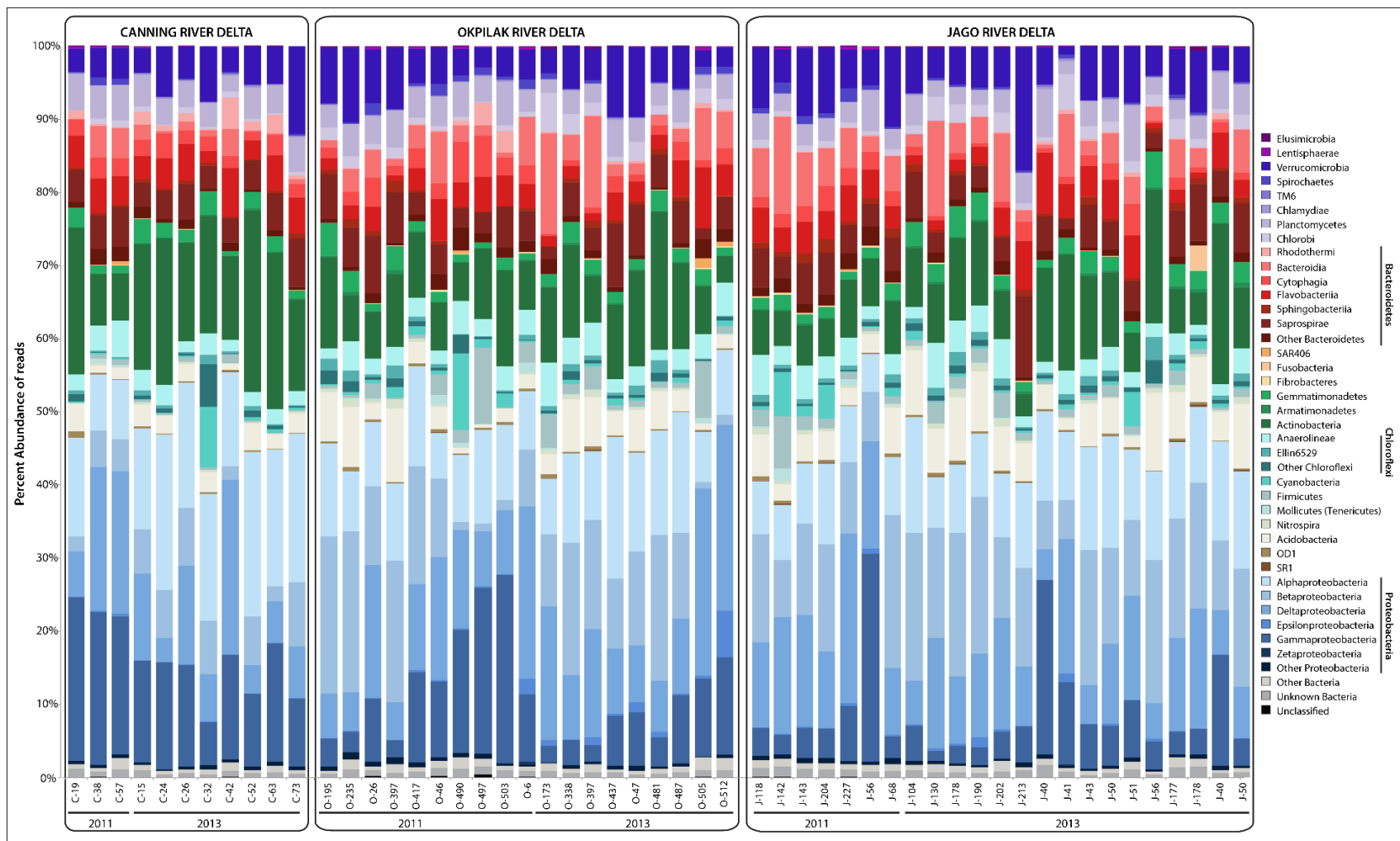


Figure. 4.1. Relative proportion of bacterial taxa across all samples, as calculated from 16S amplicon Illumina MiSeq sequence analyses. These data were randomly subsampled to 6802 sequences per sample to avoid potential biases in diversity based on uneven sample sizes. After subsampling, 13,463 taxa (OTUs) were observed among these 53 samples.

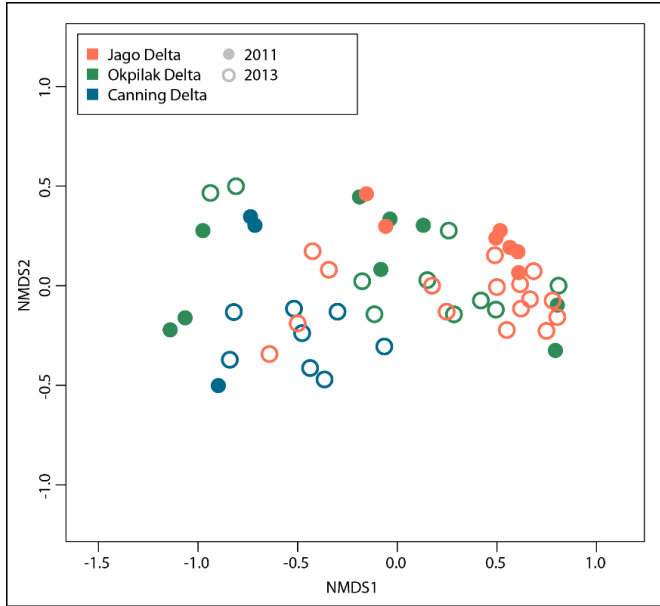


Figure 4.2. Ordination of nonmetric multidimensional scaling plot of subsampled mudflat bacterial communities from the Jago, Okpilak/Hulahula, and Canning river deltas, northern Alaska. Sequence reads were first normalized using a Hellinger transformation and then Bray-Curtis distance was used for calculation of beta diversity.

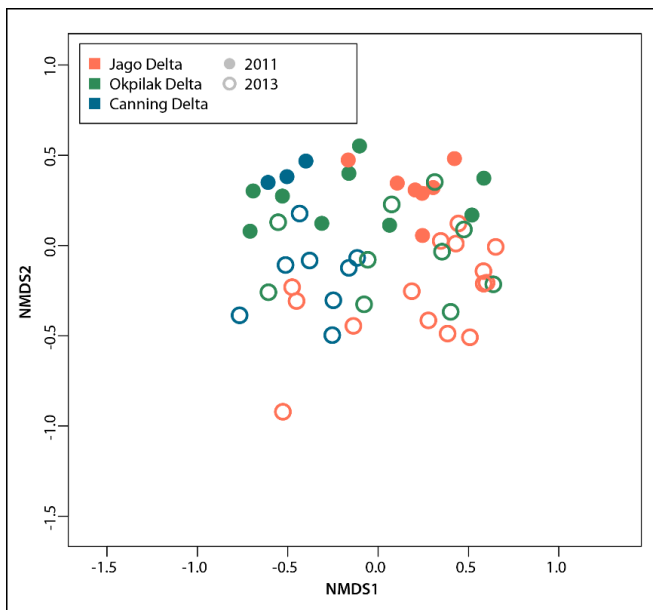


Figure 4.3. Ordination of nonmetric multidimensional scaling plot of subsampled mudflat eukaryotic communities from the Jago, Okpilak/Hulahula, and Canning river deltas, northern Alaska. Sequence reads were first normalized using a Hellinger transformation and then Bray-Curtis distance was used for calculation of beta diversity.

4.4 References

- Al-Mailem DM, Sorkhoh NA, Salamah S, Eliyas M, Radwan SS. 2010. Oil-bioremediation potential of Arabian Gulf mud flats rich in diazotrophic hydrocarbon-utilizing bacteria. *International Biodeterioration and Biodegradation*. 64:218-225.
- Andresen, M, Kristensen E. 2002. The importance of bacteria and microalgae in the diet of the deposit-feeding polychaete *Arenicola marina*. *Ophelia*. 56:179-196.
- Aronesty, E. 2013. Comparison of sequencing utility programs. *Open Bioinformatics J*. 7:1-8.
- Auguet, JC, Barberan A, Casamayor, EO. 2010. Global ecological patterns in uncultured Archaea. *ISME Journal*. 4:182-190.
- Beazley MJ, Martinez RJ, Rajan R, Powell J, Piceno YM, Tom LM, Andersen GL, Hazen TC, Van Nostrand JD, Zhou JZ. 2012. Microbial community analysis of a coastal salt marsh affected by the Deepwater Horizon oil spill. *PLoS ONE*. 7:10.1371.
- Bowen, JL, Crump BC, Deegan LA, Hobbie JE. 2009. Salt marsh sediment bacteria: their distribution and response to external nutrient inputs. *ISME Journal*. 3:924-934.
- Brakstad, OG, Nonstad I, Faksness LG, Brandvik PJ. 2008. Responses of microbial communities in Arctic sea ice after contamination by crude petroleum oil. *Microbial Ecology*. 55:540-552.
- Caporaso, JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Pena AG, Goodrich JK, Gordon JI, Huttley GA, Kelley ST, Knights D, Koenig JE, Ley RE, Lozupone CA, McDonald D, Muegge BD, Pirrung M, Reeder J, Sevinsky JR, Tumbaugh PJ, Walters WA, Widmann J, Yatsunenko T, Zaneveld J, Knight R. 2010. QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*. 7:335-336.
- Carlsson, P, Segatto AZ, Graneli E. 1993. Nitrogen bound to humic matter of terrestrial origin - a nitrogen pool for coastal phytoplankton. *Marine Ecology-Progress Series*. 97:105-116.
- Crump, BC, Hopkinson CS, Sogin ML, Hobbie JE. 2004. Microbial biogeography along an estuarine salinity gradient: combined influences of bacterial growth and residence time. *Applied and Environmental Microbiology*. 70:1494-1505.
- Crump, BC, Kling GW, Bahr M, Hobbie JE. 2003. Bacterioplankton community shifts in an arctic lake correlate with seasonal changes in organic matter source. *Applied and Environmental Microbiology*. 69:2253-2268.

- Crump, BC, Peterson BJ, Raymond PA, Amon RMW, Rinehart A, McClelland JW, Holmes RM. 2009. Circumpolar synchrony in big river bacterioplankton. *Proceedings of the National Academy of Sciences*. 106:21208-21212.
- Deppe, U, Richnow HH, Michaelis W, Antranikian G. 2005. Degradation of crude oil by an arctic microbial consortium. *Extremophiles*. 9:461-470.
- dos Santos, HF, Cury JC, do Carmo FL, dos Santos AL, Tiedje J, van Elsas JD, Rosado AS, Peixoto RS. 2011. Mangrove bacterial diversity and the impact of oil contamination revealed by pyrosequencing: bacterial proxies for oil pollution. *PLoS ONE* 6.
- Edgar, RC 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nature Methods*. 10:996-998.
- Feng, BW, Li XR, Wang JH, Hu ZY, Meng H, Xiang LY, Quan ZX. 2009. Bacterial diversity of water and sediment in the Changjiang estuary and coastal area of the East China Sea. *Fems Microbiology Ecology*. 70:236-248.
- Fortunato, CS, Crump BC. 2011. Bacterioplankton community variation across river to ocean environmental gradients. *Microbial Ecology*. 62:374-382.
- Gauthier, MJ, Lafay B, Christen R, Fernandez L, Acquaviva M, Bonin P, Bertrand JC. 1992. *Marinobacter hydrocarbonoclasticus* gen-nov, sp-nov., a new, extremely halotolerant, hydrocarbon-degrading marine bacterium. *International Journal of Systematic Bacteriology*. 42:568-576.
- Gerlach, SA 1978. Food-chain relationships in subtidal silty sand marine sediments and role of meiofauna in stimulating bacterial productivity. *Oecologia*. 33:55-69.
- Gilbert, JA, Jansson JK, Knight R. 2014. The Earth Microbiome Project: successes and aspirations. *BMC Biology*. 12:69.
- Hamels, I, Sabbe K, Muylaert K, Vyverman W. 2004. Quantitative importance, composition, and seasonal dynamics of protozoan communities in polyhaline versus freshwater intertidal sediments. *Microbial Ecology*. 47:18-29.
- Herlemann, DPR, Labrenz M, Jurgens K, Bertilsson S, Waniek JJ, Andersson AF. 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME Journal*. 5:1571-1579.

- Judd, KE. 2004. Dissolved organic matter dynamics in an arctic tundra catchment: linking DOM chemistry, bioavailability, and microbial community composition. Doctoral dissertation. University of Michigan.
- Judd, KE, Crump BC, Kling. 2006 GW. Variation in dissolved organic matter controls bacterial production and community composition. *Ecology*. 87:2068-2079.
- Jurelevicius, D, Alvarez VM, Marques JM, Lima L, Dias FD, Seldin L. 2013. Bacterial community response to petroleum hydrocarbon amendments in freshwater, marine, and hypersaline water-containing microcosms. *Applied And Environmental Microbiology*. 79:5927-5935.
- Kostka, JE, Prakash O, Overholt WA, Green SJ, Freyer G, Canion A, Delgardio J, Norton N, Hazen TC, Huettel M. 2011. Hydrocarbon-degrading bacteria and the bacterial community response in Gulf of Mexico beach sands impacted by the Deepwater Horizon Oil Spill. *Applied and Environmental Microbiology*. 77:7962-7974.
- Lamendella, R, Strutt S, Borglin S, Chakraborty R, Tas N, Mason OU, Hultman J, Prestat E, Hazen TC, Jansson JK. 2014. Assessments of the Deepwater Horizon oil spill impact on Gulf coast microbial communities. *Frontiers in Microbiology*. 5:1-13.
- Lin, XZ, Yang BJ, Shen JH, Du N. 2009. Biodegradation of crude oil by an arctic psychrotrophic bacterium *Pseudoalteromonas sp* P29. *Current Microbiology*. 59:341-345.
- McCallister, SL, Bauer JE, Cherrier JE, Ducklow HW. 2004. Assessing sources and ages of organic matter supporting river and estuarine bacterial production: A multiple-isotope (Delta C-14, delta C-13, and delta N-15) approach. *Limnology and Oceanography*. 49:1687-1702.
- Tankere, SPC, Bourne DG, Muller FLL, Torsvik V. 2002. Microenvironments and microbial community structure in sediments. *Environmental Microbiology*. 4:97-105.
- Tsuchiya, M, Kurihara Y. 1979. Feeding habits and food sources of the deposit-feeding polychaete, *Neanthes japonica* (izuka). *Journal of Experimental Marine Biology and Ecology*. 36:79-89.
- van Oevelen, D, Moodley L, Soetaert L, Middelburg JJ. 2006a. The trophic significance of bacterial carbon in a marine intertidal sediment: results of an in situ stable isotope labeling study. *Limnology and Oceanography*. 51:2349-2359.

- van Oevelen, D, Soetaert K, Middelburg JJ, Herman PMJ, Moodley L, Hamels I, Moens T, Heip CHR. 2006b. Carbon flows through a benthic food web: Integrating biomass, isotope and tracer data. *Journal of Marine Research*. 64:453-482.
- Yakimov, MM, Denaro R, Genovese M, Cappello S, D'Auria G, Chernikova TN, Timmis KN, Golyshin PN, Giluliano L. 2005. Natural microbial diversity in superficial sediments of Milazzo Harbor (Sicily) and community successions during microcosm enrichment with various hydrocarbons. *Environmental Microbiology*. 7:1426-1441.

5. Sediment Parameters: Chlorophyll, Microalgal Composition, Ammonium, and Stable Isotopic Measurements

Ken Dunton and Philip Bucolo, The University of Texas Marine Science Institute

5.1 Introduction

Arctic nearshore shallow river deltas are foraging sites for migratory shorebirds dependent on resident invertebrate food sources for pre-migratory fattening (Brown 2006). Following freshet, Arctic river freshwater discharge mixes with marine waters at the mouth of these shallow river deltas. Dunton et al. (2012) provided strong evidence that terrestrially derived organic inputs such as those from riverine discharge and erosion are assimilated by primary consumers in several shallow Arctic lagoons. Consumers included epibenthic amphipods, mysids, and infaunal mollusks, all of which are food sources for foraging shorebirds (Craig et al. 1984). Invertebrates of this trophic guild rely on sediment-associated microalgae and bacteria, particulate organic matter (POM), and subsequent biogeochemical processes that produce dissolved organic carbon (DOC) to flourish in estuarine habitats (Dunton et al. 2012; McTigue and Dunton 2014). Overall there is a paucity of studies investigating the community structure and biogeochemical processes of the sediment microbial community and associated abiotic characteristics of Arctic river delta sediments. In order to better describe the ecological structure and biogeochemical contributions of the micro-epibenthic community, our group characterized the sediment microalgal assemblages based on pigment analysis, and sediment chemistry characteristics (including stable isotope $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, TOC, C:N ratios, levels of sediment porewater ammonium (NH_4^+), and salinity) from the Jago, Okpilak, and Canning river deltas of the Alaskan Arctic.

In addition to providing a food source for micro- and macro-invertebrates important to shorebird sustainability, sediment associated microalgae, or microphytobenthos, contribute up to 50% of primary production in mud flats (Underwood and Kromkamp 1999) and exceed pelagic production by a factor of 1.5 along the Arctic shelf to depths of 30 m (Glud et al. 2009). High pressure liquid chromatography (HPLC) pigment analyses can elucidate microphytobenthic viability and the taxonomic composition of major algal contributors to sedimentary community production. Our analyses included calculation of the universal photosynthetic pigment chlorophyll *a* (chl *a*), microalgal accessory pigments indicative of specific algal taxonomic groups, and chl *a* degradation products known as pheopigments. To further investigate primary production from

sediment microalgae of the river deltas, we also measured TOC, which reflects the total reservoir of carbon in sediments, but provides little information on source or lability. Sedimentary stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and molar C:N analyses were employed to trace terrestrial and marine contributions to the microepibenthic community. Sediment porewater measurements of salinity and NH_4^+ provided information on the relative magnitude of sediment organic decomposition and mixing of river runoff and marine waters, respectively.

5.3 Materials and Methods

Approximately 340 and 120 sediment cores were collected during summer 2011 and 2013 respectively, from sampling stations across the Jago, Canning, and Okpilak/Hulahula river deltas during two separate sampling periods, 15 July to 8 August and from 11 to 22 August. Due to inclement weather, only the Jago River delta was sampled during the second sampling period in 2013. At each station three replicate sediment cores were extracted to 5 mm into the sediment with a 20-cc (radius = 1 cm) syringe to collect material for sediment pigments, TOC, isotopic and C:N analysis. Each core was placed in a pre-labeled Falcon tube and those used for pigment analysis were wrapped in foil to avoid sunlight. Two separate 60-cc (radius = 1.46 cm) syringe cores were used to collect sediments to analyze porewater salinity and NH_4^+ , and to collect additional sediment for further microalgal analysis if needed. Those samples were placed into pre-labeled Whirl-pac® bags. All samples were immediately frozen until analysis. A representative subsample was used to quantify each parameter across each delta in each sampling period (Table 5.1).

5.3.1 Pigment Analysis

HPLC provides the most reliable method of sedimentary pigment analysis and was used here to measure chl *a* concentrations, pheopigment chl *a* degradation products, and accessory pigments indicative of specific algal groups. Prior to analysis, pigments were extracted using 10 ml of 100% acetone to account for acetone dilution by residual porewater. Volume of porewater was determined by evaporation and accounted for during extraction. Samples were sonicated for 15 min in darkness during extraction and were centrifuged for 5 min at 4000 rpm. The supernatant was decanted and filtered. This process was repeated and both filtered supernatants were

Table 5.1. Results of parameters measured (means \pm standard errors), dates collected, and the number of samples used in the analyses from 2011 and 2013 sediment sampling of Jago, Okpilak/Hulahula, and Canning river deltas.

	year	sampling period	Jago			Okpilak/Hulahula			Canning		
			collection date(s)	n	mean \pm SE	collection date(s)	n	mean \pm SE	collection dates(s)	n	mean \pm SE
$\delta^{15}\text{N}$ (‰)	2011	1	7/23,28,30	4	1.59 \pm 0.14	7/25,26,30; 8/8	5	2.39 \pm 0.39	7/30; 8/1	4	2.94 \pm 0.35
	2011	2	8/11,13,16	3	1.95 \pm 0.13	8/17,22	2	1.94 \pm 0.43	8/13	1	1.68
	2013	1	8/3,6	11	1.74 \pm 0.84	8/8	9	2.09 \pm 0.16	8/5,4	10	2.50 \pm 0.14
	2013	2	8/19	4	1.70 \pm 0.38		0			0	
$\delta^{13}\text{C}$ (‰)	2011	1	7/23,28,30	4	-26.38 \pm 0.48	7/25,26,30; 8/8	5	-24.90 \pm 0.21	7/30; 8/1	4	-25.05 \pm 0.92
	2011	2	8/11,13,16	3	-26.36 \pm 0.16	8/17,22	2	-25.65 \pm 0.59	8/13	1	-25.31
	2013	1	8/3,6	11	-25.78 \pm 0.14	8/8	9	-24.28 \pm 0.31	8/4,5	10	-24.82 \pm 0.18
	2013	2	8/19	4	-25.94 \pm 0.72		0			0	
C:N (mol/mol)	2011	1	7/28,29	4	11.27 \pm 0.56	7/25,26,30; 8/8	5	9.90 \pm 1.30	7/30; 8/1	4	12.13 \pm .72
	2011	2	8/11	3	11.20 \pm 0.86	8/17,22	2	17.09 \pm 8.11	8/13	1	24.87
	2013	1	8/3,4	11	10.22 \pm 0.54	8/8	9	12.78 \pm 2.82	8/4,5	10	13.46 \pm 1.37
	2013	2	8/19	4	13.49 \pm 1.48		0			0	
Total Organic Carbon (% g sample ⁻¹)	2011	1	7/23,28,30	3	1.73 \pm 0.10	7/25,26,31	3	2.09 \pm 0.68	7/30	3	3.46 \pm 0.39
	2011	2	8/19	3	2.44 \pm 0.17	8/17,19	3	2.48 \pm 0.78	8/14	3	4.02 \pm 0.76
	2013	1	8/3,4	11	2.24 \pm 0.24	8/8	9	1.77 \pm 0.19	8/4,5	10	3.10 \pm 0.23
	2013	2	8/19	5	2.26 \pm 0.38		0			0	
NH ₄ ($\mu\text{mol L}^{-1}$)	2011	1	7/15-30	40	169.00 \pm 18.39	7/19,25-31; 8/1,7,8	47	69.90 \pm 10.75	7/29,30; 8/1,2	47	69.90 \pm 10.75
	2011	2	8/11-16	70	203.42 \pm 15.14	8/12,15-26	91	101.46 \pm 9.46	8/12-15	92	101.46 \pm 9.46
	2013	1	8/3,4	27	79.15 \pm 17.22	8/8	34	73.38 \pm 10.77	8/4,5,8	34	73.38 \pm 10.77
	2013	2	8/18,19	18	96.67 \pm 18.60		0			0	

Chlorophyll a (mg m ⁻²)	2011	1	7/23-30	9	90.98 ± 13.52	7/23-30	10	74.03 ± 16.42	7/23-30	10	55.99 ± 8.91
	2011	2	8/11,13,16	8	74.11 ± 7.94	8/11,13,16	10	55.91 ± 16.73	8/11,13,16	10	52.84 ± 3.66
	2013	1	8/3,4,8	10	35.90 ± 9.20	8/3,4,8	10	16.29 ± 5.28	8/3,4,8	10	15.06 ± 3.4
	2013	2	8/18,19	10	64.33 ± 20.03		0			0	
Fucoxanthin (mg m ⁻²)	2011	1	7/23-30	9	36.01 ± 8.44	7/23-30	10	20.32 ± 3.43	7/23-30	10	15.10 ± 2.80
	2011	2	8/11,13,16	8	30.23 ± 3.83	8/11,13,16	10	26.64 ± 6.04	8/11,13,16	10	23.90 ± 2.48
	2013	1	8/3,4,8	10	10.84 ± 2.07	8/3,4,8	10	4.60 ± 1.06	8/3,4,8	10	5.45 ± 1.99
	2013	2	8/18,19	10	14.41 ± 2.51		0			0	
Total Pheopigment (mg m ⁻²)	2013	1	8/3,4,8	10	40.17 ± 9.78	8/3,4,8	10	24.58 ± 7.04	8/3,4,8	10	26.80 ± 4.22
	2013	2	8/18,19	10	44.06 ± 11.39		0			0	
Pheophytin a (mg m ⁻²)	2013	1	8/3,4,8	10	13.42 ± 3.67	8/3,4,8	10	8.35 ± 2.26	8/3,4,8	10	8.55 ± 2.04
	2013	2	8/18,19	10	11.62 ± 3.04		0			0	
Pheophorbide a (mg m ⁻²)	2013	1	8/3,4,8	10	13.28 ± 2.89	8/3,4,8	10	11.22 ± 3.61	8/3,4,8	10	9.77 ± 2.18
	2013	2	8/18,19	10	19.80 ± 5.94		0			0	
Pyropheophytin a (mg m ⁻²)	2013	1	8/3,4,8	10	12.89 ± 4.75	8/3,4,8	10	5.01 ± 2.07	8/3,4,8	10	8.48 ± 1.61
	2013	2	8/18,19	10	13.22 ± 4.17		0			0	
Salinity (ppt)	2011	1	7/28	2	2.00 ± 2.00	7/19,25-31; 8/1,8	40	7.00 ± 1.90		0	
	2011	2		0		8/19,22	30	3.00 ± 0.61		0	
	2013	1	8/3,4	28	4.00 ± 0.90	8/8	33	6.00 ± 1.58	8/4,5,8	18	11.00 ± 1.91

combined for HPLC analysis. HPLC pigment analysis followed the protocol of the Danish Hydraulic Institute in a C₈ HPLC column (Agilent Eclipse XDB, 3.5µm, 4.6 mm diameter x 150 mm length) where eluted pigments were detected by ultraviolet-vis absorbance. Pigment peaks were compared to certified commercial standards to determine concentrations of each compound (mg m⁻²). Pigments targeted for analysis were chl *a*, accessory pigments chlorophyll *b*, fucoxanthin, zeaxanthin from samples collected during 2011 and 2013; lutein, violaxanthin, and alloxanthin from 2011; and peridinin, 19-hex-fucoxanthin and pheopigments from 2013. Chl *a* was targeted as a proxy for fresh algal organic matter in sediments. Chl *b* was targeted to identify chlorophytes, fucoxanthin for the diatom lineage, the carotenoid zeaxanthin for cyanobacteria, chlorophytes and land plants. From 2011 sampling, lutein was targeted for presence of rhodophytes and glaucophytes, violaxanthin for chlorachniophytes, and alloxanthin for cryptomonads. Due to a lack of signatures of those pigments from 2011, targeted pigments were altered for 2013 analysis. In 2013 pigment analysis peridinin was targeted for dinoflagellate signals, 19-hex-fucoxanthin targeted haptophytes, and pheopigments were used to assess the standing stock of chl *a* breakdown derivatives where the formation of these breakdown products depends on specific diagenic events. Herbivorous metazoan grazing primarily forms pheophorbide *a* and secondary degradation product pyropheophorbide *a* while bacterial degradation of the chl *a* compound forms pheophytin *a*.

5.3.2 Isotopic Analysis, C:N Ratios, and TOC

Stable isotope analyses were performed on sediment cores on automated systems for coupled δ¹³C and δ¹⁵N measurements using a mass spectrometer and elemental analyzer. Samples were combusted at 1020°C and injected into mass spectrometer with continuous flow. Isotopic ratios are denoted in standard δ notation relative to carbon and nitrogen standards of Vienna PeeDee Belemnite and atmospheric N₂ respectively where

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

and X is either ¹³C or ¹⁵N of the sample and R corresponds to the ¹³C:¹²C or ¹⁵N:¹⁴N ratio.

Instrumental analytical error was ± 0.20‰ based on internal standards (casein and glutamic acid) checked against certified standards from the US National Institute of Science and Technology

and the International Atomic Energy Agency. Sediment isotopic signatures and C:N (mol/mol) ratios were calculated from these analysis.

TOC samples were dried at 105°C and weighed, combusted at 550°C for 4 h and reweighed. The weight loss is proportional to the amount of organic carbon contained in the sample. Carbon lost on ignition during combustion was calculated where

$$\text{Loss on Ignition (\%)} = [(DW_{105} - DW_{550} / DW_{105}) \times 100]$$

and DW is dry weight of samples at 105°C or 550°C in drying oven or muffle furnace respectively resulting in TOC (%).

5.3.3 Porewater Salinity and Ammonium

Sediment porewater was extracted by centrifuging thawed sediments at 10,000 rpm for 20 min and analyzing the supernatant for salinity and NH_4^+ . Salinity was measured with a refractometer. Sediment NH_4^+ ($\mu\text{mol L}^{-1}$) concentrations were calculated following Parsons et al. (1984) with colorimetric analysis based on comparisons at 640 nm absorbance on spectrophotometer and regressing to a standard curve.

5.4 Results and Discussion

Representative subsamples of sediment collections from both sampling periods during 2011 and 2013 sampling were averaged for each parameter measured and reported here (Table 5.1).

Although attempts were made to quantify subsampled pigments and sediment chemistry from the same stations across sampling periods for each delta, some materials only allowed for analysis of samples from stations in close geographic proximity. Number of subsamples dedicated to quantify each parameter varied only slightly across most parameters but sediment porewater salinity and NH_4^+ varied greatly within and between deltas due to an insufficient amount of water available for extraction for the analysis. As reported previously, due to inclement weather, Okpilak/Hulahula and Canning deltas could not be sampled during the second sampling period of 2013 (Table 5.1).

5.4.1 Pigment and TOC Analysis

Chl *a* concentrations ranged from 3.58 to 203.91 mg m⁻² which are within recently reported ranges for Arctic subtidal sediments (McTigue et al. 2015 and references therein). Jago, Okpilak, and Canning chlorophyll concentrations ranged from 3.58 to 203.91, 5.48 to 191.58, and 4.58 to 116.18 mg m⁻² respectively for each delta. These values are reflective of a strong signal for viable microphytobenthos. Mean concentrations of chl *a* from the Jago River Delta were consistently greater than the Okpilak/Hulahula and Canning deltas across both years with the Okpilak/Hulahula and Canning deltas following in order for each period (Figure 5.1). All chl *a* concentrations were significantly higher during 2011 than the first sampling period of 2013. However chl *a* concentrations from the late sampling of 2013 Jago River delta were similar to previous year's findings (Figure 5.1). The presence of chl *a* throughout these deltas is an indicator of a healthy microphytobenthic community inhabiting the upper layer of these sediments.

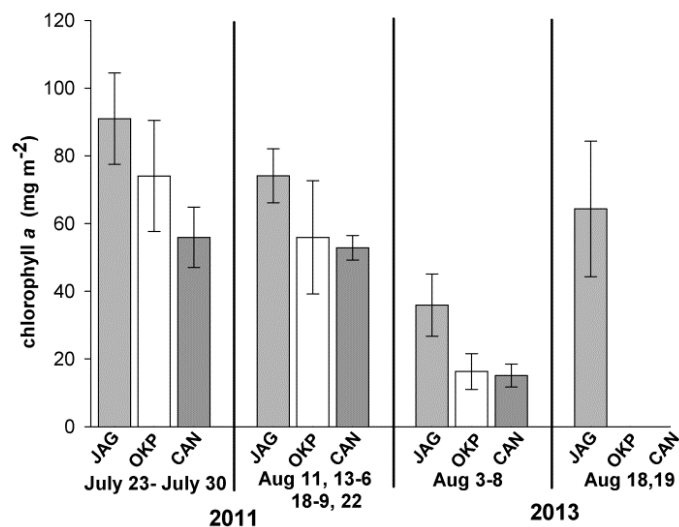


Figure 5.1. Average chlorophyll *a* concentrations from three Arctic river deltas (Jago: JAG; Okpilak/Hulahula: OKP; Canning: CAN) during 2011 and 2013 sampling regimes across two sampling periods. Error bars represent standard errors.

Evaluation of accessory pigments yielded a strong fucoxanthin signal reaching 92.96 mg m^{-2} with a steady signal throughout each delta at each sampling period. This result illustrates an established diatom community throughout each delta (Figure 5.2). Average sediment concentration of zeaxanthin from the Jago River delta during the second sampling period of 2011 reached 9.22 mg m^{-2} but never reached $> 2.74 \text{ mg m}^{-2}$ in any other delta at any other period of sampling. This signal could be indicative of decaying plant matter, cyanobacteria, or chlorophyte presence. However, the signal is very slight and not common throughout the sampling periods of any other delta. All other targeted pigments were found at very low concentrations ($\bar{x} < 5 \text{ mg m}^{-2}$) and sporadically throughout sampling periods in different deltas without trend. However, the presence of the strong diatom signal suggests an autogenous source of primary productivity during the summer months which is in congruence with our chl *a* findings. We confirmed the presence of a rich diatom community via light microscopy following a ludox extraction and centrifugation of additional sediment samples following HPLC results. The community consisted of large ($> 40 \text{ }\mu\text{m}$) naviculoid diatoms with high concentrations of lipids providing a nutrient rich food source for primary consumers.

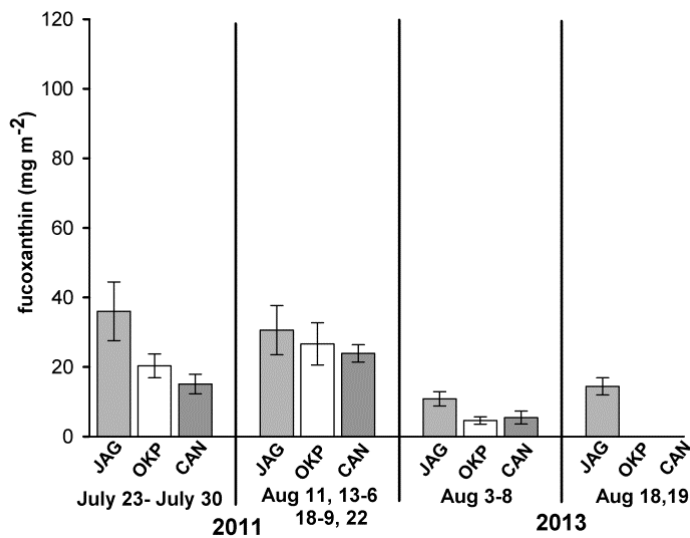


Figure 5.2. Average chlorophyll *a* concentrations from three Arctic river deltas (Jago: JAG; Okpilak/Hulahula: OKP; Canning: CAN) during 2011 and 2013 sampling regimes across two sampling periods. Error bars represent standard errors.

Total pheopigment concentrations combining pheophytin *a*, pheophorbide *a*, and pyropheophorbide *a* signals from each delta in early August 2013, and from the Jago River delta in 2013, were relatively high for pheopigments ranging up to 113.00 mg m⁻². In the early sampling period (3–8 August) average chl *a* : total pheopigment concentrations were < 1 in each of the deltas, although late season Jago sampling showed the opposite trend (Figure 5.3). This indicates that bacterial cleaving and metazoan grazing have led to a higher concentration of chl *a* breakdown products than live, intact chl *a* compounds in these deltas. Each of the degradation products was analyzed individually across each delta, and there was no statistical difference between concentrations of the bacterial breakdown product pheophytin *a* and metazoan breakdown products pheophorbide *a* and pyropheophorbide *a* in any delta (Figure 5.4). Overall, the pigment analyses from all three deltas reveal the strong presence of chl *a*. This is indicative of a healthy microphytobenthic community consisting mostly of diatoms identified by consistent signals of fucoxanthin across deltas and sample periods. However, chl *a*:total pheopigment ratios < 1 and high pheopigment concentrations show that bacterial and metazoan populations are dependent on microphytobenthic availability. Clearly, nitrogen is not a limiting resource for these benthic microalgal populations based on the high levels of porewater ammonium measured in the sediments (see porewater section).

Sedimentary total organic carbon ranged from 1.52–5.21% indicative of active carbon fixation via microphytobenthic photosynthesis across the three Arctic river deltas as expected from the strong chl *a* concentrations previously reported above. There was no significant difference in TOC (%) between sampling periods in any delta (Figure 5.5) which can be attributed to the widespread deposition of terrestrial organic matter from local sources and consistent photosynthetic fixation by microphytobenthos during each period. Curiously, Canning River delta sedimentary TOC (%) were significantly greater than Jago or Okpilak/Hulahula deltas (Figure 5.5) even though Canning had the lowest chl *a* concentrations and lowest chl *a*:total pheopigments ratios (Figure 5.3). This observation may simply reflect the overarching importance of terrestrial materials in the sediments, which was confirmed isotopically (see next section). Nonetheless, the photosynthetically active microphytobenthos does contribute substantially to in situ primary production but also acts as a source of nutrients for the microbial heterotrophs as illustrated by the high signals of pheopigments.

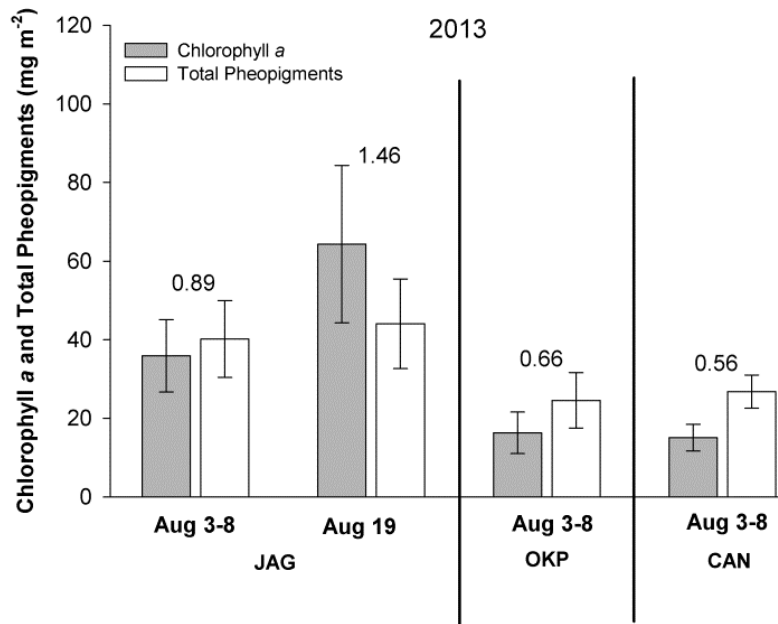


Figure 5.3. Average chlorophyll a:total pheopigment concentrations from three Arctic river deltas (Jago: JAG; Okpilak/Hulahula: OKP; Canning: CAN) during 2013 sampling regimes. Error bars represent standard errors. Numbers above bars are calculated ratio of chlorophyll a:total pheopigments.

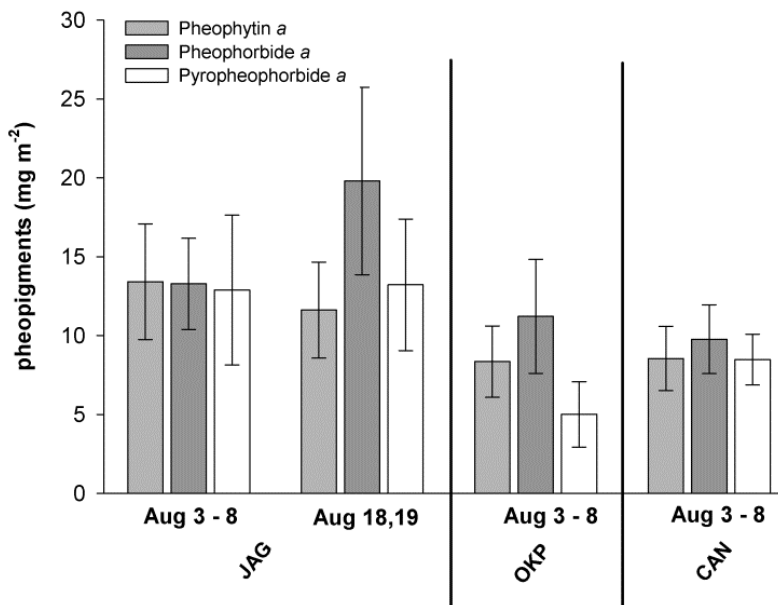


Figure 5.4. Average pheopigment concentrations from three Arctic river deltas (Jago: JAG; Okpilak/Hulahula: OKP; Canning: CAN) during 2013 sampling regimes across two sampling periods. Error bars represent standard errors.

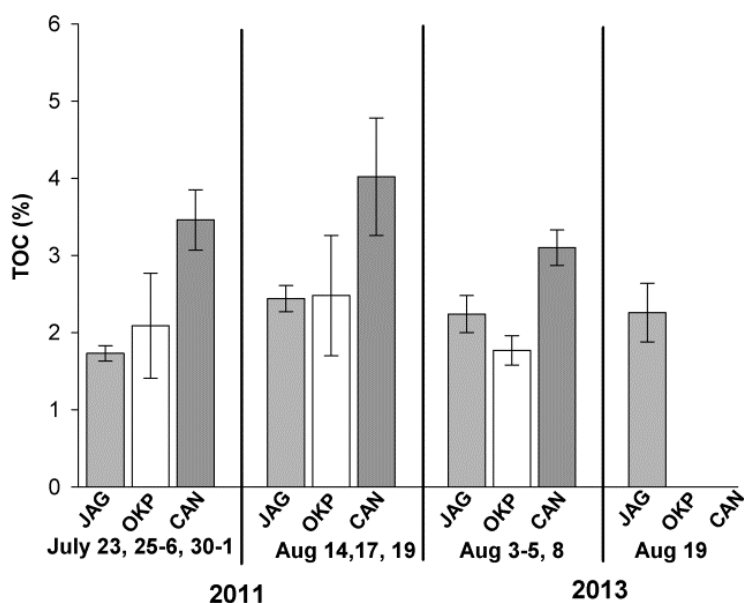


Figure 5.5. Average total organic carbon concentrations from three Arctic river deltas (Jago: JAG; Okpilak/Hulahula: OKP; Canning: CAN) during 2011 and 2013 sampling regimes across two sampling periods. Error bars represent standard errors.

5.4.2 Isotope and C:N Analysis

Stable isotopic composition of organic matter in sediments reflected strong terrestrial contributions based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranging from -27‰ to -24‰ and 1‰ to 3.5‰ respectively (Dunton et al. 2012). These were well constrained throughout sampling (Table 5.1; Figures 5.6 and 5.7). There were no significant differences within or between deltas during all sampling periods. In addition C:N ratios averaging 4 to 10:1 are indicative of terrestrial signatures within sediments as well as high lipid content (Post et al. 2007). Mean of C:N ratios were > 9:1 across all deltas and sampling periods. These data show significant influences of terrestrial matter in sediments of these three Arctic river deltas as well as high lipid content from the terrestrial matter. High lipid content in the sediments is most likely a product of the lipid-rich diatom community observed microscopically and quantified in the high fucoxanthin concentrations from pigment analysis.

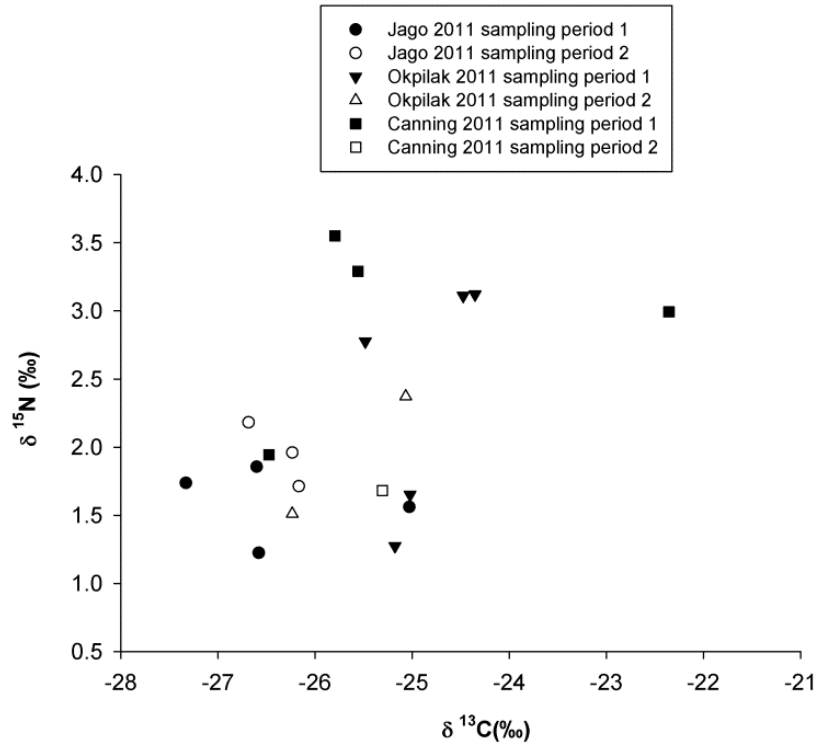


Figure 5.6. Isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for sediment samples from three Arctic river deltas (JOHC) during 2011 sampling periods.

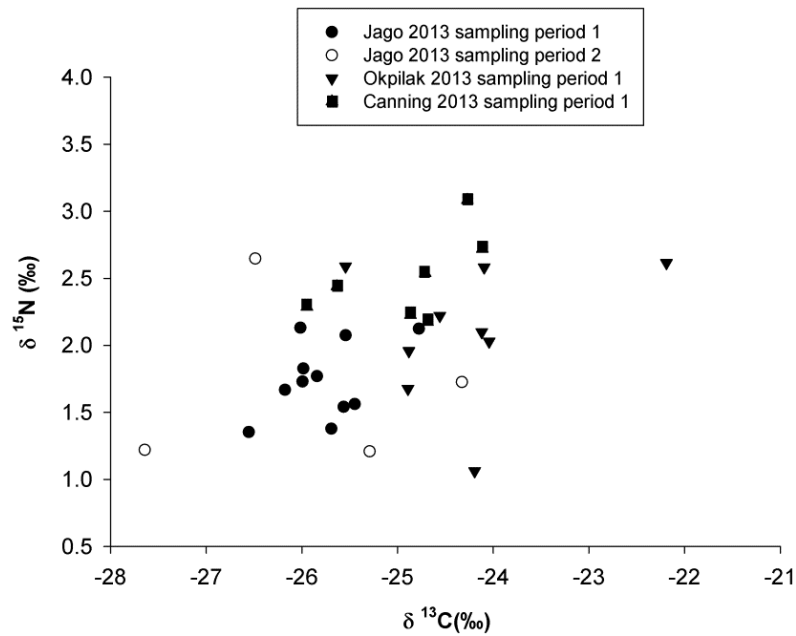


Figure 5.7: Isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for sediment samples from three Arctic river deltas (JOHC) during 2013 sampling periods.

5.4.3 Porewater Salinity and NH_4^+

Sediment porewater salinities ranged from 0 – 42 across the three deltas. However, average salinities in all three deltas were relatively low for estuarine habitats (< 12 ; Table 5.1). These values reflect brackish water conditions which are a product of the large amounts of freshwater inflow into the deltas from rivers, even during periods of lower flow following the June freshet.

Concentrations of sediment NH_4^+ reached as high as $417.62 \mu\text{mol L}^{-1}$ but averages across three deltas never rose above $203.42 \mu\text{mol L}^{-1}$ (Figure 5.8). Ammonium is a reduced nitrogen species and although normally present in concentrations within the range reported here, the compound is usually associated with active aerobic organic matter decomposition, or in deeper soils, processes of nitrate or sulfate reduction in the presence of organic matter (Fenchel and Riedl 1970). Mean concentrations of NH_4^+ were highest in the Jago River delta during 2011 (Figure 5.8) which correlates with the low TOC (%) as a result of carbon remineralization. The Jago also possessed the highest concentrations of chl *a* that we can attribute to the high NH_4^+ concentrations found in these sediments that would support appreciable algal biomass. Interestingly, terrestrial organic matter may be more important as a substrate for bacterial production of inorganic-N for benthic microalgae than as a carbon source for sediment consumers such as amphipods, polychaetes, and small molluscs.

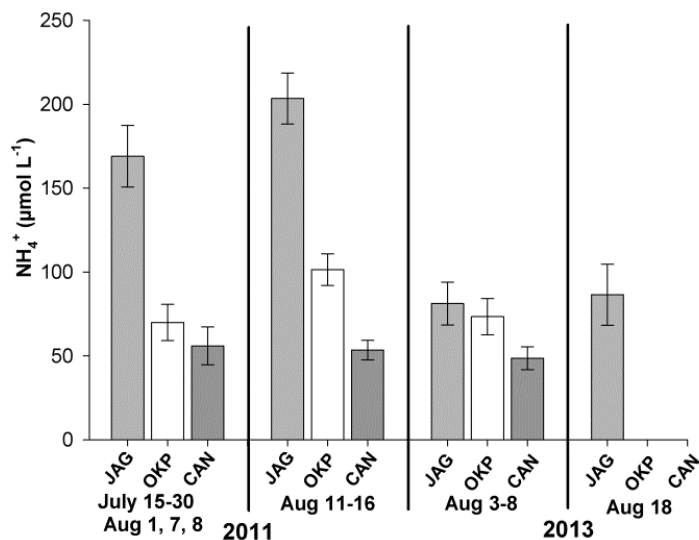


Figure 5.8. Average sediment ammonium concentrations from three Arctic river deltas (Jago: JAG; Okpilak/Hulahula: OKP; Canning: CAN) during 2011 and 2013 sampling regimes across two sampling periods. Error bars represent standard errors.

5.5 References

- Craig PC, Griffen WB, Johnson SR, Schell D. 1984. Trophic dynamics in an arctic lagoon. In *The Alaskan Beaufort Sea-a review*. Transactions of the American Fisheries Society. 113: 265-282.
- Dunton KH, Schonberg SV, Cooper LW. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. *Estuaries and Coasts*. 35:416-435.
- Fenchel TM, Riedl JR. 1970. The sulfide system: A new biotic community under the oxidized layer of marine sandy bottoms. *Marine Biology*. 7:255-268
- Glud RN, Woelfel J, Karsten U, Kuhl M, Rysgaard S. 2009. Benthic microalgal production in the Arctic: applied methods and status of the current database. *Botanica Marina*. 52:559-571.
- Kazlowski S, Stewart M. 2006. Arctic wings: birds of the Arctic National Wildlife Refuge. Brown S, editor. Seattle (WA): Mountaineers Books.
- McTigue ND, Bucolo P, Liu Z, Dunton KH. 2015. Pelagic-benthic coupling, food webs, and organic matter degradation in the Chukchi Sea: insights from sedimentary pigments and stable carbon isotopes. *Limnology and Oceanography*. 60:429-445.
- McTigue ND, Dunton KH. 2014. Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. *Deep-Sea Research*. 102:84-96.
- Parsons TR, Maita Y, Lalli CM. 1984. A manual of chemical and biological methods for seawater analysis. Oxford: Pergamon Press.
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analysis. *Oecologia*. 152:179-189.
- Underwood GJC, Kromkamp J. 1999. Primary production by phytoplankton and microphytobenthos in estuaries. *Advances in Ecological Research*. 29:93-153.

6. Environmental Variables and Sediment Macroinvertebrates

Roy Churchwell, University of Alaska Fairbanks

Abby Powell, U S Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit

Ken Dunton, The University of Texas Marine Science Institute

6.1 Introduction

Tens of thousands of shorebirds use Alaska's Beaufort Sea coastal river deltas as stopover sites and as first stops on their fall migration to forage on invertebrates and deposit fat stores to fuel their long-distance flights (Taylor et al. 2010; Brown et al. 2012; Churchwell 2015). There is a paucity of information on the macroinvertebrate community inhabiting these intertidal habitats or the physical and chemical characteristics of deltaic sediments. In fact, these deltas have been reported as uninhabited by benthic macroinvertebrates (Crane 1974; Feder and Schamel 1976; Gutt 2001), despite the fact that shorebirds have been observed foraging there. However, few unpublished reports describe persistent intertidal macroinvertebrate communities (Connors and Risebrough 1977; Andres 1989).

Our first objective was to identify the macroinvertebrate taxa at the JOHC deltas. Second, we examined within-year variability of invertebrate abundance during three time periods corresponding to shorebird migration. Because invertebrate abundance is partially determined by the environmental factors, we modeled the association between abundance and environmental variables while accounting for spatial and temporal effects. Specifically, we predicted that invertebrate abundance would show a positive relationship with the proportion of fine sediment and soil moisture. Glaciers are a major source of fine sediments in some of these river deltas, but they are expected to disappear in the future, which may ultimately change the characteristics of mudflats (Nolan et al. 2011).

Finally, we used stable isotope comparisons to determine whether intertidal invertebrates were freshwater- or marine-carbon based, and to describe trophic structure of shorebird food webs. Stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes quantify trophic level and forage dynamics, respectively. Nitrogen isotope values increase about 3.4‰ through fractionation with each step up in trophic level, and thus can estimate relative placement of taxa within a food web (Fry 2006; Dunton et al. 2012). Carbon isotopic values distinguish marine from terrestrial sources based on

photosynthetic processes and carbon assimilation through the food chain (Fry 2006). There is a significant east-west gradient in carbon isotopic values of sediments from the Mackenzie River westward along the Beaufort Sea coast, owing to the large input of terrestrial organic carbon from the Mackenzie and the advection of marine carbon from the Chukchi Sea on the west (Dunton et al. 2006). Within lagoons, isotopic signatures of amphipods become more terrestrial with proximity to freshwater inputs and drainages (Craig et al. 1984). We hypothesized that freshwater invertebrate taxa collected on deltaic mudflats would have a terrestrial isotopic signature while marine taxa would have a marine signature, and that there may be a gradient from marine to terrestrial from the lagoon to the high water mark on a mudflat.

6.2 Methods

We collected invertebrate data in July and August 2010 and 2011 on the JOHC deltas. One sample was collected from a random location within 250 m² grid cells, which covered all available shorebird foraging habitat at each site (Figure 6.1). We collected samples across the grids at each delta during three sessions representing fall migration of shorebirds: early (21 July–1 August), mid- (1–8 August), and late season (10–22 August). Sampling occurred in areas accessible to feeding shorebirds: water depths ≤ 5 cm and up to the tundra edge of the delta mudflat. At each sampling location, we collected an invertebrate core and a sediment core, and recorded water depth to the nearest cm. The invertebrate core was collected with a piece of PVC pipe (1/100 m²) pushed in the sediment to 5-cm depth (volume = 501.2 cm³). We sifted the core through a 500- μ m sieve and stored the macroinvertebrates and residual sediment in a plastic jar with 70% alcohol for preservation. The sediment core was obtained using a 50-cc syringe barrel and analyzed later for grain size, moisture, and carbon/nitrogen. The syringe plunger was pushed in the sediment 5 cm (volume = 24.5 cm³), and the sample was stored in a Whirl-pac® and frozen as soon as possible. All samples were shipped back to the University of Alaska Fairbanks for analysis.

We sorted invertebrate samples by taxa to the family level when possible. We identified samples to a higher taxonomic level than family when individuals were difficult to identify and required

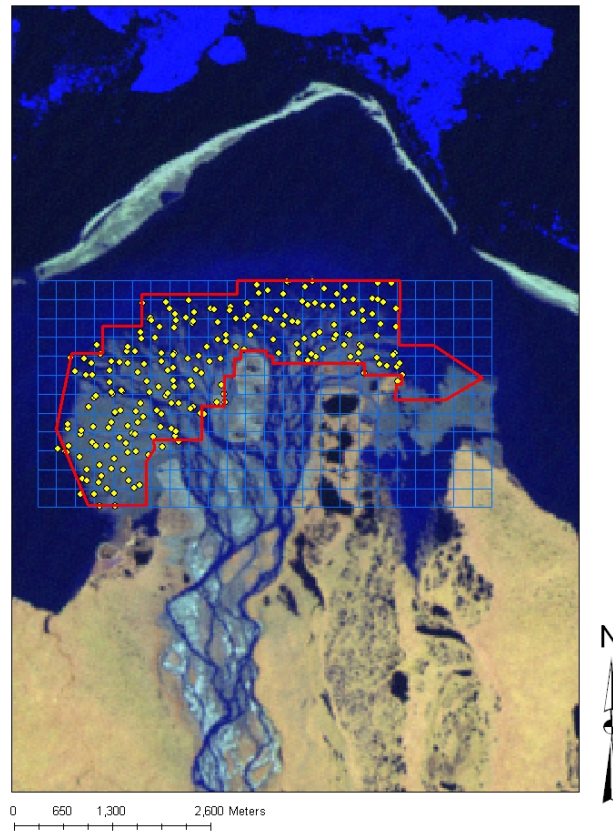


Figure 6.1. Grid used for sampling sediment characteristics and macroinvertebrates on the Jago River Delta.

an expert in the taxon. Nematoda were not counted in 2010 because they are not considered a shorebird food, but were quantified in 2011. We counted individuals in the invertebrate core and extrapolated this to m^2 (\pm S.E.) to obtain a density estimate. The percent occurrence estimate was calculated as the number of cores where the taxon was present divided by the total number of cores for that sampling session x 100.

We weighed and dried at 65°C sediment cores for 48 h to a constant weight to determine percent moisture by weight. We also subsampled two 0.1-g samples that were analyzed using a TruSpec Carbon/Nitrogen Determinator® to calculate percentage by weight for total carbon and nitrogen. The remaining sample was used to determine grain size. In 2010, sediment samples were weighed and suspended in water using a mixer; then the sand was allowed to settle for 40 sec. Then the solution containing the silt and clay portion was decanted leaving the sand, which was

sifted using a 46- μm sieve to make sure all of the silt and clay were removed. After drying once more, the sample was weighed a final time to determine percent sand. We used the percentage silt/clay determined by $100 - \text{sand}$. In 2011, after the subsamples for carbon and nitrogen were taken, the remaining sample was suspended in 100 ml of 70% hydrogen peroxide (H_2O_2) for 48 h to remove any organic material. The silt/clay portion was removed using a 63- μm sieve. Both the sand and silt/clay portions were dried to constant mass.

We also determined stable isotopic (^{13}C and ^{15}N) values for macroinvertebrate samples collected on the delta and nearby terrestrial tundra ponds. Samples of the dominant taxa were collected throughout the season as time allowed from areas where they were present during past sampling using a core and sieve, and then were frozen as soon as possible. Soft-bodied taxa were dried at 65°C for 48 h to a constant weight, and then the sample was homogenized and weighed into aluminum capsules. Taxa with a calcified exoskeleton were immersed in 2 M HCL for 24 h, rinsed in deionized water, and dried at 65°C for 48 h until constant weight was achieved; the sample was homogenized and weighed into aluminum capsules. Samples were analyzed at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) using continuous flow stable isotope-ratio mass spectrometry in a Costech ECS4010 Elemental Analyzer (Costech Scientific, Valencia, CA) and Finnigan Delta Plus XP isotope ratio mass spectrometer through the ConFlo III interface (Thermo-Finnigan, Bremen, Germany). We report our results in delta (δ) notation ‰ relative to the international standard (^{13}C = Vienna PeeDee Belemnite; ^{15}N = atmospheric nitrogen) using the equation: $\delta^{13}\text{C} = [\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1] \times 1,000$ with R representing the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Laboratory standards (peptone) were run with samples, and using the standard deviation of replicate measurements the analytical error was estimated to be $< \pm 0.2\%$.

6.2.1 Species Diversity, Distribution, and Statistical Analyses

We calculated diversity indices using data from 2011 to compare the invertebrate communities among the three study deltas using both Simpson's and Shannon's log base 10 diversity indices and evenness (Krebs 1989). Data from 2011 were selected because we had better detection of rare species that year. We are uncertain if the low number of rare species in 2010 was due to observer bias or a lack of rare species. We used both diversity indices because the Simpson's Index reduces bias of rare species, while Shannon's Index reduces bias of abundant species, but

both indices increase with the number of species detected (Krebs 1989). We made identifications to different taxonomic levels, but most to the family level, and so we have to assume each taxon that we made identifications to at our sites has only one family, because it is the lowest taxonomic level of the analysis.

We developed models using the statistical program R version 2.15.2 (R Development Core Team 2013) to evaluate the effect of site, year, session, and environmental factors on invertebrate abundance. We created linear mixed-effects (random and fixed effects) restricted maximum likelihood (REML) models using the R library lmerTest (Kuznetsova et al. 2013) and used stepwise model selection using backwards elimination of non-significant factors that were then further evaluated for fit. The dependent variable was invertebrate abundance of Chironomidae and Oligochaeta modeled respectively, which were the only two taxa with a significant sample size for this analysis. Chironomidae were only modeled for the Jago and Okpilak/Hulahula deltas because they were not present at the Canning. Modeled random effects included year, session, and delta, as well as interactions between these three variables. Modeled fixed effects included delta; spatial variables latitude and longitude from sample locations; and continuous variables for nitrogen, carbon, water depth, moisture, and percent silt/clay from sample locations. We started with a full model containing the interaction ‘delta x longitude x water depth x moisture x silt/clay’ and the other variables as non-interactive terms, based on past experience from modeling invertebrate populations in benthic habitats. We tested model and variable diagnostics using the variance inflation factor in the R library car (Fox et al. 2013) and Q-Q plots and residual plots in the lme4 library (Bates et al. 2013). Significance was set at $\alpha = 0.05$.

To determine invertebrate distribution, we used kriging with the R library geoR (Ribeiro and Diggle 2013). Kriging is a geostatistical technique that uses the spatial variance between pairs of sample points to model the predicted values from each sample location, which is then extrapolated across the study area (Fortin and Dale 2005). We created variograms using an exponential model, fit the model, and projected the model as a predictive map.

In order to calculate the spatial extent of invertebrate patches, we used Moran’s I with R library spatial (Ripley 2013) for each year, sample session, and major taxa combination. Moran’s I is a

spatial parameter that describes the spatial autocorrelation of a dataset by distance class (Fortin and Dale 2005). Moran's I can also be used to interpret patch size as a linear distance across the patch.

Finally, we used MANOVA in R to test for differences between isotopic values of invertebrates collected in delta (marine) and tundra pond (terrestrial) habitats from three ponds in tundra habitat < 2 km from the Jago River Delta. We calculated trophic level for invertebrates using a fractionation coefficient of 3.4‰ (Dunton et al. 2012), and the equation: $TL(POM) = \delta^{15}N_{Consumer} - \delta^{15}N_{POM} / 3.4 + 1$ (Iken et al. 2010). The variable TL = trophic level and POM = particulate organic matter, which is the base measurement for $\delta^{15}N$ in the food chain.

6.3 Results

6.3.1 Taxa and Occurrence

We collected samples at 247, 525, and 487 sites over two years on the Canning, Okpilak/Hulahula, and Jago deltas respectively. Salinity and water temperature were similar at the Jago and Okpilak/Hulahula Delta (Figure 6.2), and most values were near zero with patches of saline water near gaps in the barrier islands. The Canning Delta had higher salinity values and lower temperatures (Figure 6.2) because of the proximity of this delta to an outlet to the ocean. Overall, we collected 18 taxa: 11 freshwater, 3 marine, 3 terrestrial, and 1 taxon that inhabits all habitats (Table 6.1). Indices of diversity and evenness were highest at the Jago Delta and lowest at the Canning Delta (Figure 6.3).

Six taxa regularly occurred in our samples: Oligochaeta, Chironomidae, Tipulidae, Amphipoda, Chaetiliidae, and Spionidae (Table 6.2, Figure 6.4), but these taxa were not found at all sites. Chironomidae larvae were never observed at the Canning Delta (although a few adults were present) despite the fact that they were sometimes the most common taxa at other deltas. Likewise, Tipulidae larvae were only found on one occasion at the Canning Delta, but were common at the other two deltas. In contrast, Spionidae were common at the Canning Delta but uncommon at the Okpilak/Hulahula Delta and never found at the Jago Delta. Overall, marine

Table 6.1. Taxonomic list of invertebrates sampled at Beaufort Sea river deltas (JOHC), 2010 – 2011. Taxa are underlined at the level at which we conducted the analysis. Superscript ^F = freshwater taxa, ^S = saltwater taxa, ^B = commonly found in both salt and freshwater, and ^T = terrestrial taxa.

Phylum	Class	Order	Family	Genus	Species
<u>Nematoda</u>^B					
Annelida					
	Clitellata				
		<u>Oligochaeta</u> ^F			
	Polychaeta				
		Canalipalpata			
			<u>Spionidae</u> ^S		
				<i>Spio</i>	<i>filicornis</i>
Arthropoda					
	Maxillipoda				
		<u>Copepoda</u> ^F			
	Malacostraca				
		<u>Amphipoda</u> ^S			
			Lysianassidae		
				<i>Orchomene</i>	
			Pontoporeiidae		
				<i>Pontoporeia</i>	<i>femorata</i>
		Isopoda			
			<u>Chaetiliidae</u> ^S		
				<i>Saduria</i>	<i>entomon</i>
	Arachnida				
		<u>Araneae</u> ^T			
		Trombidiformes			
			<u>Hydrachnidae</u> ^F		
	Entognatha				
		<u>Collembola</u> ^F			
	Insecta				
		<u>Hymenoptera</u> ^T			
		Hemiptera			
			<u>Cicadellidae</u> ^T		
		Plecoptera			
			<u>Capniidae</u> ^T		
		Diptera			
			<u>Chironomidae</u> ^F		
				<i>Diplocladius</i>	
				<i>Chironomus</i>	

Tipulidae^F

Ormosia

Culicidae^F

Empididae^F

Ephydriidae^F

Ceratopugonidae^F

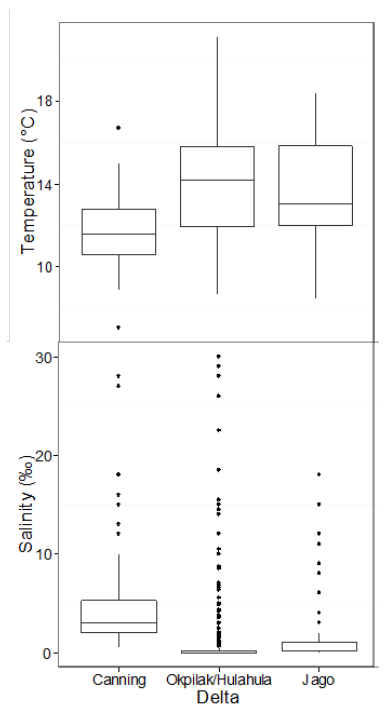


Figure 6.2. Mean salinity and temperature for each Beaufort Sea river delta (JOHC), 2010 – 2011. The box represents the first and third quartile, the whiskers represent one standard deviation, and the dots are outliers.

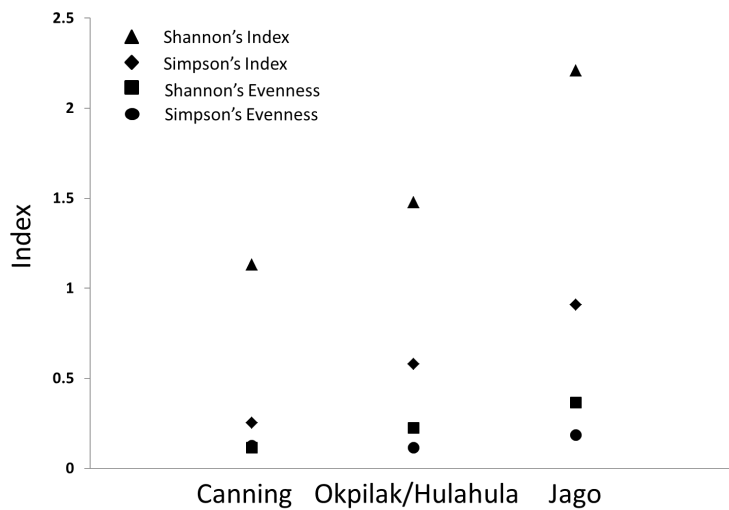


Figure 6.3. Shannon and Simpson's diversity indices and evenness for taxa sampled on Beaufort Sea river deltas (JOHC) 2011. Individuals were identified to the family level or assumed to contain one family if identified at a higher taxonomic level.

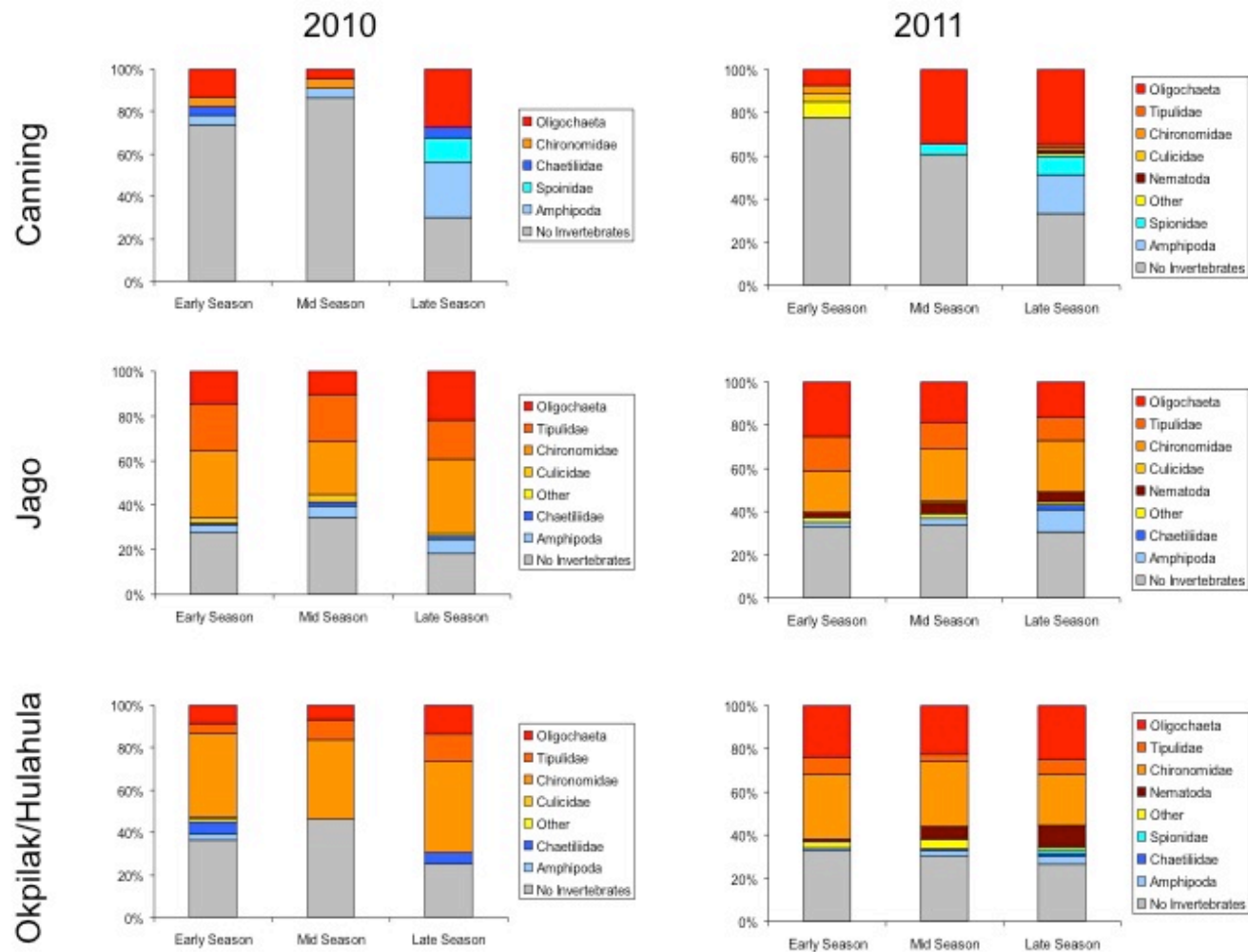


Figure 6.4. Percent occurrence of macroinvertebrates sampled at Beaufort Sea river deltas (JOHC) in 2010 and 2011.

invertebrates were more prominent at the Canning Delta compared to the other two deltas where freshwater invertebrates dominated. Variation in invertebrate occurrence within deltas was similar between years (Table 6.2, Figure 6.4). The Canning tended to have fewer invertebrates during early and mid-season sessions, but invertebrate occurrence, especially for marine invertebrates, increased in the late session.

6.4.2 Invertebrate Abundance and Distribution

We determined invertebrate abundance at all three deltas for each year and sampling session (Table 6.3). Environmental variables were sampled for each invertebrate sample location at each delta (Figures 6.5 and 6.6). In summary, the Jago and Okpilak/Hulahula deltas had similar sediment environmental characteristics, but the Canning Delta had four times higher salinity and carbon values and tended to be cooler and drier on average than the other two sites.

Chironomidae and Oligochaeta were the only two taxa common enough to make visual comparisons across years and sessions and to model abundance (Table 6.4a and b). There was a significant interaction between the random temporal variables year and session for both Chironomidae ($P < 0.05$; Table 6.4a) and Oligochaeta ($P = 0.04$; Table 6.4b). In the Chironomidae regression model the spatial variable Latitude was significant with a positive effect ($P < 0.001$), but spatial variables were not significant in the Oligochaeta model. The fixed environmental variables related to resources (total carbon and nitrogen) were not significant model predictors for either Chironomidae or Oligochaeta abundance. However, environmental variable interactions for moisture were significantly positive (delta:moisture $P = 0.003$; silt:moisture $P = 0.011$) for Chironomidae, but negative (delta:moisture $P < 0.001$) for Oligochaeta (Tables 6.4a and b).

Spatial maps demonstrated consistent distribution but varying abundance patterns across the spatial domain, which we were able to relate to invertebrate life history. Kriged maps of all invertebrates combined indicate invertebrate distributions were generally similar among years with core patches found on the edges and middle of the Jago Delta, but abundance within patches varied (Figure 6.5). We saw similar consistency in patches at the other deltas, but were limited in our ability to present all of the data. The kriged abundances for some taxa were quite variable

Table 6.2. The percentage that each taxa contributed to invertebrate occurrence for each river delta and season on the Beaufort Sea coast. Percentage is the number of cores where taxon was present divided by total cores collected for that period x 100. Nematodes were only quantified in 2011. Species in the Other category include those species that only occurred once within a season and delta, including Capniidae, Cicadellidae, Arachnida, Copepoda, Empididae, Ephydriidae, Hydrachnidia, and Hymenoptera. The “***” represents no detection of a taxa.

	<u>Canning 2010</u>			<u>Canning 2011</u>		
	Early Season	Mid Season	Late Season	Early Season	Mid Season	Late Season
Amphipoda	4.4	4.6	26.3	**	**	18.1
Chaetiliidae	4.4	**	5.0	**	**	**
Chironomidae	4.4	4.6	**	3.7	**	1.4
Culicidae	**	**	**	3.7	**	**
Oligochaeta	13.0	4.6	27.5	7.4	34.2	34.7
Spionidae	**	**	11.2	**	4.9	8.3
Tipulidae	**	**	**	**	**	1.4
Other	**	**	**	7.4	**	1.4
No Invertebrates	73.9	86.4	30.0	77.8	61.0	33.3
	<u>Jago 2010</u>			<u>Jago 2011</u>		
Amphipoda	3.3	5.2	6.5	2.3	3.0	10.5
Chaetiliidae	1.1	1.7	1.1	**	**	2.2
Chironomidae	30.0	24.1	33.7	19.3	24.0	23.9
Culicidae	2.2	3.5	**	**	1.0	**
Nematoda	**	**	**	2.3	5.0	4.5
Oligochaeta	14.4	10.3	21.7	25.0	19.0	16.4
Tipulidae	21.1	20.7	17.4	15.9	12.0	10.5
Other	**	**	1.1	2.3	2.0	1.5
No Invertebrates	27.8	34.5	18.5	33.0	34.0	30.6
	<u>Okpilak/Hulahula 2010</u>			<u>Okpilak/Hulahula 2011</u>		
Amphipoda	3.2	**	**	1.3	2.4	3.6
Chaetiliidae	5.4	**	5.3	**	0.8	1.2
Chironomidae	39.8	37.2	42.7	30.3	30.4	23.8
Culicidae	1.1	**	**	**	**	**
Nematoda	**	**	**	1.3	5.6	10.1
Oligochaeta	8.6	7.0	13.3	23.7	22.4	25.0
Spionidae	**	**	**	**	**	1.8
Tipulidae	4.3	9.3	13.3	7.9	3.2	6.6
Other	1.1	**	**	2.6	4.8	1.2
No Invertebrates	36.6	46.5	25.3	32.9	30.4	26.8

Table 6.3. Abundance estimates (mean \pm S.E.) of macroinvertebrate taxa from the Canning, Jago, and Okpilak/Hulahula river deltas. Measurements are abundance m⁻². The “***” represents no detection of a taxa.

	Canning 2010			Canning 2011		
	Early Season	Mid Season	Late Season	Early Season	Mid Season	Late Season
Amphipoda	8.7 \pm 8.7	4.6 \pm 4.6	172.5 \pm 59.1	**	**	158.9 \pm 85.8
Chaetiliidae	4.4 \pm 4.4	**	5.0 \pm 5.0	**	**	**
Chironomidae	4.4 \pm 4.4	**	10.0 \pm 10.0	3.7 \pm 3.7	**	3.6 \pm 3.6
Collembola	**	**	**	7.4 \pm 7.4	**	**
Culicidae	**	**	**	3.7 \pm 3.7	**	**
Ephydriidae	**	**	**	**	**	1.8 \pm 1.8
Nematoda	**	**	**	**	**	3.6 \pm 3.6
Oligochaeta	69.6 \pm 56.7	9.1 \pm 9.1	490.0 \pm 139.8	55.6 \pm 48.4	943.6 \pm 293.6	876.8 \pm 294.4
Spionidae	**	**	52.5 \pm 22.3	**	5.1 \pm 3.6	28.6 \pm 15.7
Tipulidae	**	**	**	**	**	1.8 \pm 1.8
	Jago 2010			Jago 2011		
Amphipoda	4.3 \pm 2.6	31.7 \pm 24.2	28.6 \pm 22.1	2.9 \pm 2.0	3.8 \pm 2.2	69.5 \pm 31.5
Arachnida	**	**	**	**	1.3 \pm 1.3	**
Capniidae	**	**	**	1.5 \pm 1.5	**	1.1 \pm 1.1
Chaetiliidae	1.1 \pm 1.1	1.7 \pm 1.7	1.1 \pm 1.1	**	**	3.2 \pm 1.8
Chironomidae	235.5 \pm 68.7	185.0 \pm 70.9	575.8 \pm 123.5	108.7 \pm 36.9	496.2 \pm 141.8	539.0 \pm 118.5
Cicadellidae	**	**	1.1 \pm 1.1	**	**	**
Collembola	**	**	**	1.5 \pm 1.5	**	1.1 \pm 1.1
Copepoda	**	**	**	**	**	1.1 \pm 1.1
Culicidae	2.2 \pm 1.5	3.3 \pm 2.3	**	**	1.3 \pm 1.3	**
Ephydriidae	**	**	**	**	1.3 \pm 1.3	**
Nematoda	**	**	**	2.9 \pm 2.9	21.5 \pm 12.7	10.5 \pm 4.6
Oligochaeta	211.8 \pm 100.4	15.0 \pm 7.5	205.5 \pm 62.8	349.3 \pm 132.6	311.4 \pm 203.8	543.2 \pm 206.9
Tipulidae	36.6 \pm 9.6	56.7 \pm 22.1	51.7 \pm 15.2	40.6 \pm 12.4	40.5 \pm 15.0	72.6 \pm 26.8

	Okpilak/Hulahula 2010			Okpilak/Hulahula 2011		
Amphipoda	8.7 ± 6.7	**	**	1.7 ± 1.7	4.1 ± 2.5	17.3 ± 11.0
Capniidae	1.1 ± 1.1	**	**	**	2.1 ± 2.1	
Chaetiliidae	6.5 ± 3.0	**	5.3 ± 2.6	**	1.0 ± 1.0	2.4 ± 1.8
Chironomidae	226.1 ± 70.3	143.2 ± 60.1	228.0 ± 56.1	198.3 ± 80.7	217.5 ± 49.0	178.7 ± 42.1
Collembola	**	**	**	3.5 ± 3.5	1.0 ± 1.0	1.6 ± 1.6
Copepoda	**	**	**	**	3.1 ± 3.1	0.8 ± 0.8
Culicidae	1.1 ± 1.1	**	**	**	**	**
Empididae	**	**	**	**	1.0 ± 1.0	**
Hydrachnidia	**	**	**	**	1.0 ± 1.0	**
Hymenoptera	**	**	**	1.7 ± 1.7	1.0 ± 1.0	**
Nematode	**	**	**	1.7 ± 1.7	59.8 ± 34.3	68.5 ± 29.3
Oligochaeta	130.4 ± 85.6	161.4 ± 115.8	109.3 ± 57.8	613.8 ± 224.1	857.7 ± 245.0	1339.4 ± 305.7
Spionidae	**	**	**	**	**	7.1 ± 5.6
Tipulidae	5.4 ± 2.8	25.0 ± 13.5	17.3 ± 5.5	31.0 ± 21.0	10.3 ± 6.6	32.3 ± 20.1

Table 6.4. Effects of environmental factors on Chironomidae abundance (a) and Oligochaeta abundance (b) on Beaufort Sea river deltas based on a linear model in which we found a significant interaction between the random temporal variables year and session for both Chironomidae ($p < 0.05$) and Oligochaeta ($p = 0.04$). All variables for the best model are shown and only significant random variables are reported. Significance of fixed factors was used in a stepwise model selection using backwards elimination of non-significant factors.

a.

<u>Random Factors</u>			<u>Fixed Factors</u>				
Variable	Variance	S.D.	Variable	Estimate	S.E.	t-value	p-value
Year:Session	0.00	0.06	Intercept	-629.60	128.40	-4.91	0.000
Residual	0.18	0.42	Latitude	8.99	1.83	4.91	0.000
			Delta	-1.09	0.22	-4.95	0.000
			Moisture	-0.01	0.01	-1.32	0.188
			Silt/clay	-0.01	0.01	-2.38	0.018
			Delta:Moisture	0.03	0.01	2.96	0.003
			Moisture:Silt/clay	0.00	0.00	2.56	0.011

<u>Random Factors</u>			<u>Fixed Factors</u>				
Variable	Variance	S.D.	Variable	Estimate	S.E.	t-value	p-value
Year:Session	0.01	0.07	Intercept	-0.77	0.27	-2.88	0.004
Residual	0.26	0.51	Delta	0.44	0.12	3.74	0.000
			Moisture	0.06	0.01	4.52	0.000
			Delta:Moisture	-0.02	0.01	-4.39	0.000

Table 6.5. Carbon and nitrogen isotopic values for benthic macroinvertebrates (mean \pm SE) and the C:N ratio for corresponding samples collected from Beaufort Sea river deltas and three tundra ponds < 2 km from the Jago Delta, 2010–2011.

	N	$\delta^{15}\text{N}$ (‰ \pm SE)	$\delta^{13}\text{C}$ (‰ \pm SE)	C:N (Moles/mole \pm SE)
<u>Delta</u>				
Amphipoda	5	4.5 \pm 0.3	-22.0 \pm 0.7	5.6 \pm 0.2
Chironomidae	2	3.0 \pm 0.5	-22.3 \pm 1.6	5.8 \pm 0.4
Culicidae	1	3.3	-31.3	4.1
Oligochaeta	1	5.2	-22.0	5.3
Saduria	2	6.6 \pm 2.0	-19.8 \pm 0.7	4.8 \pm 0.1
Spionidae	2	5.1 \pm 0.0	-24.2 \pm 0.4	5.9 \pm 0.0
Tipulidae	6	1.3 \pm 0.4	-23.7 \pm 0.1	5.8 \pm 0.2
<u>Tundra Ponds</u>				
Anostraca	2	1.4 \pm 0.0	-36.2 \pm 0.6	4.1 \pm 0.1
Chironomidae	6	1.7 \pm 0.3	-31.6 \pm 0.9	4.8 \pm 0.1
Cladocera	1	0.2	-34.6	5.1
Coleoptera	3	2.6 \pm 0.4	-31.8 \pm 1.9	4.7 \pm 0.4
Oligochaeta	5	0.7 \pm 0.2	-31.7 \pm 0.9	4.7 \pm 0.1
Ostracoda	1	0.8	-34.4	5.1
Plecoptera	1	1.1	-35.4	4.8

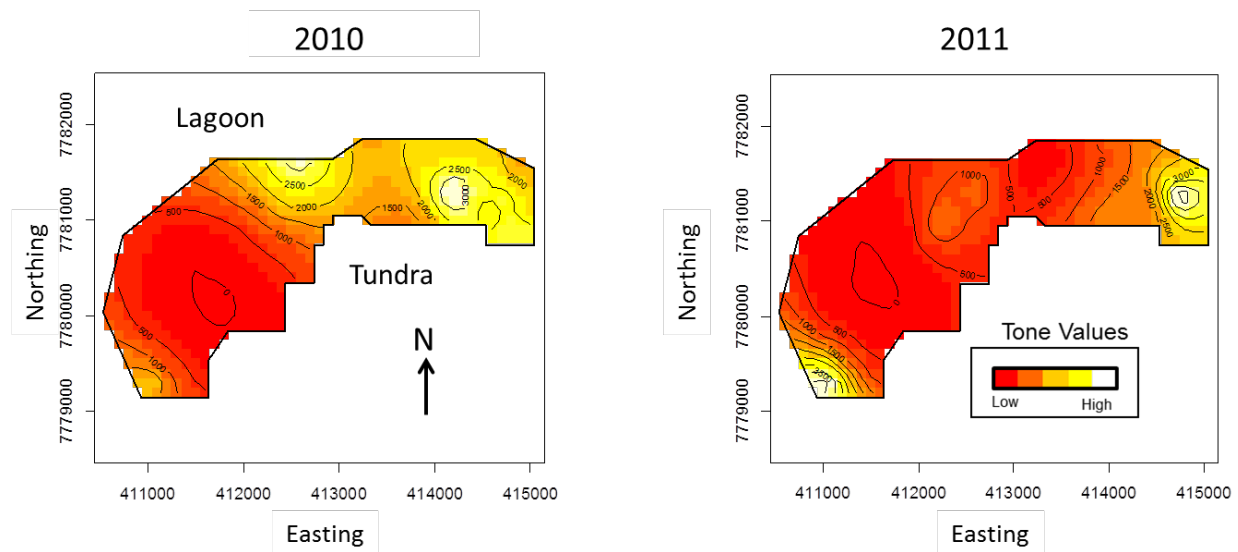


Figure 6.5. Predicted distribution of all invertebrate taxa combined during late-season sampling at the Jago River Delta 2010 – 2011.

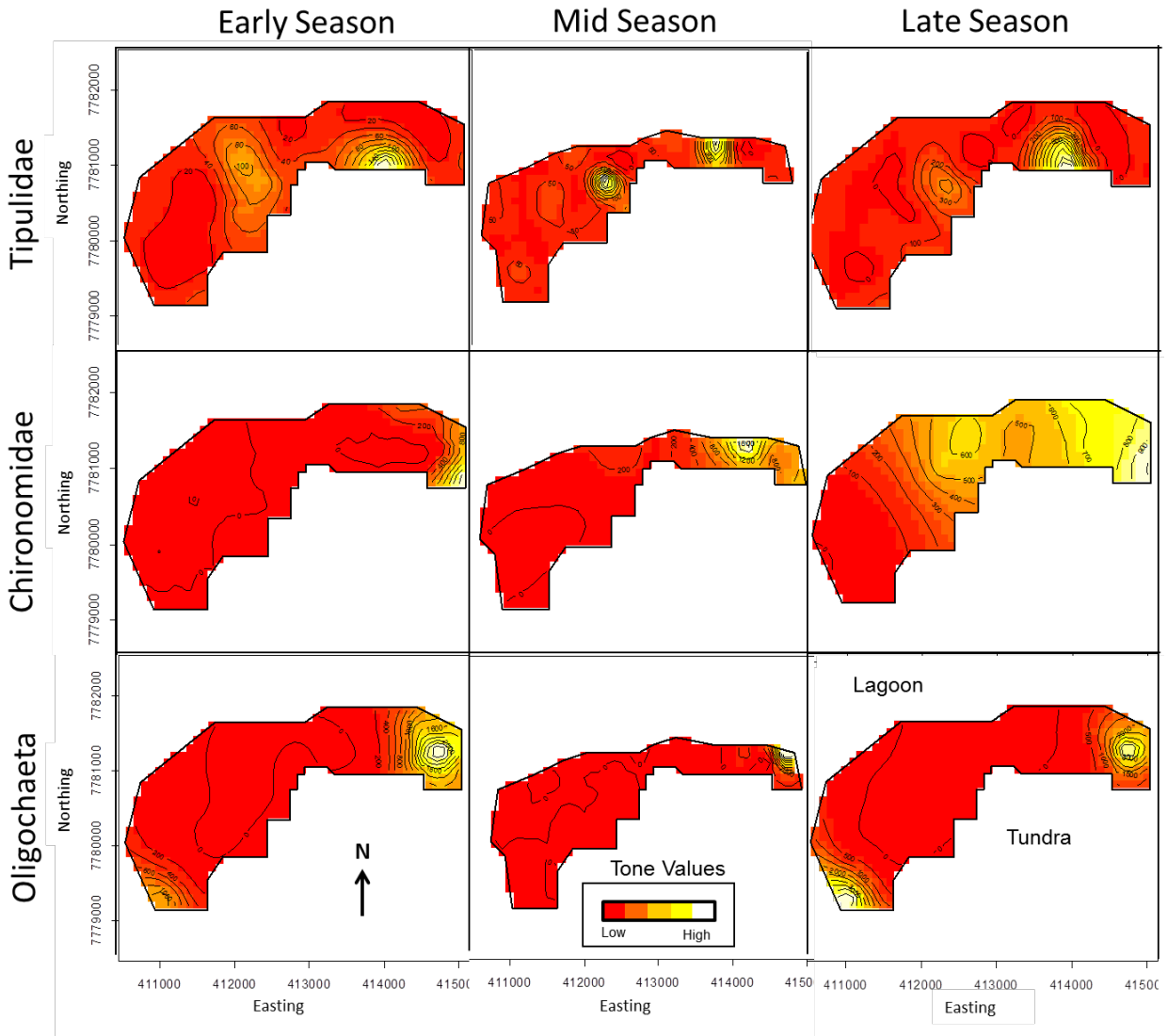


Figure 6.6. Predicted distribution of invertebrate taxa through three sampling sessions (early = 21 July – 1 August, mid = 1 – 8 August, late = 10 – 22 August) at the Jago River Delta 2011. The area of the delta changes during the mid-season due to lower water levels during that session.

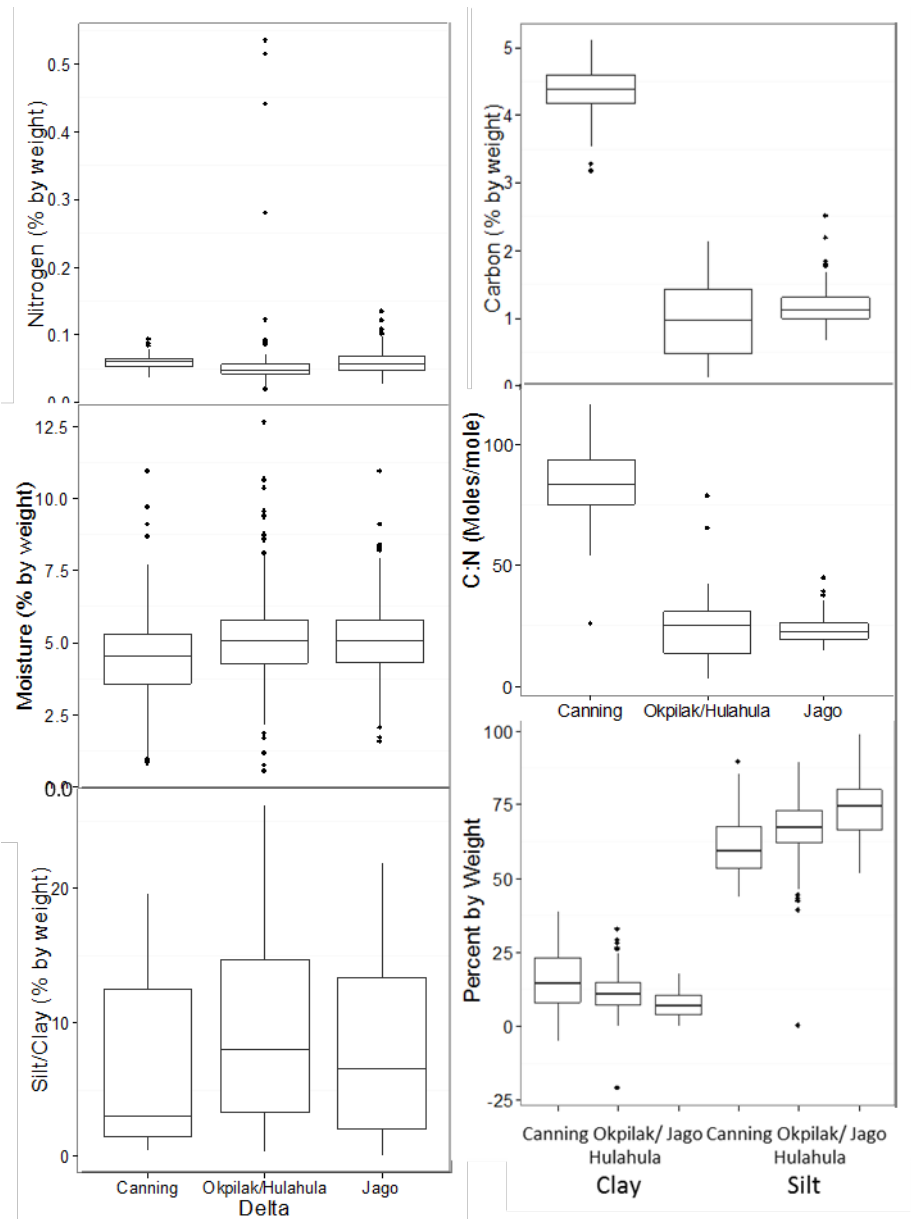


Figure 6.7. Sediment grain size with respect to the silt/clay fraction (bottom left panel), soil moisture, and C:N data from Beaufort Sea river deltas, 2010-2011. The unquantified portion of the sample is sand. The proportion of clay or silt in the combined silt/clay fraction by weight fraction for each delta sediment sample is included (bottom right panel).

within the delta and among survey session, with abundances increasing later in the season (Figure 6.6). Seasonally, patches of Tipulidae larvae expanded from terrestrial tundra origins as summer progressed, while patches of Chironomidae larvae expanded from east to west. In contrast, Oligochaeta were consistently found in the same patches throughout the season. Moran's I estimates of patch size for all invertebrates combined and individual taxa were 400 – 600 m. Almost all estimates were \approx 400 m except there were a few estimates of \approx 600 m measured for the Okpilak/Hulahula.

6.3.3 Stable Isotopes

With just one exception (noted below), freshwater and marine taxa collected on Beaufort Sea river deltas had average $\delta^{13}\text{C}$ values ranging from -19.8 to -24.2‰, compared to organisms collected on tundra ponds on the Jago Delta that had more depleted mean $\delta^{13}\text{C}$ signatures ranging from -31.7 to -36.2‰. Most invertebrate consumers were characterized as either dependent on terrestrial organic carbon as defined by isotopic values less than about -28‰ or mainly by autochthonous sources of carbon as denoted by values greater than -24‰ (Figure 6.8, Table 6.5). There was a significant difference in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signature between delta and terrestrial samples ($P < 0.001$). The one exception were the Culicidae; although they were collected on the delta, they had a strong terrestrial signature ($\delta^{13}\text{C}$ -31.0‰). We suspect that these organisms had likely just hatched and migrated from nearby tundra ponds to the delta. The mean nitrogen isotopic signature for delta invertebrates ranged from $\delta^{15}\text{N}$ 1.3 to 6.6‰, and based on a trophic step fractionation of 3.4‰, delta consumers likely fall within two trophic levels, assuming that the $\delta^{15}\text{N}$ values for ultimate carbon sources on the deltas fall between 0 and 3‰ (Dunton et al 2012; Figure 6.8). Based on $\delta^{15}\text{N}$ values of 4.7‰ and 8.7‰, *Saduria* was the only taxon that spanned multiple trophic levels, which reflects the opportunistic feeding behavior of this invertebrate.

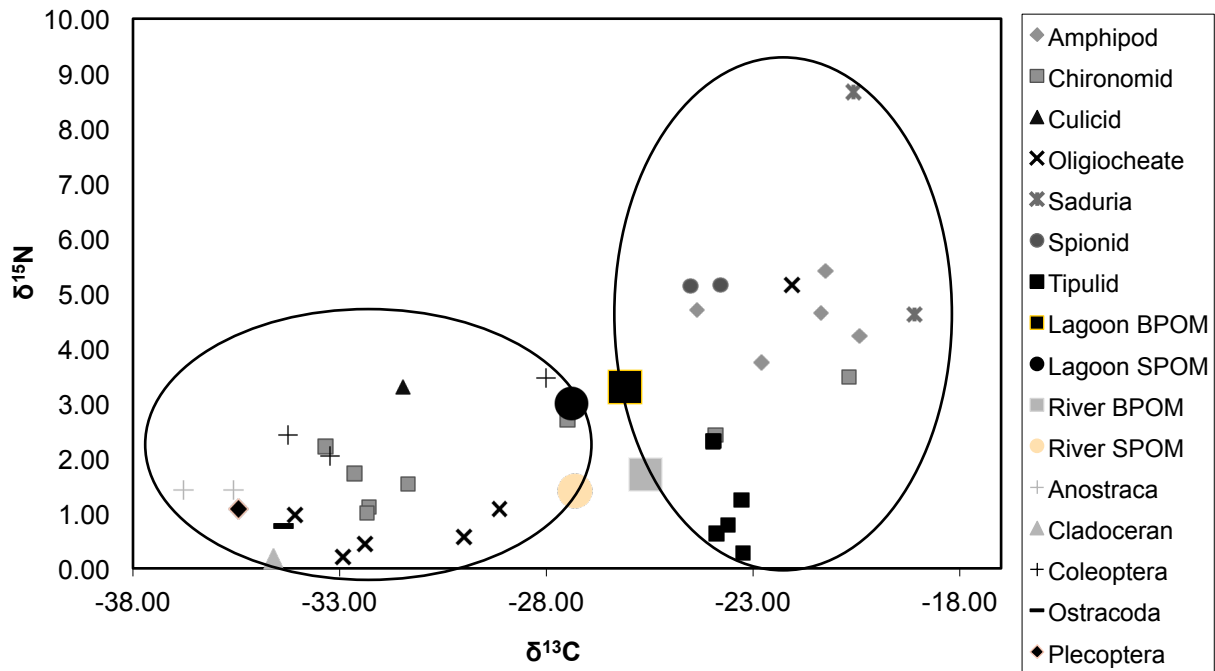


Figure 6.8. Stable isotopic values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of the major invertebrate taxa found on Beaufort Sea river deltas. Separate circles encompass all of the samples collected on the delta and within tundra ponds except for Culicidae, which were collected on the delta as adults that we believe had just migrated from nearby tundra ponds as reflected in their depleted $\delta^{13}\text{C}$ values. The four larger circles and squares are isotopic values of suspended particulate organic matter (SPOM) and benthic particulate organic matter (BPOM) from the lagoons and rivers (estimates from Dunton et al. 2012) that we hypothesized would be the base food source for delta invertebrates.

6.4 Discussion

6.4.1 Taxa and Occurrence

The fauna of the Beaufort Sea river deltas (70°N) are comparably more depauperate than the faunal communities of river deltas at more boreal latitudes (Lees et al. 1979; Lees et al. 1980; Powers et al. 2002). Taxa found at coastal sites of the Gulf of Alaska in southcentral Alaska (Copper River Delta, Port Valdez, and Cook Inlet at ~60°N) included Amphipoda, Chironomidae, and Polychaeta, but at most sites the dominant group was *Macoma* in the family Tellinidae (Lees et al. 1979; Lees et al. 1980; Powers et al. 2002). Although we did not find adult bivalves at our study sites, we found bivalve larva in a few locations (Baguley, unpublished data). *Macoma* and other bivalves were found in a nearby lagoon at 4.5-m depth providing a source population for young-of-the-year bivalves found on the mudflats (Dunton et al. 2012). In high Arctic regions, ice drove community dynamics of intertidal areas including Spitsbergen (near 78°N) where all marine benthic invertebrates except Nematoda disappeared each winter (Weslawski and Szymelfenig 1999) and in the Canadian high Arctic (65°N-70°N), which had reduced or no macroinvertebrate benthic community in solid ice zones (Dale et al. 1989).

Previous studies have attributed the absence of marine fauna in the Beaufort Sea intertidal to the damaging physical disturbances of ice scour (Crane 1974; Feder and Schamel 1976; Gutt 2001). However, while ice scour likely contributes to the loss of relatively large metazoans, the multiple generations of freshwater dipteran larvae indicate that they survive total freezing of the intertidal and that such disturbances do not permanently eliminate all macroinvertebrates from the sediments. At the nearby Mackenzie Delta, scouring was less common at water depths < 2 m, perhaps because the entire water column is frozen at this depth (Hill et al. 2001). The lack of dynamic tides in lagoons on the Beaufort Sea coast may also minimize scouring, although Baffin Island intertidal fauna did survive in areas where tidal fluctuations prevented freezing to the bottom (Dale et al. 1989).

Freezing of the water column and sediments that annually kills some taxa during the winter, as observed on Spitsbergen and Baffin Island, likely drives the low diversity in marine invertebrates in Beaufort Sea deltas. There is considerable evidence that marine invertebrates survive at depths where freezing to the bottom is prevented (Dale et al. 1989; Dunton et al. 2012). Hard-shelled

taxa like bivalves, periwinkles, and barnacles in hard bottom environments can withstand freezing temperatures to -10°C (Ellis and Wilce 1961; Gutt 2001), but bivalves dwelling in soft sediments do not survive freezing (Gutt 2001). Freezing is lethal to Amphipoda, Spionidae, and Chaetiliidae as well (Weslawski and Szymelfenig 1999), but these species can recolonize the intertidal each year from nearby lagoons (Zajac 1991; Drolet et al. 2013), where source populations can escape freezing (Dale et al. 1989; Weslawski and Szymelfenig 1999).

The low diversity of our study areas reflects responses to a highly stressed environment. Strong disturbances exceeding a community's resilience (Boesch and Rosenberg 1981) have a negative effect on invertebrate occurrence. Also, the intermediate disturbance hypothesis predicts highly disturbed areas will have lower species diversity (Huston 1979). Annual freezing of Beaufort Sea intertidal habitats is a strong disturbance that exceeds the resilience of some taxa with the effect of reduced species diversity. Likewise, invertebrate occurrence at high Arctic deltas on Spitsbergen was low. Only one taxa was found at a similar depth as our sites (Wlodarska-kowalczyk et al. 2007), and another study found four to nine taxa in samples collected at unknown depths at six different deltas (Weslawski and Szymelfenig 1999). In the Canadian high Arctic on Baffin Island, macroinvertebrate taxa were few to absent (Dale et al. 1989). Lower species diversity is due to greater disturbance in shallow water habitat (Kendall 1996) and the lack of resistance and resilience in marine species to freezing (Boesch and Rosenberg 1981). Thus, Beaufort Sea intertidal habitats are populated with pioneering marine species that recolonize the benthos annually.

Unlike marine invertebrates, freshwater invertebrates are capable of surviving freezing events within the sediment (Strathdee and Bale 1998; Danks 2007). Beaufort Sea delta sediments probably freeze all the way through to the underlying permafrost (Walker 1998); thus the strategy of burrowing deep into sediments to escape the ice is not possible. Chironomidae (Danks 1971; Andrews and Rigler 1985), Oligochaeta (Andrews and Rigler 1985), and Tipulidae (Pritchard 1983) survive freezing events through freeze tolerance and supercooling (reviewed by Danks 1971; Strathdee and Bale 1998). Another strategy to withstand freezing events is seen in Chironomidae; they may withstand the mechanical stresses due to changes in sediment structure with ice crystal formation during freezing events by burrowing into fine silt/clay sediments

(Danks 2007). Indeed, we found that Chironomidae abundance was associated with fine sediments. This finding is important as climate change will likely alter delta sediments; fine grain sediment accretion will decrease as glaciers in the Brooks Range disappear in the next 50-75 years (Nolan et al. 2011). A final adaptation to this cold and variable environment is found in the order Diptera including Chironomidae, which has a population consisting of multiple generations (MacLean and Pitelka 1971; Butler 1982; Danks 2007). This trait is thought to increase persistence of a population in harsh environments in the event that one generation is unsuccessful (MacLean 1975).

6.4.2 Invertebrate Abundance

Environmental extremes like desiccation, freezing, predation, and other factors in large part determine the survival and vertical distribution of intertidal biota (Anderson 1983). For deltas that have little vertical relief, the fauna still reflect habitat heterogeneity, food availability, exposure to predators and physical dynamics. We investigated the association between invertebrates and some environmental variables by testing interactions between water depth, moisture, and fine sediments and found they were important predictors of Chironomidae and Oligochaeta abundance. In comparison, inundation time and fine sediment grain size were positively correlated with invertebrate abundance in other studies (Yates et al. 1993; Powers et al. 2002; Kraan et al. 2010), but they did not investigate interactions. The significant interactions in the present study indicate that associations between abundance and environmental variables may be more complex than previously reported. Sediment grain-size is usually a covariate with physical dynamics such that finer sediments persist in areas with reduced dynamics (Naidu and Mowatt 1983; Naidu and Klein 1988). Here, due to freezing, low tidal influences, and reduced available carbon due to glacial sediments (Wlodarska-Kowalczyk and Pearson 2004; Hood and Scott 2008), the complexity of environmental interactions may be greater.

6.4.3 Invertebrate Distribution

Survival strategies preventing freshwater invertebrates from freezing allow them to survive on the deltas, but we propose that freezing also plays an important role in shaping invertebrate distribution. For example, we found the distribution of Oligochaeta was constant from one year

to the next and within a season, but patches were small and habitat may be limited due to the frozen sediment in winter. In contrast, Chironomidae distribution increased across the mudflats as the summer progressed suggesting that in areas where populations were negatively impacted by freezing, they were able to recolonize through the summer. Tipulidae larvae radiated from the tundra's edge with increasing abundance over the summer coupled with a spread from the shore towards the water. Tipulidae adults lay eggs in south-facing tundra slopes, which collect heat early in the summer helping to initiate egg hatching (MacLean 1975; Pritchard 1983). Tipulidae pupae and adults were very rare in our samples, suggesting that these life stages occur outside delta habitats. Tipulidae may migrate out onto deltas during the larval stage to feed, but then migrate back to upland tundra to pupate and finish their life cycle. Their tracks stretching for meters are common on the sediment surface. If this is a true migration by this taxon, then, future research should address how these insects return to specific habitats during different life stages, and how the linkages between the marine and terrestrial environments enhance survival in these river deltas.

6.4.4 Isotopic Analysis of the Trophic Community

The macroinvertebrate community of Beaufort Sea river deltas was composed of two life history strategies, one marine and one with terrestrial freshwater origins. We hypothesized that these two groups would maintain some degree of fidelity to their natal carbon sources, with one reflecting a marine signature and the other a terrestrial signature. However, our data did not support this hypothesis; the range in $\delta^{13}\text{C}$ values for biota collected on the deltas clearly reflects a fauna that preferentially assimilates marine-derived carbon, with some fauna exhibiting a greater proportion of autochthonous carbon than others (e.g. *Saduria* compared to *Spio filicornis*) regardless of the life history strategy of the taxa. In addition, carbon isotopic values for some species are similar to those of the same species collected in Beaufort Sea lagoons at ≤ 4.5 m depth (*Spio filicornis* - 22.3‰, *Gammarus setosus* -23.4‰, and *Saduria entomon* -21.0‰; Dunton et al. 2012).

We did not observe a gradient of enriched to depleted $\delta^{13}\text{C}$ values from the lagoon to the delta as found by researchers on the Colville River Delta (Craig et al. 1984), but these three deltas are relatively small in comparison. The isotopic signatures we observed from resident delta fauna were distinctly more ^{13}C enriched than values observed in nearby tundra ponds, although a

representative of the Culicidae collected on deltaic mudflats had a $\delta^{13}\text{C}$ value of -31.5‰. It is likely that this organism had just emigrated from its tundra pond base since Culicidae are an infrequent component of the delta community assemblage (Table 5.3) and larvae are never found. Thus, our data clearly show the importance of terrestrial sources of carbon for freshwater species that reside in the ponds, but also demonstrate the clear assimilation of marine sources of carbon by benthic fauna that inhabit the deltas. Other recent work (Dunton, unpublished data) has shown that sediment chlorophyll concentrations range up to 204 mg m^{-2} , which would provide a significant source of labile carbon for the benthic infauna living on the tidal flats of the these deltas. In addition, concentrations of various phaeopigments reveal very active grazing of the sediment microalgae by benthic metazoans (Dunton, unpublished data). This information, along with the evidence from stable isotope data, indicates that the food webs of the high latitude river deltas may shift from allochthonous (terrestrial) to autogenous (marine benthic microalgae) sources of carbon once the deltas become ice-free.

6.4.5 Study Implications

The disturbance prone intertidal habitats we surveyed had fewer taxa than temperate areas, and furthermore, the marine taxa were generalists. However, some of the freshwater taxa were specialists that could be impacted by climate change including changes in sediment aggregation, erosion from storm surges, and sea level rise. Sediment accretion in river deltas of the Beaufort Sea may be greater now than in the past due to increased melting of glaciers in the Brooks Range (Hinzman et al. 2005; Nolan et al. 2011). However, sediment transport will decline in the next 50-75 years when glacial ice disappears and is replaced by annual snow fields (Nolan et al. 2011). Changes in sedimentation rates will likely transform sediment structure by increasing grain size, a change that could further affect some invertebrates, especially those associated with more fine-grain sediments (e.g. the Chironomidae).

Glacial sediments in particular have unique characteristics due to high ion exchange and low carbon content that will impact the invertebrate community from the bottom up with more available carbon if glacial sediments are absent (Naidu and Klein 1988; Hood and Scott 2008). In our samples we find a four-fold increase in total carbon measurements between glacial fed and non-glacial fed deltas (Figure 5.5). Storm surge frequency is increasing on the Beaufort Sea coast

(Hinzman et al. 2005; Walsh 2008), and storm surges are often observed first-hand (Crane 1974; Martin 1983). However, the effects of these events on deltaic habitats are unknown, although the invasion of seawater likely increases salinity in brackish water areas and increases erosion. Sea level rise could also change delta habitats, but with little knowledge of the extent of the change in the Beaufort Sea it is difficult to predict actual impacts to river deltas (Proshutinsky and Bourke 2001). Regardless, expectations are that sedimentation rates will not counter sea level rise (Weston 2014).

Resource development for oil could also impact coastal delta areas; offshore drilling has already begun within 7 km of the Canning River Delta, and more development along the coast is expected. Oil spills adversely affect invertebrate communities (Percy 1976; Miller et al. 1986; Feder et al. 1990; Peterson et al. 2003). The full impact of an Arctic oil spill is currently unknown, but biodegradation of oil in Arctic conditions is being researched to prepare for spill response and assess Arctic conditions (this study; McFarlin et al. 2011; Prince et al. 2013). Our data provide baseline information on pre-development invertebrate communities of the Beaufort Sea that could help assess impacts and restore habitats to their previous condition. Our data also provide insights into the potential resilience of macroinvertebrate communities. The absence of many marine fauna on deltaic mudflats suggests source populations from nearby lagoons. In the event of a large but temporally short disturbance, the perturbation may have limited effects as marine fauna repopulate rapidly on an annual basis. Freshwater fauna would likely recolonize from source populations in the river.

In conclusion, invertebrate communities on the Beaufort Sea coast are dominated by disturbances (prolonged annual freezing) unique to high latitudes. Beaufort Sea river deltas are important sources of food for wading birds and migrating estuarine fishes during the summer. The availability of food resources is a product of the survival of various freshwater invertebrate species that are resilient to freezing and the active annual migration and colonization of invertebrates from protected marine invertebrate “source” populations in adjacent lagoons. Because of their contributions to estuarine ecology as well as their contributions to migrating birds, future research of lagoon ecosystems on the Beaufort Sea should include intertidal habitats

and the freshwater taxa that live in these highly physically stressed habitats, which will require new sampling approaches.

6.5 References

- Anderson FE. 1983. The northern muddy intertidal: seasonal factors controlling erosion and deposition - a review. *Canadian Journal of Fisheries and Aquatic Sciences*. 40:143-159.
- Andres BA. 1989. Littoral zone use by post-breeding shorebirds on the Colville River Delta, Alaska [master's thesis]. [Columbus (OH)]: Ohio State University.
- Andrews D, Rigler FH. 1985. The effects of an Arctic winter on benthic invertebrates in the littoral zone of Char Lake, Northwest Territories. *Canadian Journal of Zoology*. 63: 2825-2834.
- Bates D, Maechler M, Bolker B, Walker S. 2013. Package lme4. <http://lme4.r-forge.r-project.org/>.
- Boesch DF, Rosenberg R. 1981. Response to stress in marine benthic communities. In Barrett GW, Rosenberg R, editors. *Response to stress in marine benthic communities*. Chichester (UK): John Wiley & Sons Ltd. p. 179-200.
- Brown S, Kendall S, Churchwell R, Taylor A, Benson A-M. 2012. Relative shorebird densities at coastal sites in the Arctic National Wildlife Refuge. *Waterbirds*. 35:546-554.
- Butler MGG. 1982. A 7-year life cycle for two Chironomus species in arctic Alaskan tundra ponds (Diptera: Chironomidae). *Canadian Journal of Zoology*. 60:58-70.
- Churchwell RT. 2015. Stopover ecology of semipalmated sandpipers (*Calidris pusilla*) at coastal deltas of the Beaufort Sea, Alaska. PhD Dissertation, University of Alaska, Fairbanks. 149 pp.
- Connors PG, Risebrough RW. 1977. Shorebird dependence on Arctic littoral habitats. In *Environmental Assessment of the Alaskan Continental Shelf (Annual Reports of Principal Investigators)*, Volume 3:402-524. Outer Continental Shelf Environmental Assessment Program.
- Craig PC, Griffiths WB, Johnson SR, Schell DM. 1984. Trophic dynamics in an Arctic lagoon. Barnes PW, Schell DM, Reimnitz E, editors. *The Alaskan Beaufort Sea: ecosystems and environments*. Orlando (FL): Academic Press, Inc. p. 347-380.

- Crane JJ. 1974. Ecological studies of the benthic fauna in an arctic estuary [master's thesis]. [Fairbanks (AK)]: University of Alaska, Fairbanks.
- Dale JE, Aitken AE, Gilbert R, Risk MJ. 1989. Macrofauna of Canadian arctic fjords. *Marine Geology*. 85:331-358. doi:10.1016/0025-3227(89)90159-X.
- Danks HV. 1971. Overwintering of some north temperate and arctic Chironomidae. *The Canadian Entomologist*. 103:1875-1910.
- Danks HV. 2007. How aquatic insects live in cold climates. *The Canadian Entomologist*. 139:443-471.
- Drolet D, Coffin MRS, Barbeau MA, Hamilton DJ. 2013. Influence of intra- and interspecific interactions on short-term movement of the Amphipod *Corophium volutator* in varying environmental conditions. *Estuaries and Coasts*. 36:940-950.
- Dunton KH, Schonberg SV, Cooper LW. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. *Estuaries and Coasts*. 35:416-435.
- Dunton KH, Weingartner T, Carmack EC. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. *Progress in Oceanography*. 71:362-378. doi:10.1016/j.pocean.2006.09.011.
- Ellis DV, Wilce RT. 1961. Arctic and subarctic examples of intertidal zonation. *Arctic*. 14:224-235.
- Feder HM, Naidu AS, Paul AJ. 1990. Trace element and biotic changes following a simulated oil spill on a mudflat in Port Valdez, Alaska. *Marine Pollution Bulletin*. 21:131-137.
- Feder HM, Schamel D. 1976. Shallow-water benthic fauna of Prudhoe Bay. In *Assessment of the Arctic marine environment: selected topics*. University of Alaska Fairbanks. p. 329-359.
- Fortin M-J, Dale M. 2005. *Spatial analysis*. Cambridge: Cambridge University Press.
- Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Firth D, et al. 2013. Package car. <https://r-forge.r-project.org/projects/car/>.
- Fry B. 2006. *Stable isotope ecology*. New York: Springer Verlag.
- Gutt J. 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biology*. 24:553-564.
- Hill PR, Lewis CP, Desmarais S, Kauppaymuthoo V, Rais H. 2001. The Mackenzie Delta: sedimentary processes and facies of a high-latitude, fine-grained delta. *Sedimentology*. 48:1047-1078.

- Hinzman LD, Bettez ND, Bolton WR, Chapin FS, Dyurgerov MB, Fastie CL, Griffith B, et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*. 72:251-298.
- Hood E, Scott D. 2008. Riverine organic matter and nutrients in southeast Alaska affected by glacial coverage. *Nature Geoscience*. 1:583-587. doi:10.1038/ngeo280.
- Huston M. 1979. A general hypothesis of species diversity. *American Naturalist*. 113:81-101.
- Iken K, Bluhm B, Dunton KH. 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 57. Elsevier. p. 71-85.
- Kendall MA. 1996. Are arctic soft-sediment macrobenthic communities impoverished? *Polar Biology*. 16:393-399.
- Kraan C, Aarts G, van der Meer J, Piersma T. 2010. The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. *Ecology*. 91:1583-1590.
- Krebs CJ. 1989. *Ecological methodology*. New York (NY): Harper Collins Publishers.
- Kuznetsova A, Brockhoff PB, Chris-Tensen RHB. 2013. Package lmerTest. <http://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf>.
- Lees DC, Erikson DE, Driskell W, Boettcher DE. 1979. Intertidal and shallow subtidal biological studies: Valdez Port Expansion Project. Anchorage (AK).
- Lees DC, Houghton JP, Erickson DE, Driskell W, Boettcher DE. 1980. Ecological studies of intertidal and shallow subtidal habitats in lower Cook Inlet, Alaska.
- MacLean SF. 1975. Ecological adaptations of tundra invertebrates. In: Vernberg FJ, editor. *Physiological Adaptation to the Environment*. New York: Intext Educational Publishers. p. 269-300.
- MacLean SF, Pitelka FA. 1971. Seasonal patterns of abundance of tundra Arthropods near Barrow. *Arctic*. 24:19-40.
- Martin PD. 1983. Bird use of arctic tundra habitats at Canning River Delta, Alaska [master's thesis]. [Fairbanks (AK)]: University of Alaska, Fairbanks.
- McFarlin KM, Perkins RA, Gardiner WW, Word JD, Word JQ. 2011. Toxicity of physically and chemically dispersed oil to selected arctic species. *International Oil Spill Conference Proceedings*. 2011: 1-7.

- Miller MC, Stout JR, Alexander V. 1986. Effects of a controlled under-ice oil spill on invertebrates of an arctic and a subarctic stream. *Environmental Pollution Series A*. 42:99-132.
- Naidu AS, Klein LH. 1988. Sedimentation processes. In: Shaw DG, Hameedi MJ, editors. *Environmental studies in Port Valdez, Alaska: a basis for management*. Berlin: Springer-Verlag. p. 69-92.
- Naidu AS, Mowatt TC. 1983. Sources and dispersal patterns of clay minerals in surface sediments from the continental-shelf areas off Alaska. *Geological Society of America Bulletin*. 94:841-854.
- Nolan MR, Churchwell R, Adams J, McClelland J, Tape KD, Kendall S, Powell A, Dunton K, Payer D, Martin P. 2011. Predicting the impact of glacier loss on fish, birds, floodplains, and estuaries in the Arctic National Wildlife Refuge. In: Medley CN, Patterson G, Parker MJ, editors. *Observing, studying, and managing for change*. Reston (VA): US Geological Survey Scientific Investigations Report 2011- 5169. p. 49-54.
- Percy JA. 1976. Responses of arctic marine crustaceans to crude oil and oil-tainted food. *Environmental Pollution*. 10:155-162.
- Peterson CH, Rice SD, Short JW, Esler D, Bodkin JL, Ballachey BE, Irons DB. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. *Science*. 302:2082-2086.
- Powers SP, Bishop MA, Grabowski JH, Peterson CH. 2002. Intertidal benthic resources of the Copper River Delta, Alaska, USA. *Journal of Sea Research*. 47:13-23.
- Prince RC, McFarlin KM, Butler JD, Febbo EJ, Wang FCY, Nedwed TJ. 2013. The primary biodegradation of dispersed crude oil in the sea. *Chemosphere*. 90:521-526.
- Pritchard G. 1983. Biology of Tipulidae. *Annual Review of Entomology*. 28:1-22.
- Proshutinsky A, Bourke RH. 2001. Sea level rise in the Arctic Ocean. *Geophysical Research Letters*. 28:2237-2240.
- R Development Core Team. 2013. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Ribeiro PJ, Diggle PJ. 2013. Package geoR. <http://www.leg.ufpr.br/geoR>.
- Ripley B. 2013. Package spatial. <http://www.stats.ox.ac.uk/pub/MASS4/>.
- Strathdee AT, Bale JS. 1998. Life on the edge: insect ecology in arctic environments. *Arctic*. 43:85-106.

- Taylor AR, Powell AN, Nigro DA, Kendall SJ. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. *Arctic*. 63:451-467.
- Walker HJ. 1998. Arctic deltas. *Journal of Coastal Research*. 14:718-738.
- Walsh JE. 2008. Climate of the Arctic marine environment. *Ecological Applications*. 18:S3-S22.
- Weslawski JM, Szymelfenig M. 1999. Community composition of tidal flats on Spitsbergen: consequence of disturbance? In: Gray, JS, et al., editors. *Biogeochemical cycling and sediment ecology*. NATO ASI Series, Series E. 59:185-193.
- Weston NB. 2014. Declining sediments and rising seas: an unfortunate convergence for tidal wetlands. *Estuaries and Coasts*. 37:1-23.
- Wlodarska-Kowalczyk M, Pearson TH. 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology*. 27:155-167. doi:10.1007/s00300-003-0568-y.
- Wlodarska-Kowalczyk M, Szymelfenig M, Zajickowski M. 2007. Dynamic sedimentary environments of an Arctic glacier-fed river estuary (Adventfjorden, Svalbard). II: meio- and macrobenthic fauna. *Estuarine, Coastal and Shelf Science*. 74:274-284.
- Yates MG, Goss-Custard JD, McGrorty S, Lakhani KH, dit Durell S, Clarke RT, Rispin WE, et al. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology*. 30:599-614.
- Zajac R. 1991. Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. *Marine Ecology Progress Series*. 77:197-206.



The Department of Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under US administration.



The Bureau of Ocean Energy Management

As a bureau of the Department of the Interior, the Bureau of Ocean Energy (BOEM) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS) in an environmentally sound and safe manner.

The BOEM Environmental Studies Program

The mission of the Environmental Studies Program (ESP) is to provide the information needed to predict, assess, and manage impacts from offshore energy and marine mineral exploration, development, and production activities on human, marine, and coastal environments.