

To the Graduate Council:

I am submitting herewith a thesis written by Arianne Lynn Balsom entitled “Macroinfaunal community composition and biomass, and bacterial and viral abundances from the Gulf of Alaska to the Canadian Archipelago: A biodiversity study.” I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Dr. Jacqueline Grebmeier

Major Professor

We have read this thesis and
recommend its acceptance:

Dr. Steven Wilhelm

Dr. Lee Cooper

Dr. Tom Hallam

Acceptance for the Council:

Dr. Anne Mayhew

Vice Provost and Dean of
Graduate Studies

(Original signatures are on file with official student records.)

**MACROINFAUNAL COMMUNITY COMPOSITION AND BIOMASS, AND
BACTERIAL AND VIRAL ABUNDANCES FROM THE GULF OF ALASKA TO
THE CANADIAN ARCHIPELAGO: A BIODIVERSITY STUDY**

A Thesis
Presented for the
Masters of Science
Degree
The University of Tennessee, Knoxville

Arianne Lynn Balsom
May 2003

Acknowledgements

I wish to thank my committee members Dr. Jackie Grebmeier, Dr. Lee Cooper, Dr. Tom Hallam, and Dr. Steve Wilhelm for their time, efforts, and advice throughout this entire process. Many thanks to my lab co-workers Jackie Clement, Rebecca Pirtle-Levy, Becky Brown, Catherine Lalande, and Kim Harmon for their help and emotional support. I would also like to thank Captain John Anderson, Captain Norman Thomas, and the crews of the CCGC *Sir Wilfrid Laurier* for their assistance in the field, and Bon Von Hardenberg and Reg Bigham for CTD data collection. Funding was provided by National Science Foundation grants OPP-0003241 and OPP-9910319.

Abstract

Hydrographic, sediment, and biological (chlorophyll *a*, bacteria, viruses, and macroinfauna) samples were collected on a several thousand mile long transect spanning from the Gulf of Alaska, through the Bering and Chukchi Seas, the Beaufort Sea, and into the Canadian Archipelago/Northwest Passage in the summer of 2000.

Water column hydrographic parameters (temperature, salinity, and chlorophyll *a*), water column bacterial and viral abundances and distributions, as well as benthic measurements of sediment bacterial and viral abundances and distribution, sediment grain size, and sediment organic carbon and organic nitrogen content were measured. In addition, macroinfaunal community composition and diversity were examined.

The Bering and Chukchi Seas had the highest overall mean abundances of bacterial, viral, and macroinfaunal parameters. Of all areas measured, the Beaufort Sea and Gulf of Alaska stations exhibited the lowest values, and Canadian Archipelago stations showed intermediate, varied values. Statistical analysis indicated significant positive correlations among many parameters. For example, the significant relationship between macroinfaunal diversity and sediment viral abundance suggests that Arctic benthic macroinfaunal communities may be influenced by viral parameters coincident with sediment grain size and the quantity and quality of surface-water derived primary production food supply.

TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
Study Rationale: Biodiversity	1
Study Rationale: Parameters to be examined	4
Overview of the 2000 field program	7
Study objectives	9
Description of study areas	10
II. HYDROGRAPHIC PARAMETERS	20
Introduction	20
Selection of samples	21
Materials and methods: Temperature, salinity, and water column chlorophyll <i>a</i>	21
Results	22
Discussion	28
Chapter summary	29
III. MACROINFAUNAL COMMUNITY COMPOSITION AND BIOMASS	31
Introduction	31
Materials and Methods: Macroinfaunal and sediment tracer parameters	37
Results	40
Discussion	63
Chapter summary	67
IV. BACTERIAL AND VIRAL ABUNDANCES AND DISTRIBUTION	70
Introduction	70
Materials and methods	79
Results	81
Discussion	96
Chapter summary	100
V. RELATIONSHIPS AMONG INFAUNAL, BACTERIAL, AND VIRAL COMPONENTS	103
Introduction	103
Materials and methods	104
Results	105
Discussion	107
Chapter summary	109
VI. BENTHIC CARBON FLOW MODEL	110
Introduction	110
Methods and assumptions	111

TABLE OF CONTENTS. Continued.

Chapter	Page
Results	115
Global warming scenarios	118
Discussion	121
VII. FINAL DISCUSSION AND CONCLUSIONS	123
LIST OF REFERENCES	125
APPENDICES	146
VITA	189

LIST OF TABLES

Table	Page
1. Regional mean values for bottom water and integrated water column parameters	27
2. A comparison of bottom water and integrated water column parameters among study regions.	30
3. Regional mean values for macroinfaunal parameters.	44
4. Mean values for cluster group macroinfaunal parameters	50
5. Regional mean values for sediment parameters.....	56
6. A comparison of mean sediment tracer parameter values between study regions.	67
7. A comparison of mean macroinfaunal parameter values between study regions.....	69
8. Regional means for bacterial and viral abundance (surface and bottom water) values.	86
9. Regional means for sediment bacterial and viral parameters	95
10. A comparison of mean water column bacteria and viral parameter values among study regions.	100
11. A comparison of mean sediment bacteria and viral parameter values among study regions.....	101
12. Stations and mean sediment oxygen rates used for model assumptions.....	113

LIST OF FIGURES

Figure	Page
1. Cruise track of Laurier 2000, showing locations of all stations occupied during the cruise.	11
2. Bathymetry (indicated by colored lines; see legend above for depth values) and general directional flow (indicated by black arrows) for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).....	12
3. Laurier 2000 station locations for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA)	14
4. Regional names of geographical locations in study areas (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA)	19
5. Bottom water salinity for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.	23
6. Bottom water temperature for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.	24
7. Integrated total water column chlorophyll <i>a</i> concentrations for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.....	26
8. Macroinfaunal organic carbon mass for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.	41
9. Macroinfaunal abundance for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA). ...	42
10. Dominant station animal by total organic biomass for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA)	43
11. Cluster analysis grouped by macroinfaunal abundance.....	47
12. Locations of cluster groups based on abundance, for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA)	49

LIST OF FIGURES. Continued.

Figure	Page
13. Sediment chlorophyll <i>a</i> concentrations for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).....	55
14. Sediment total organic carbon (TOC) content for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).....	57
15. Sediment total organic carbon to total organic nitrogen ratios (weight/weight) for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	58
16. Regional comparisons between macroinfaunal and sediment tracer statistical Spearman's rho relationships for Bering Sea and Chukchi Sea stations (BC), Canadian Archipelago stations (CA), and cruise stations combined overall (O)	61
17. An illustration of the microbial loop including the viral shunt component, modified from Wilhelm and Suttle (1999).....	72
18. Surface water bacterial (bacterial-like particle) abundances for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	82
19. Bottom water bacterial (bacterial-like particle) concentrations for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	83
20. Surface water virus (virus-like particle) abundances for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	84
21. Bottom water viral (virus-like particle) abundances for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	85
22. Regional statistical Pearson's product-moment relationships of discrete depth water column bacterial and viral abundances versus hydrographic parameters; Gulf of Alaska stations (GOA), Bering/Chukchi Sea stations (BC), Beaufort Sea stations (B), Canadian Archipelago stations (CA), and stations combined overall (O)..	88

LIST OF FIGURES. Continued.

Figure	Page
23. Sediment bacterial (bacteria-like particle) abundances for the 4 study regions; see legend above for values (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	92
24. Sediment virus (virus-like particle) concentrations for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).	93
25. Regional comparisons between bacterial, viral, and sediment tracer values	94
26. A regional comparison of bacterial, viral, and macroinfaunal correlations. Bering/Chukchi Sea stations (BC), Canadian Archipelago stations (CA), stations combined overall (O)	106
27. Conceptual box model of benthic carbon flow through a high productivity (Northern Bering Sea, top numbers) region and a low productivity (Beaufort Sea, bottom numbers) region	116
28. A graphical representation of global warming scenarios in a low productivity (Beaufort Sea) marine system.	119
29. A graphical representation of global warming scenarios in a high productivity (Northern Bering Sea) marine system.....	120

LIST OF DEFINITIONS AND ABBREVIATIONS

Definitions

Bacterial-Like Particles (BLP)	bacteria have not been cultured for identification
Polynya	an ice-free or relatively ice-free region surrounded by ice
Psychrotolerant	organisms resistant to cold conditions
Psychrophilic	organisms exhibiting optimal function and growth in cold conditions
Virus-Like Particles (VLP)	viruses that have not been cultured to identify their hosts

Abbreviations

ACC	Alaska Coastal Current, also known as Alaska Coastal Water (ACW)
ACW	Alaska Coastal Water, also known as the Alaska Coastal Current (ACC)
AW	Anadyr Water
BSAW	Bering-Shelf Anadyr Water
CA	Canadian Archipelago
CTD	Conductivity-Temperature Depth profiler used to sample parameters of the water column
DOM	dissolved organic matter
GOA	Gulf of Alaska
POC	particulate organic carbon
SBI	Western Arctic Shelf-Basin Interactions project
TEM	transmission electron microscopy
TOC	total organic carbon

Abbreviations used in statistical comparison charts and matrices

Depth	station depth in meters
Bot Sal	bottom water salinity (ppt)
Bot Temp	bottom water temperature (°C)
Euph.	water column euphotic zone (upper 20-25 m)
Int Chl	integrated water column chlorophyll <i>a</i> concentration (mg m ⁻²)
Sed Chl	surface sediment chlorophyll <i>a</i> content (mg m ⁻²)
Abund	macroinfaunal abundance (number of individuals m ⁻²)
Bio gC	macroinfaunal organic carbon biomass (grams of carbon m ⁻²)
Modal	modal sediment phi grain size (Ø)
TOC	surface sediment total organic carbon content (%)
C/N	surface sediment total organic carbon to total organic nitrogen ratio (weight/weight)
Diversity	Shannon-Weaver diversity index (H')
Evenness	Shannon-Weaver evenness index (J)
Bact L ⁻¹	bacterial-like particle abundance per L
VLP L ⁻¹	viral-like particle abundance per L
Sed Virus	surface sediment viral-like particle abundance (per gram sediment dry weight)
Sed Bact	surface sediment bacterial-like particle abundance (per gram sediment dry weight)
TWC	total water column

I. INTRODUCTION

Study Rationale: Biodiversity

The importance of biodiversity within ecosystems is a subject of great scientific interest. Biodiversity as defined by the 1992 Biodiversity Convention is “the variability among living organisms from all sources including *inter alia*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems” (Angel, 1997). The importance of biodiversity to the success and persistence of communities has been observed in both aquatic and terrestrial systems (Naeem and Li, 1997; Naeem et al., 2000). Increases in biodiversity appear to stabilize ecosystems, acting as a buffer against future extinction events. Environmental disruptions that cause extinction events could very well include a regime shift or change such as global warming.

While studies continue to mount on either side of the debate concerning whether or not increased diversity automatically leads to increased ecosystem stability (resistance to change; reviewed by Loreau, 2000), there does not seem to be much disagreement in the observation that a greater number of community members often, if not usually, leads to a greater number of functional group (a specific ecological role within that ecosystem) options. If one member of a functional group is removed, then there is an increased chance of adequate trophic level replacements keeping the community functioning without substantial disruption if the biodiversity within that community is maintained or increased. Previous studies indicate that greater numbers of species within trophic levels resulted in greater consistencies of biomass and density measurements between

experimental replicates, suggesting that biodiversity may act as “biological insurance” to counteract the loss of species and poor species performance through “compensatory growth” and functional group redundancy (Naeem and Li, 1997).

Several studies indicate that decreases in community biodiversity may lead to decreased nutrient retention, decreased productivity rates, and decreased community stability, all suggested to result from the decreased number of available functional group options in selective pressure scenarios (Tilman, 1996; McGrady-Steed et al., 1997; Naeem and Li, 1997). In other words, there is a decreased chance of important functional group components surviving a disturbance (i.e. climatic, pathogenic, invasive, and/or predatory) because there is a decreased variation in the adaptive strategies of the functional group members (Loreau, 2000). Several reasons for increased nutrient retention within sediments (resulting from a lower inorganic nutrient supply which is less susceptible to leaching), increased primary productivity, and increased stability of standing stock biomass have been suggested to arise from increased biodiversity, resulting from the “reservoir” of phenotypic and genetic variation acting as insurance against fluctuating environmental conditions (Loreau, 2000).

Decreasing biodiversity within communities resulting from habitat modifications and disturbances may have far-reaching, complex, and unexpected affects (Naeem et al., 2000)—as an example of these unexpected affects, Naeem et al. (2000) demonstrated a surprising “co-dependency” between heterotrophic bacteria and aquatic algae which resulted in increased algal production corresponding to the increased algal and bacterial diversities that could not be explained solely by one factor, but instead could only be explained by the interaction of the two increased diversities. Complex interactions

similar to this example could be prevalent between many trophic levels in many environments.

A reduction in biodiversity could therefore destabilize ecosystem function (Elmgren and Hill, 1997) by reducing the available pool of potential functional group contributors. Ecosystems where high levels of biodiversity already exist may not suffer any functional losses with the extinction of only a few species; however, in species-poor, often food-limited geographic areas such as the Arctic, there are inherently fewer options per functional group because of its decreased diversity compared to temperate and tropical ecosystems. When an ecosystem is destabilized, it is less tolerant to environmental disruptions due to the increased likelihood that the key players within the major functional groups could be removed by pathogenic or by climatic means (Pimm, 1984).

An ecosystem's processes could be largely affected by this removal of "key players", and in low-diversity environments, a loss or reduction of only one species may in fact result in the loss of an entire functional group (Elmgren and Hill, 1997). Arctic data sets spanning from the early 1900's to the present day have illustrated a large decrease in annual ice pack cover (Rothrock et al., 1999), an atmospheric and hydrographic warming trend (Oechel and Vourlitis, 1994; Grotefendt et al., 1998), an increase in freshwater runoff (Peterson et al., 2002) and modification of several species' distributions and abundances (Highsmith and Coyle, 1992; Grebmeier and Cooper, 1994; Grebmeier and Dunton, 2000; Grebmeier and Cooper, 2002). In the geologically young, species-poor Arctic marine environment (Dunton, 1992), these ensuing climatic events could certainly contribute to the possibility of its ecosystem destabilization.

The Arctic's lower level of ecosystem functional group redundancy, coupled with the predicted magnified effects of global warming in the polar regions, suggests that ecosystem disruption could have significant consequences for the Arctic trophic food web structure as a whole if community biomass and diversity change substantially. Changes in the community species diversity of "key players" such as macroinfauna, bacteria, and viruses, could feasibly affect everything from microbial nutrient cycling dynamics to regional benthic macroinfaunal community standing stocks to apex predator success if vital functional groups are lost, without functional group replacement options, to habitat disturbances.

Study Rationale: Parameters to be examined

The key forcing functions of arctic benthic biodiversity have been determined by previous studies to include bottom water temperature, bottom water salinity, the quantity and quality of carbon supply reaching the sea floor, and sediment grain size (Gray, 1981; Grebmeier et al., 1989; Feder et al., 1994; Grebmeier et al., 1995; Cooper et al., 2002). Species vary in their tolerances of hydrographic parameters such as temperature, which can limit the ranges of organisms due to metabolic restraints, and freshwater input, which lowers salinity and often supplies a less nutritious terrigenous-based carbon supply to the marine benthos. Integrated water column chlorophyll *a* concentration can be used as a proxy measurement of primary productivity-derived carbon existing in the overlying water column, and sediment chlorophyll *a* content can serve as a proxy measurement of primary productivity that has reached the benthos. The quality of this carbon supply can be measured by the sediment total organic carbon to total organic nitrogen ratio (C/N)

which indicates the amount of organic material that has been degraded. Sediment grain size is also important because it governs how and if animal burrows and tubes can be built (a predominance of gravel could impede burrowing); in addition to regulating whether suspension-feeding or deposit-feeding strategies are suitable for that environment. This study examines these important forcing factors (bottom water temperature, bottom water salinity, integrated water column chlorophyll *a* concentration, sediment chlorophyll *a* content, sediment C/N ratios, sediment TOC content, and sediment modal grain size) relationships with macroinfaunal carbon biomass, macroinfaunal abundance, and macroinfaunal species diversity. The Shannon-Weaver species diversity index (H' ; a measure of species richness and the proportion of that species within a community) is used as a surrogate measurement for “biodiversity.”

In addition, these same forcing function hydrographic and sediment parameters could also be related to bacterial/bacterial-like particle (BLP) and viruses/viral-like particle (VLP) abundances in both the water column (BLP L^{-1} and VLP L^{-1}) and in the sediment (BLP g^{-1} and VLP g^{-1}) because these environmental parameters define how food-rich and habitable a system is. Bacteria and viruses are addressed in this study in addition to sediment parameters because microbial activity may influence macroinfaunal biodiversity through food supply degradation and nutrient mineralization rates. Because of this possible effect, bacterial and viral community abundances and their distributions are notable components of ecological dynamics. It has long been known that bacteria break down detritus into biologically available nutrients. These nutrients can then either be incorporated into primary producers' metabolic products or be buried within sediment complexes and consequently lost to the active food web (Azam et al., 1983).

These bacteria also function as food sources themselves for deposit- and suspension-feeding organisms, two feeding strategies adapted by many infaunal organisms (Plante et al., 1990). When examining bacterial abundance, it is also important to examine corresponding viral abundance, which is thought to limit the abundance of bacteria. The influential role of viruses on bacterial mortality rates, and subsequently on the availability of bacteria-processed nutrients, is an important interaction that should not be overlooked (Wilhelm and Suttle, 1999).

Bacterial and viral distributions and abundances in Arctic waters are examined in a select few studies (e.g. Steward et al., 1996; Wells and Deming, 2002). Since bacteria and viruses play a large role in the breakdown and recycling of both water column and sediment biotic material (Azam et al., 1983), it is important to quantify a “baseline” of Arctic microbial and viral abundances, as a contribution to the understanding of how bacteria and viruses are related on larger spatial scales, before temporal impacts can be assessed. The relationships between microbial abundances and the parameters of macroinfaunal abundance, biomass, and diversity were examined using non-parametric correlations. These relationships were then discussed in the context of future global warming scenarios using a conceptual box model.

In addition to hydrographic and sediment parameters influencing macroinfaunal biodiversity, macroinfaunal organisms have also been shown in many studies to impact their regional environmental conditions by ecological feedback mechanisms (Ray et al., 1997), meaning that a change in biotic parameters, in turn, can cause a change in environmental processes in response to the biotic component. Therefore, as regional environmental parameters change, it is useful to track changes in the corresponding

biological parameters in order to elucidate often complex causes. The need to quantify Arctic North American benthic infaunal standing stocks have been recognized (Carey, 1991). Historical biological surveys in the Beaufort Sea and Canadian Archipelago (CA) regions did not utilize standardized sampling procedures, and many of the studies reported results in preserved wet weights rather than in organic carbon biomass, which has been determined to be a more useful biological comparative measurement (Carey, 1991). The northern Bering and Chukchi Seas have been the focus of long-term biological monitoring (e.g. Grebmeier and Cooper, 1994) and therefore, community structures have been well-described, allowing for the spatial and temporal variations existing within these communities to be closely monitored. The Beaufort Sea and CA infaunal communities, thus far have been largely undescribed, limiting analysis of pan-arctic trends and patterns (Carey, 1991). One of this thesis's primary goals was to apply standardized sampling techniques of benthic organic carbon biomass to previously unstudied areas of the western CA in order to examine benthic community composition variations among the known hot spot stations in the northern Bering and Chukchi Seas and stations occupied in the Beaufort Sea and CA.

Overview of the 2000 field program

In 2000, the Voyage of Rediscovery, a reenactment of the Royal Canadian Mounted Police (RCMP) schooner *St. Roch*'s accomplishment of the first west-to east passage through the CA/Northwest Passage (1940-1942) and the first circumnavigation of the North American continent (1942) provided an unusual scientific opportunity to sample along a several thousand-mile continental shelf cruise track through the Canadian

Archipelago/Northwest Passage. The expedition began on July 1, 2000 and ended in December 2000 upon return to Vancouver. In addition to the Voyage of Rediscovery's historical re-enactment and the benthic studies described here, the mission also supported scientific activities ranging from gathering forensic evidence of Sir John Franklin's lost expedition, to studies of Arctic biodiversity.

Research was conducted on board the CCGS *Sir Wilfrid Laurier* in conjunction with the *St. Roch* reenactment, including sampling in previously unsampled areas of the Canadian Archipelago, and a key objective was to construct a better understanding of Arctic biocomplexity (text modified from E. Carmack, unpubl. report). CTD hydrographic data, benthic sediment samples, and water column samples reported in this thesis were taken at 165 scheduled and opportunistic stations along the continental shelf from the Gulf of Alaska (GOA), the Bering, Chukchi and Beaufort Seas, and within the CA as far east as Spence Bay, Nunavut. Benthic parameters measured included: macroinfaunal biomass (gram wet weight and carbon content), macroinfaunal abundance, sediment chlorophyll *a* content, sediment grain size, viral and bacterial abundance, and total organic carbon. In addition, water samples were collected for chlorophyll *a* content, viral and bacterial abundance, oxygen-18, and nutrients. Scientists from the Institute of Ocean Sciences in Sidney, British Columbia, the University of Alaska Fairbanks, the University of Washington, and the University of Victoria also sampled phytoplankton and zooplankton, microbial activity, turbulence, nutrient content, physical parameters of water movement, and observed marine bird and mammal activity for portions of the cruise. Most of these data will be shared among the participating laboratories.

Study objectives

The objectives of this master's thesis study are to:

1. Compare variations in benthic community composition and biomass among the study regions (GOA, Bering and Chukchi Seas, Beaufort Sea, CA).
2. Document the role of bacteria and viruses in relation to macroinfaunal community assemblages, in order to elucidate ecological impacts.
3. Investigate pelagic-benthic coupling across the study areas using parameter patterns in order to evaluate the potential impacts that global warming may have on the Arctic ecosystem.

The hypotheses pertaining to these objectives are:

1. The macroinfaunal community biomass and diversity will be highest in the Bering and Chukchi Sea stations (previously established hot spot stations), followed by the GOA (a well-known productive fishery), then the CA (possessing a wide range of depths and environments), and lastly, the Beaufort Sea (known to have shallow depths, large freshwater inflow from the Mackenzie River, and seasonal ice scour).
2. Bacterial and viral abundance will both be significantly correlated to macroinfaunal biomass, abundance, and diversity, due to the utilization of the same surface-derived carbon supply.
3. Significant pelagic-benthic coupling will exist throughout the study regions between chlorophyll *a* concentration and macroinfaunal community biomass (previously established for the Bering and Chukchi Seas but unstudied in the Beaufort Sea and CA). Significant pelagic-benthic coupling will also exist throughout the study regions between

chlorophyll *a* concentration and both bacterial and viral abundances since they may depend on a pelagic food source reaching the bottom, or may be dependent on pelagic abundances of bacteria and viruses to “reseed” sediment abundances.

Description of study areas

The Laurier 2000 cruise track traversed 4 major geographically distinct marine systems; (1) the Pacific Ocean’s GOA, (2) the Bering/Chukchi Seas region, (3) the Beaufort Sea, and (4) the CA/Northwest Passage (Figure 1). The Bering/Chukchi Seas region and CA were the most extensively sampled due to the focus on standard Bering Strait Long Term Observatory stations in the Bering/Chukchi region during Leg 1 of the cruise (Cooper et al. 2002; also see <http://arctic.bio.utk.edu>) and the focus on the CA as part of the St. Roch II reenactment in Leg 2 of the cruise. Sampling in the Beaufort Sea was limited by both time and ice extent.

Gulf of Alaska (GOA): Currents on the northern GOA shelf are dominated by the Alaskan Stream, a high-flow westward flowing current, and the inner shelf Alaska Coastal Current (ACC), which also flows to the west, nearer-shore than the Alaskan Stream. (Figure 2a; modified from directional current flow diagram available at <http://www.pmel.noaa.gov/foci/brochure/Map.html>). These two currents also have a large mixing region between the two water masses (Schumacher et al., 1986). The Alaska Stream is one of the fastest currents in the world (Stabeno et al. 1995), with flows between 25 to 100 cm s⁻¹. The Alaska Stream branches off from the easterly flowing North Pacific Current, which continues south along the west coast of the United States as the California Current. The ACC originates in the southeastern GOA, flowing for

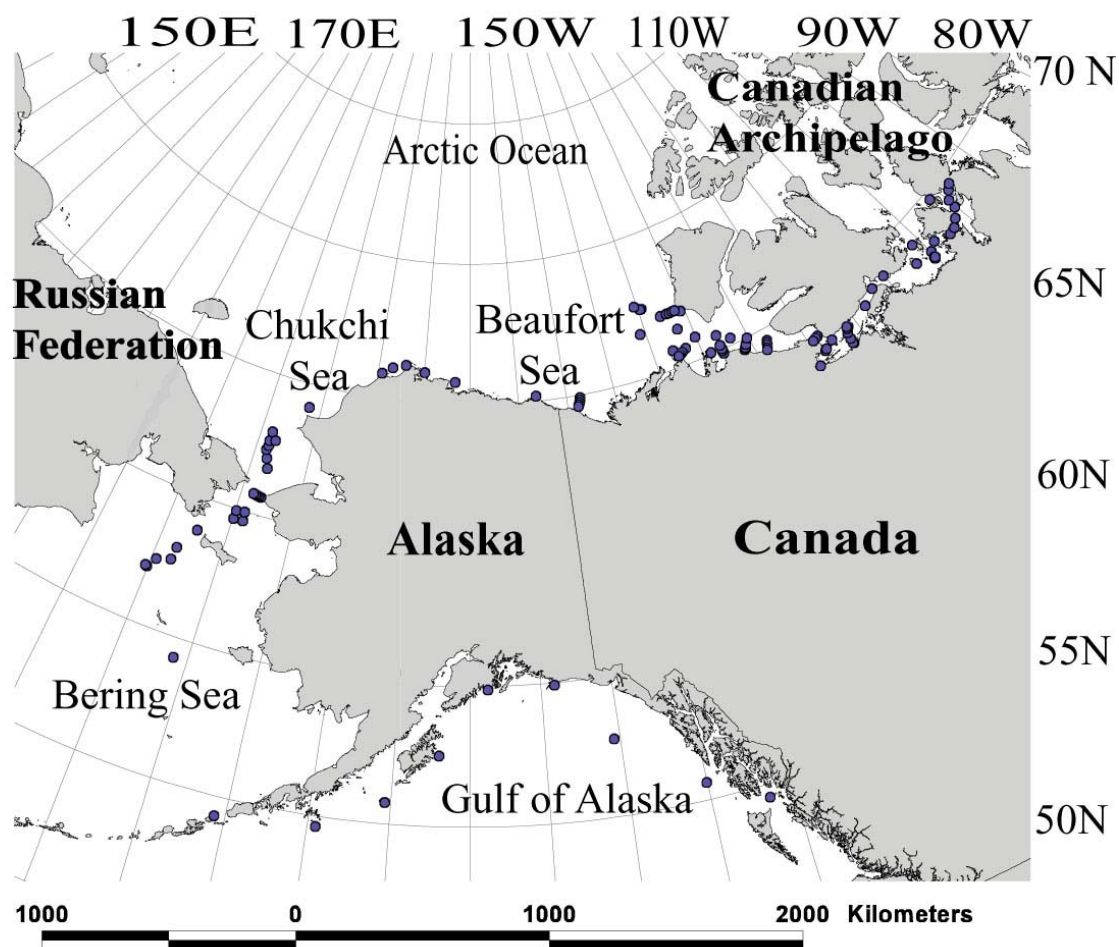


Figure 1. Cruise track of Laurier 2000, showing locations of all stations occupied during the cruise.

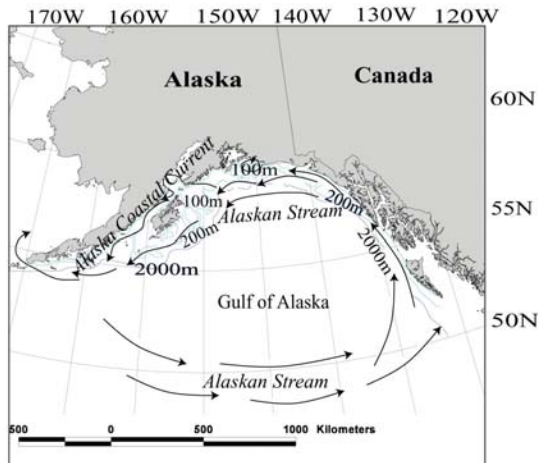


Figure 2a. Gulf of Alaska

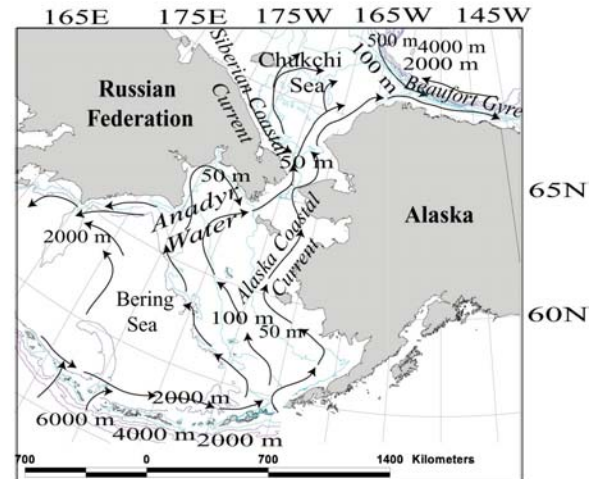


Figure 2b. Bering and Chukchi Seas

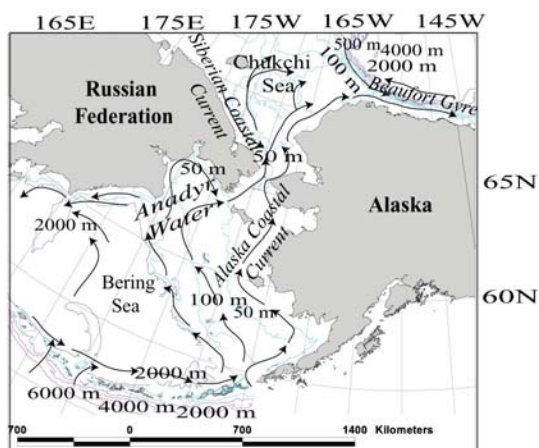


Figure 2c. Beaufort Sea

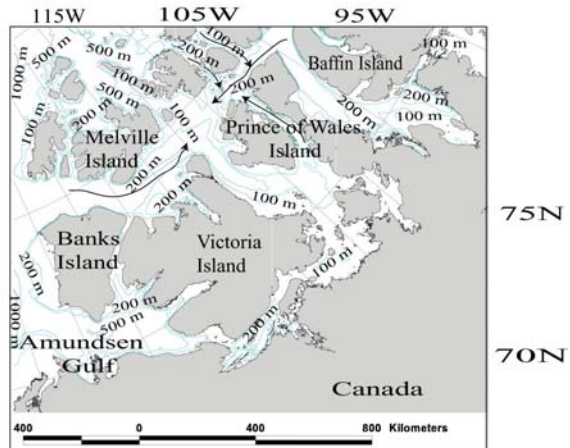


Figure 2d. Canadian Archipelago

Bathymetry legend

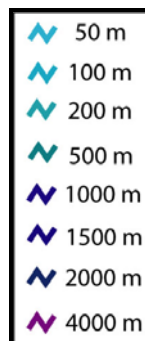


Figure 2. Bathymetry (indicated by colored lines; see legend above for depth values) and general directional flow (indicated by black arrows) for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

over 2000 kilometers across the continental shelf to the southwestern GOA, where it then flows northerly into the Bering Sea (Reed et al., 1987). The GOA region is seasonally exposed to wintertime storms along the Aleutian Chain, associated with the Aleutian Low. These storms, combined with riverine outflow, contribute to a very high regional freshwater input (Royer, 1982). The continental shelf has a steep drop off from 200 m to 2000-4000 m depths (Figure 2a; modified from bathymetry data available at <http://walrus.wr.usgs.gov/infobank/gazette/html/regions/ak.html> and <http://www.absc.usgs.gov/research/walrus/bering/bathy/>). Eight stations were occupied in this region (Figure 3a).

Bering and Chukchi Seas: These seas possess wide, shallow continental shelves (Figure 2b; modified from bathymetry data available at <http://www.absc.usgs.gov/research/walrus/bering/bathy/>) influenced primarily by three Pacific-origin water masses flowing northerly across the shallow shelf of 30-70 m (Grebmeier, 1993). The ACC continues northward as a near-shore water mass along Alaska from the GOA, through the Bering Strait into the Chukchi Sea, maintaining its distinct low-nutrient, high-temperature water mass signatures (Figure 2b; modified from figure in Hunt, 2002). Parallel to the ACC, low-temperature, high-nutrient Anadyr Water (AW) from the Russian Gulf of Anadyr is transported northward, entering the southern Chukchi Sea (Walsh et al., 1989; Grebmeier, 1993). Some of the world ocean's highest primary productivity measurements have been observed in this region, where summertime integrated water column values can reach approximately $1000 \text{ mg m}^{-2} \text{ chl } a$ in the southern Chukchi Sea (Walsh et al., 1989).

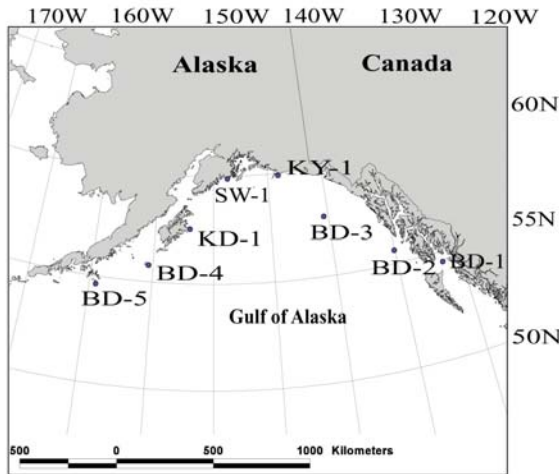


Figure 3a. Gulf of Alaska

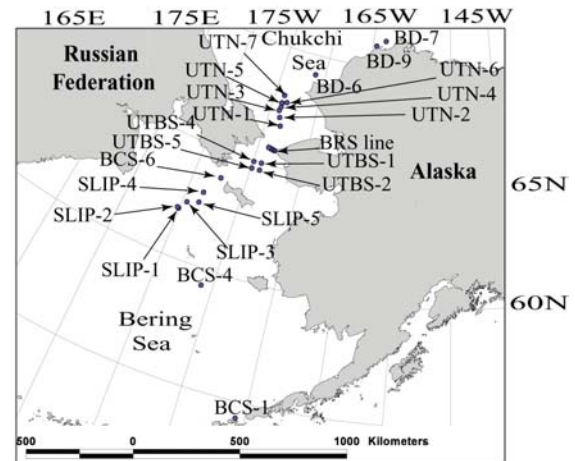


Figure 3b. Bering and Chukchi Seas

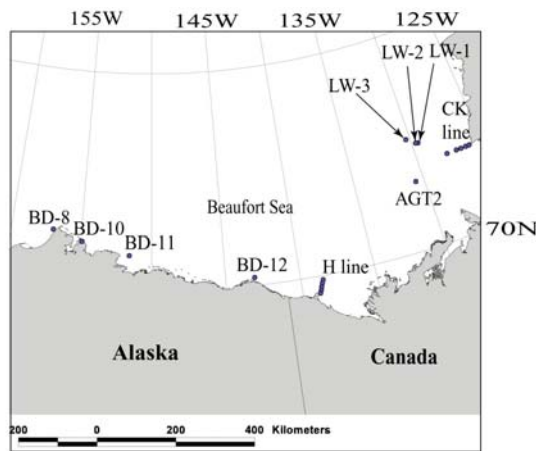


Figure 3c. Beaufort Sea

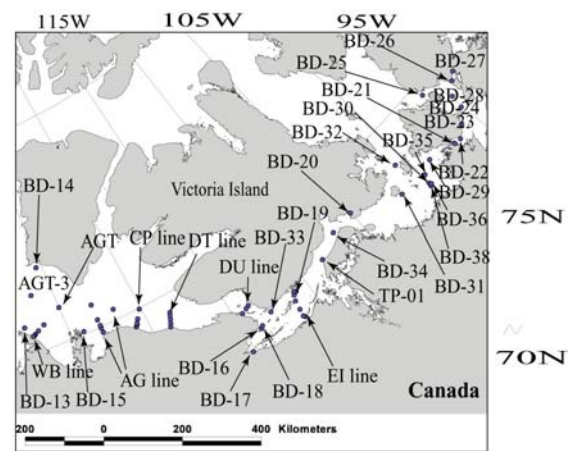


Figure 3d. Canadian Archipelago

Figure 3. Laurier 2000 station locations for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

The Chukchi Sea is also influenced by the Siberian Coastal Current, which is intermittently present during some summers and autumns but absent in the winter and spring, flowing southeasterly from the Siberian coast into the central Chukchi Sea, although some reversal occurs (Münchow et al., 1999). Bathymetry influences water mass movement here, including Herald Shoal, which divides the AW into a western high-nutrient current flowing northerly through Herald Valley into the Arctic Ocean basin, and an eastern lower-nutrient current flowing northward and eastward (Weingartner et al., 2001 and references contained therein). Twenty-six stations were occupied in this region (Figure 3b).

The Chukchi and Bering Seas are seasonally covered by winter and spring ice pack, forming at polynyas, which are ice-free or relatively ice-free regions surrounded by ice. This ice moves southward to a maximum extent coinciding with the 200 m Bering Sea isobath (Niebauer, 1981). Seasonal ice functions as a critical ecosystem component. The moving ice pack provides a large surface area environment, serving as a platform for marine mammals (seals, walrus, and polar bears) to haul out, to hunt, and to give birth (Stirling, 1997 and references therein). In addition, sea ice is a habitat for epontic ice algae (Stirling, 1997 and references therein; Gutt, 2001) and an undersurface community for invertebrates and their predators (Stirling, 1997 and references therein; Werner and Gradinger, 2002). Large abundances of bacteria and viruses have also been observed within brine veins, brine channels, surface melt pools, and within the ice matrix itself (Deming, 2002).

The seasonal break-up of this pack ice provides a “highway” of open water for the migration of whales (e.g. bowhead, beluga, narwhal) (Stirling, 1997 and references

therein) . Seasonal ice break up also functions as a growth stimulus (due to increasing light levels in the water column) for an ice-edge phytoplankton bloom (Niebauer et al., 1995) that serves as a large food source for both pelagic and benthic organisms. Ice melt releases nutrients and organic carbon derived from ice-rafted deposits of terrigenous and atmospheric dust (Reimnitz et al., 1998 and references therein). In addition, ice algae, algal-grazing invertebrates, bacteria, viruses, and detritus are released from the ice surface and the ice matrix.

Beaufort Sea: This region is exposed to persistent near-shore easterly track of ACC water that passes through Barrow Canyon. In addition, a southeasterly flow of bottom flowing Atlantic water is transported along the Arctic Ocean's Northwind Ridge into Chukchi Sea and Beaufort Sea waters (Figure 2c; modified from figure in Weingartner et al., 2001). The Mackenzie River's massive freshwater outflow ($340 \text{ km}^3 \text{ yr}^{-1}$; Aagaard and Carmack, 1989) greatly impacts coastal regions of the Beaufort Sea, causing near-shore estuarine conditions in areas proximal to the Mackenzie River mouth (Carmack and Macdonald, 2002, and references contained therein). This riverine output is substantially regulated by seasonal discharge—approximately 90% of annual outflow occurs between June and September, with minimal wintertime discharge (Carmack et al., 1989). This seasonal discharge is an important contributing factor to continental shelf freshwater mixing and dispersal (Carmack et al., 1989). The reduced winter freshwater outflow also facilitates the formation of dense water (Melling, 1993), which contributes to Arctic Ocean halocline formation (Aagaard et al., 1981). Because of this large fluvial outflow, massive amounts of riverine sediments ($130 \times 10^6 \text{ T yr}^{-1}$; Carmack and Macdonald, 2002) are also deposited on the near-shore Canadian continental shelf. In

comparison with the Bering and Chukchi Seas' wide continental shelves (Figure 2b) and seasonal ice cover, the Beaufort Sea has a narrow continental shelf approximately 120 km wide (Carmack and Macdonald, 2002; Figure 2c; modified from bathymetry data available at <http://walrus.wr.usgs.gov> and <http://www.absc.usgs.gov/research/walrus/bering/bathy/>) and is persistently exposed to ice-pack cover, though the ice extent varies seasonally. Near-shore Beaufort Sea benthic communities are subject to intense currents and substantial ice scour—pressure ridges and ice keels have been observed to scour up to 100% of the Canadian Shelf from the shoreline to depths of approximately 70 meters (Carmack and Macdonald, 2002 and references contained therein). This scouring not only physically removes and destroys benthic populations; benthic scour depressions can also form large anoxic brine pockets known as benthic “black pools of death” (Conlan et al., 1998; Kvitek et al., 1998) which also contribute to benthic population mortality. Eighteen stations were occupied in this region (Figure 3c).

Canadian Archipelago (CA): Located on the shallow continental shelf contiguous with the Beaufort Sea, the CA is characterized by central shallow depths (85-140 meters) and deeper western sills (350-450 meters), which function to limit the free exchange of waters between the Arctic Ocean and Baffin Bay (Prinsenberg and Bennett, 1987; Figure 2d; bathymetry data available at <http://walrus.wr.usgs.gov> and <http://www.absc.usgs.gov/research/walrus/bering/bathy/>). These shallow depths (85-140 meters), comparable to the Bering Strait (50-100 meters), permit only waters near the surface to pass over it, blocking deeper water masses from easy exchange. Thus both inflow from the Arctic Ocean to the CA, and outflow from the CA to Baffin Bay are both

limited to a considerable extent (Prinsenberg and Bennett, 1987). The boundaries of the CA system are delineated by Baffin Bay and by Greenland which border the CA to the east, and by the Canadian Basin of the Arctic Ocean, which borders the CA to the west (Prinsenberg and Bennett, 1987). The central area of the CA (near Barrow Strait and Resolute on Cornwallis Island; see Figure 4 for names of locations mentioned throughout text) is generally covered by land-fast ice ten months out of the year, with a brief respite of open water during August and September (Markham, 1981). As ice reforms in October, it is transported through Barrow Strait into the eastern CA, attaining a maximum thickness of approximately 2 meters by April (Environment Canada, 1972).

The CA is an important area of Arctic Ocean surface water modification, where it warms the halocline by several degrees (Melling et al., 1984). This occurs as the water passes southeasterly through the sheltered waterways of the CA. The CA's islands act as effective barriers that prevent large volumes of cold, near-freezing continental shelf water from entering the area. This separation from continental shelf waters allows the heat of the underlying Atlantic water mass, which is considerably warmer than the Arctic Ocean water, to diffuse upwards and warm the surface water (Prinsenberg and Bennett, 1987). Sixty-nine stations were occupied in this region (Figure 3d).

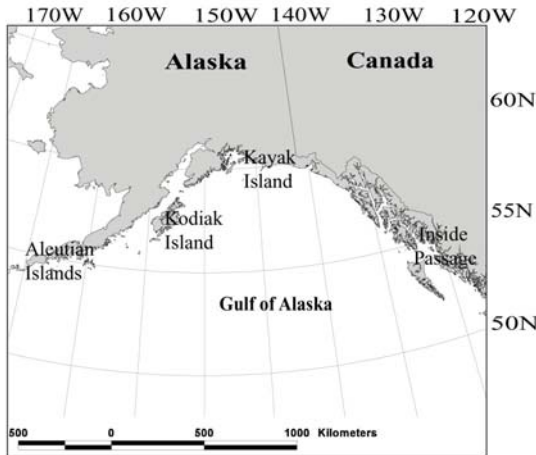


Figure 4a. Gulf of Alaska



Figure 4b. Bering and Chukchi Seas

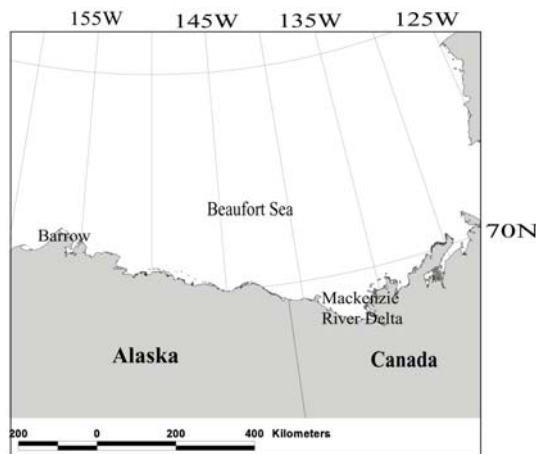


Figure 4c. Beaufort Sea

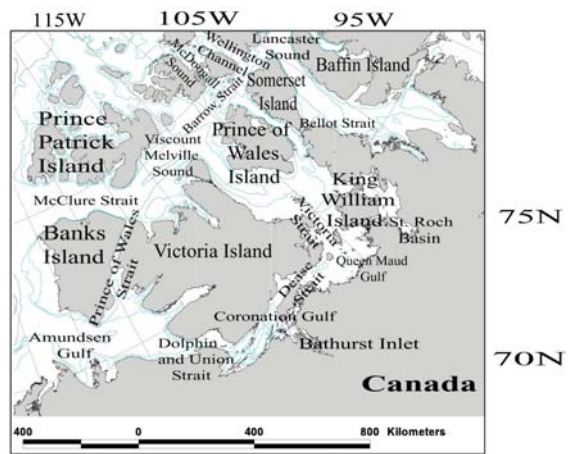


Figure 4d. Canadian Archipelago

Figure 4. Regional names of geographical locations in study areas (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

II. HYDROGRAPHIC PARAMETERS

Introduction

As discussed in the previous section, the four marine regions of this study are characterized by distinctive current, salinity and temperature dynamics. The GOA exhibits low mean bottom water salinity (31-33 ppt), high temperature inner shelf bottom water (4-7°C) (Weingartner et al., 2002), and more saline (34 ppt), colder (3-6°C), outer shelf bottom water (Weingartner et al., 2002). The Bering/Chukchi Seas have a net northern flow of the ACC, also known as Alaska Coastal Water (ACW), on their eastern shores with a bottom water salinity of ≤ 31.8 ppt and a bottom water temperature of $\geq 4^{\circ}\text{C}$ (Grebmeier et al., 1989). Colder, more saline Bering Shelf-Anadyr Water (BSAW) has a net northern flow with bottom water salinity ≥ 31.8 ppt and temperatures between 0°C and 1.5°C (Grebmeier et al., 1989). The ACW flows northeasterly along the southern shore of the Beaufort Sea, which shows a large drop in salinity due to the outflow of the Mackenzie River on its eastern edge (Carmack and Macdonald, 2002). The water masses entering the CA have been distinguished as westerly (entering from Viscount Melville Sound), southerly (entering from Peel Sound), northerly (entering from McDougall Sound and Wellington Channel), and easterly (from Lancaster Sound) in origin (Prinsenber and Bennett, 1987) (Figure 2d). Western CA water is Canadian Basin surface water in origin, and has a salinity signature of 31.5 to 32.5 ppt. Western CA water has a surface water temperature 0.2° to 0.4°C warmer than water entering from the north (Melling et al., 1984; Prinsenber and Bennett, 1987). Water entering the CA from the south has comparable temperatures to westerly water, but has salinity values less than 32.8 ppt. These temperatures and salinities generally become untraceable at sills, where

turbulent horizontal and vertical mixing of surface and subsurface waters disperse hydrographic variables' signatures (Prinsenberg and Bennett, 1987).

Selection of samples

Samples were collected along the track of the *St. Roch* II “Voyage of Rediscovery” from Victoria, British Columbia through the GOA, through the Bering, Chukchi, and Beaufort Seas, and into the CA in July, August, and September of 2000. Several stations in the Bering/Chukchi Seas (SLIP, UTN, UTBS stations) were occupied as part of on-going University of Tennessee Bering Strait Long-Term Observatory studies (<http://arctic.bio.utk.edu>). The remaining stations were opportunistic, taking advantage of locations as time and weather conditions permitted.

Materials and methods: Temperature, salinity, water column chlorophyll *a*

Water column profiles and sample collections were obtained using a Seabird CTD profiler attached to the ship's twelve-bottle Niskin bottle rosette. Water samples were collected at each station at the surface (1 meter), 5 meter, 10 meter, 25 meter, and bottom water (variable depth). Chlorophyll *a*, viral, and bacterial samples were taken for each depth. Viral and bacterial parameters will be discussed in a separate chapter.

Chlorophyll samples (250 ml) were collected into individual polypropylene containers, and kept in the dark at 4°C until processed. Samples were filtered through GF/F pre-combusted glass filters (Whatman ®) in the dark. These filters were then placed in cleaned glass vials and frozen for an hour to fracture the plant cells before the addition of 90% acetone for chlorophyll extraction. After twenty-four hour extraction in

4°C dark conditions, the acetone samples were decanted into clean glass test tubes and chl *a* concentration was determined fluorometrically (Welschmeyer, 1994). Bottom water temperature and salinity measurements are reported here because they are previous indicators of differing water mass signatures (Grebmeier et al., 1989), in comparison with surface water measurements which are usually dispersed in surface waters. Chlorophyll *a* concentrations, measured in integrated water column (mg m^{-2}) concentration, indicate the total estimated amount of carbon settling to the benthos from the overlying water column. Two integrated chlorophyll *a* water column parameters were calculated. The first integrated measurement included the entire water column depth (including both euphotic zone/active chlorophyll *a* and subeuphotic zone/transported chlorophyll *a*) which was variable between stations. The second integrated measurement included the upper euphotic water layer, estimated to be 25 m for the purposes of this study. A 20 m depth was used in many Beaufort Sea and CA stations where a 25 m measurement was not obtained. For stations shallower than 20-25 m, the entire integrated water column concentration was used for statistical comparison. Measurements are available in Appendix C.

Results

Gulf of Alaska (GOA): Bottom water salinity ranged from 31.7 ppt (near the Aleutian Islands) to 34.2 ppt at the station farthest from land, BD-3 (Figure 5a). Bottom water temperature ranged from 6-9°C, except BD-3 (3.7°C) (Figure 6a). The eastern GOA stations had the lowest range of integrated total water column chlorophyll *a* values (30-93

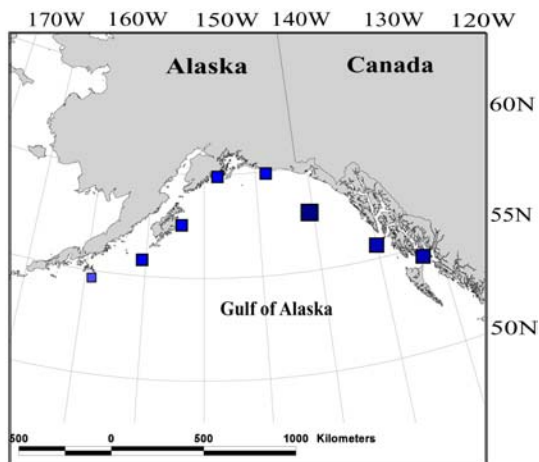


Figure 5a. Gulf of Alaska

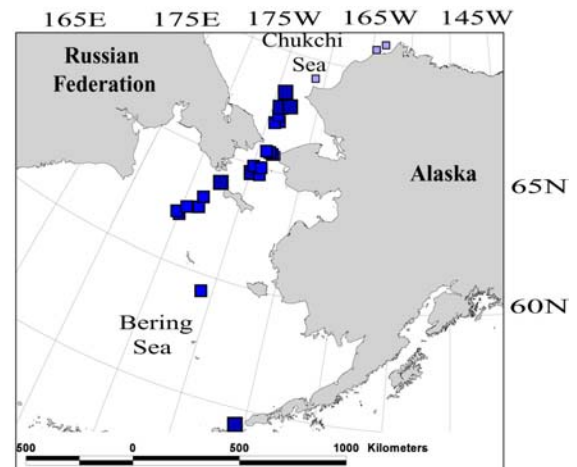


Figure 5b. Bering and Chukchi Seas

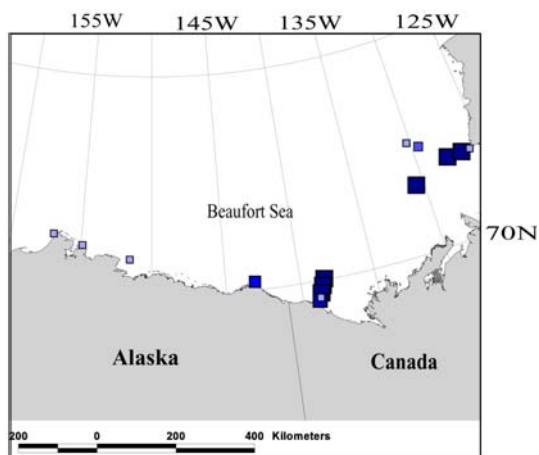


Figure 5c. Beaufort Sea

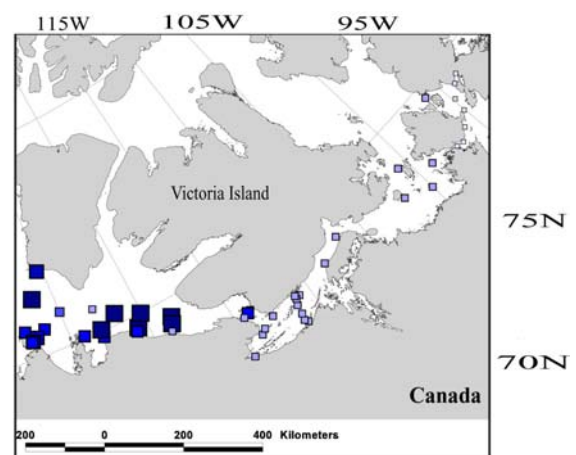


Figure 5d. Canadian Archipelago

Bottom water salinity legend

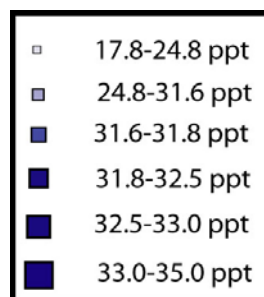


Figure 5. Bottom water salinity for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.

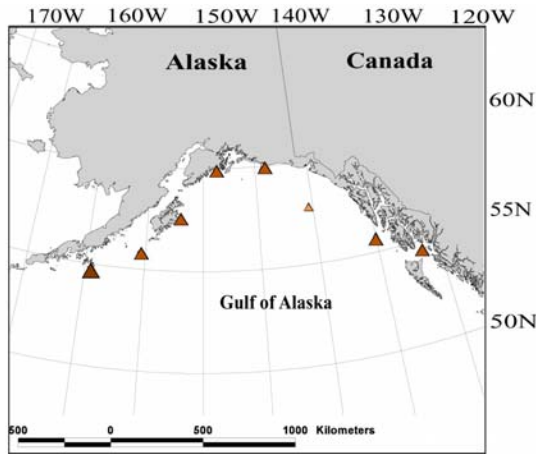


Figure 6a. Gulf of Alaska

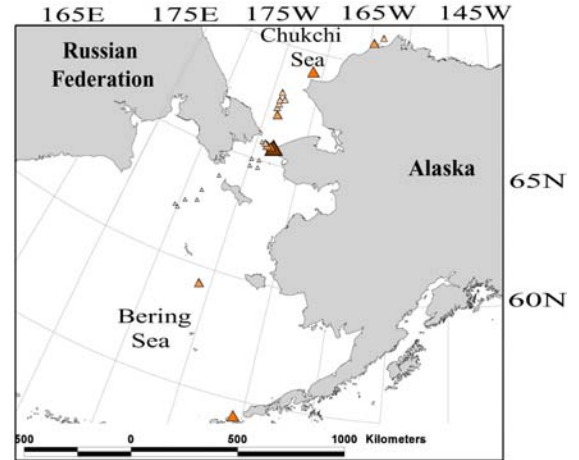


Figure 6b. Bering and Chukchi Seas

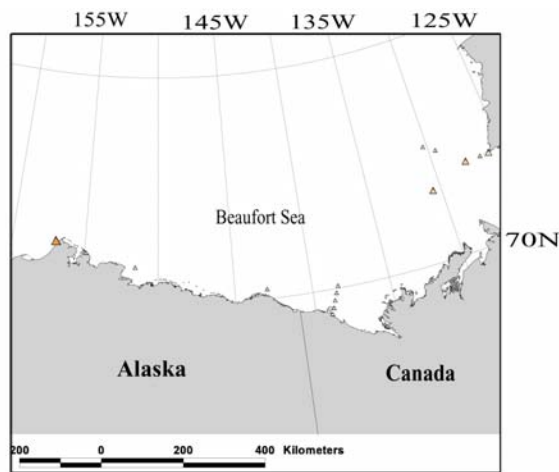


Figure 6c. Beaufort Sea

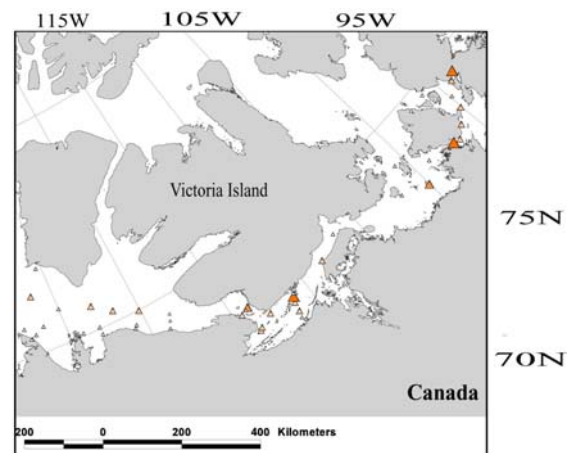


Figure 6d. Canadian Archipelago

Bottom water temperature legend

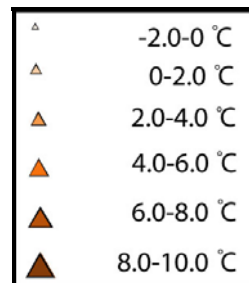


Figure 6. Bottom water temperature for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.

mg m⁻²), and the western GOA stations showed the highest range of integrated total water column chlorophyll *a* values (102-153 mg m⁻²) (Figure 7a).

Bering and Chukchi Seas: Bottom water salinity ranged from 31.8-32.5 ppt for SLIP stations and the maximum salinity (32.6 ppt) occurred in the southern Chukchi Sea (Figure 5b). Bottom water temperature ranged from -1.6 to 0°C for all stations except the northernmost Chukchi Sea station, which had a temperature of 5.2°C (Figure 6b). Integrated total water column chlorophyll *a* values ranged from 11 to 785 mg m⁻²--the minimum value occurred in the northernmost Chukchi Sea station; the highest values occurred at 5 of 6 UTN southern Chukchi Sea stations (Figure 7b).

Beaufort Sea: Bottom water salinity ranged from 29 to 34 ppt; lower values occurred in the eastern Beaufort Sea, higher salinities occurred in the western Beaufort Sea (Figure 5c). Bottom water temperature ranged from -1.6 to 3.5°C (Figure 6c). The warmest temperatures occurred in the western Beaufort Sea and the coldest temperatures occurred in the eastern Beaufort Sea. Integrated total water column chlorophyll *a* values ranged from 18 to 52 mg m⁻²; both of which occurred in the eastern Beaufort Sea (Figure 7c).

Canadian Archipelago (CA): Bottom water salinity ranged from 17-32 ppt in the eastern half of the CA study region, and predominantly 32-35 ppt in the western half of the CA region (Figure 5d). Bottom water temperature ranged from -1.2 to 2.0°C for all stations except for EI-3 in Coronation Gulf (4.5°C) and BD-27 (4.8°C) in Spence Bay (Figure 6d). Integrated total water column chlorophyll *a* ranged from 0-318 mg m⁻², with the lowest concentrations occurring in the centers of gulfs and straits; higher values were found

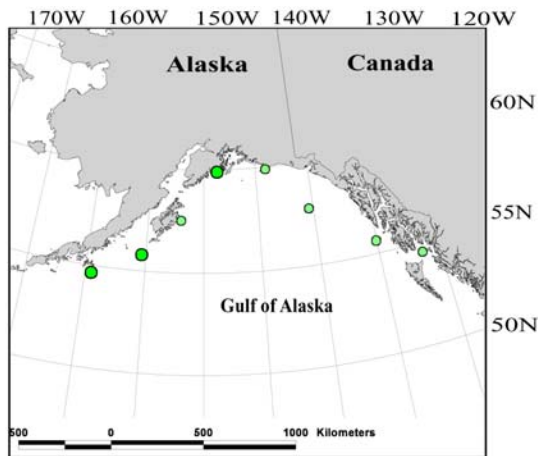


Figure 7a. Gulf of Alaska

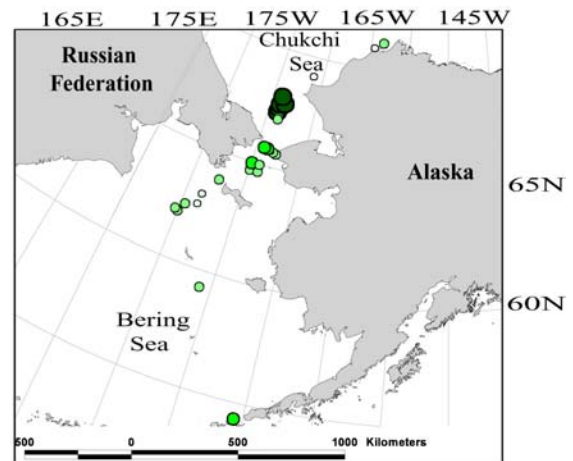


Figure 7b. Bering and Chukchi Seas

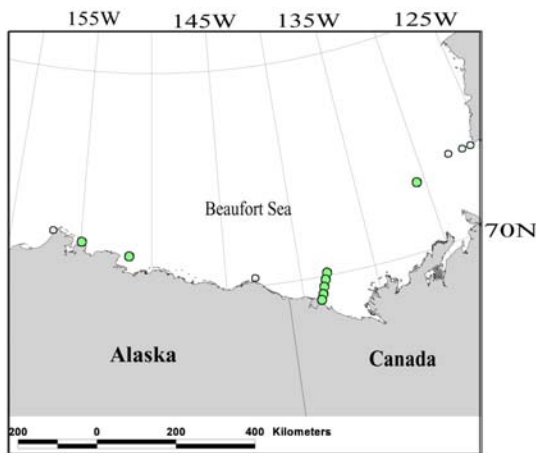


Figure 7c. Beaufort Sea

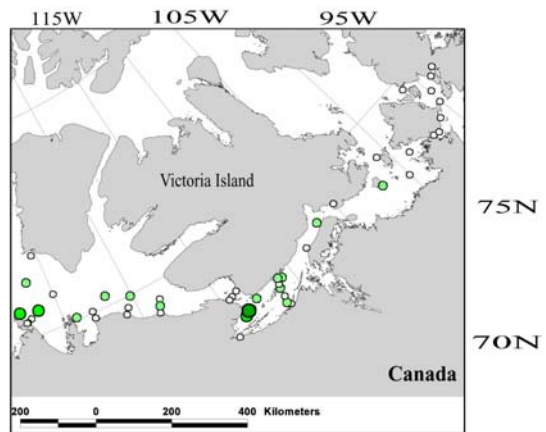


Figure 7d. Canadian Archipelago

Integrated water column chlorophyll *a* legend

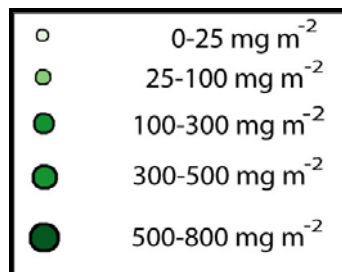


Figure 7. Integrated total water column chlorophyll *a* concentrations (mg m⁻²) for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.

near-shore, and the highest value, 318 mg m⁻² was found at BD-18, a near-shore station in Coronation Gulf (Figure 7d).

Stations from all four geographic localities combined: Mean bottom water temperatures were warmest in the GOA (6.8°C), decreasing in the Bering/Chukchi Seas (1.2°C) and remaining low in the Beaufort Sea (-0.6°C) and CA (0.2°C; Table 1), with a few warm stations in the Chukchi Sea (8.0°C) and CA where surface warming was observed (4.0-6.0°C; Figure 6). Mean bottom water salinity ranged was 32.5 in the GOA and 32.0 ppt in the Bering/Chukchi Seas, reaching a low mean value in the Beaufort Sea (31.6 ppt), before decreasing to the lowest mean value in the CA stations (29.3 ppt; Table 1). Mean integrated total water column chlorophyll *a* values were moderate to high in the GOA (85.2 mg m⁻²), and reached a maximum in the Bering and Chukchi Seas (181.7 mg m⁻²; Table 1). Mean integrated total water column chlorophyll *a* values decreased to the lowest mean value in the Beaufort Sea (31.8 mg m⁻²), then increased slightly in the CA (36.6 mg m⁻²; Table 1).

Table 1. Regional mean values for bottom water and integrated water column parameters. Standard deviations are in parentheses.

Region	Mean bottom water salinity (ppt)	Mean bottom water temperature (°C)	Mean integrated water column chlorophyll <i>a</i> (mg m ⁻²)
Gulf of Alaska	32.501 (0.786)	6.839 (1.590)	49.947 (28.427)
Bering/Chukchi	32.043 (0.602)	1.211 (2.561)	94.780 (158.310)
Beaufort	31.577 (2.391)	-0.623 (1.197)	26.677 (14.122)
Canadian Archipelago	29.369 (3.983)	0.227 (1.744)	6.690 (8.276)

Discussion

GOA hydrographic analysis confirmed ACW, with bottom water salinity values less than 31.8 ppt (Feder and Jewett, 1986; Figure 5a), except for the only station (BD-3) located off the shelf break, at 3229 m (Appendix A). Bottom water temperature followed the same pattern as bottom water salinity, with ACW temperatures (greater than 2°C) (Grebmeier et al., 1989) occurring at all stations (Figure 6a). Higher western GOA integrated chlorophyll *a* values (Figure 7c) follow an observed trend of higher western particulate organic carbon (POC) values attributed to enrichment by the westward flow of the ACC/ACW, the Alaskan Stream, and detrital contributions from the coastal Kodiak Archipelago, from the Alaska Peninsula, and from Cook Inlet (Feder and Jewett, 1986).

The Bering Sea and Chukchi Sea stations exhibited cold, high salinity bottom water to the west (Figures 5b and 6b), previously termed Bering Sea Anadyr Water (BSAW) by Grebmeier (1987), and eastern high temperature, low salinity ACW water (Figure 5b). The highest integrated total water column chlorophyll *a* values occurred in the southern Chukchi Sea (Figure 7b), where maximum values have been reported previously (Walsh et al., 1989).

The Beaufort Sea stations exhibited low bottom water salinities and low bottom water temperatures (Figures 5c and 6c), due to shallow depths and proximity to riverine outflow (Carmack and Macdonald, 2002). Bottom water salinities increased with increasing distance from shore, except for two stations west of Banks Island (Figure 5c). These near-shore low salinities reflect the large impact this river has on the Beaufort Sea coastal region, and consequently the largely estuarine nature of the Canadian Beaufort Shelf (Carmack and Macdonald, 2002). Integrated total water column chlorophyll *a*

concentrations in the Beaufort Sea are the lowest of the 4 study regions (Figure 7c); the highest concentrations of the Beaufort Sea stations occurred near the Mackenzie River (Figure 7c), possibly due to high nutrient output from the riverine outflow (Carmack and Macdonald, 2002).

The CA shows a clear trend of colder, more saline bottom water in the west, and warmer, less saline bottom water in the east (Figures 5d and 6d). This possibly indicates this region's western to eastern surface area increase in coastline, and hence increased exposure to terrestrial freshwater run-off in the eastern areas. It may also be the result of the bottom Atlantic water layer diffusing upwards and warming the surface waters within the shelter of the islands (Prinsenbergh and Bennett, 1987). Integrated total water column chlorophyll *a* values exhibited high concentrations in the area of Bathurst Polynya (Fortier et al., 2000), and the highest values were found in Coronation Gulf near the Coppermine River, possibly due to increased nutrient input [see Carmack and Macdonald's (2002) discussion of the Mackenzie River].

Chapter summary

The GOA exhibited high bottom water salinity (31.7-34.2 ppt), the warmest bottom water temperatures (3.7-9°C) of the four study regions, and moderate integrated total water column chlorophyll *a* values (30-153 mg m⁻²; Table 2). The Bering and Chukchi Seas exhibited bottom water salinity values ranging from 31.8-32.5 ppt, colder bottom water temperatures (1.6-5.2 °C) than the GOA, and the highest integrated water column chlorophyll *a* values (11-785 mg m⁻²) of all four study regions (Table 2). The

Beaufort Sea stations exhibited variable bottom water salinities (29-34 ppt), cold bottom water temperatures (-1.6-3.5 °C), and low integrated total water column chlorophyll *a* values (18-52 mg m⁻²; Table 2). The CA stations also had low to high bottom water salinities (17-35 ppt), cold bottom water temperatures (-1.2-4.8°C), and low to high integrated total water column chlorophyll *a* values (0-318 mg m⁻²; Table 2). These data support previous classifications of the GOA as a moderately productive system, the Bering and Chukchi Seas as high productivity systems, the Beaufort Sea as a low productivity system, and the CA as a mosaic of low and high productivity areas.

Table 2. A comparison of bottom water and integrated water column parameters among study regions.

Region	Mean bottom water salinity (ppt)	Mean bottom water temperature (°C)	Mean integrated water column chlorophyll <i>a</i> (mg m ⁻²)
Gulf of Alaska	High	High	Moderate
Bering/Chukchi Seas	High	Low	High
Beaufort	Low to High	Low	Moderate
Canadian Archipelago	Low to High	Low	Low

III. MACROINFAUNAL COMMUNITY COMPOSITION AND BIOMASS

Introduction

Infaunal communities are strongly influenced by overlying water column parameters including temperature, which can limit the ranges of organisms due to metabolic restraints; freshwater input, which lowers salinity and often supplies a less nutritious terrigenous-based carbon supply to the marine benthos; and integrated water column chlorophyll *a* concentration, which can be used as a proxy measurement of primary productivity-derived carbon settling to the benthos. In addition, infaunal communities are also influenced by many benthic parameters, including regional topography (Zenkevitch, 1963) and sediment characteristics (Feder et al., 1994; Grebmeier et al., 1995; Cooper et al., 2002). The sediment parameters studied include sediment grain size, sediment chlorophyll *a* content, and total organic carbon to total organic nitrogen ratios in sediments which indicate carbon quality in the sediments.

Sediment tracers

Sediment grain size: The size of sediment particles is a strong determinant of species distribution (Gray, 1981; Grebmeier, 1987). Muddy sediments (small particle size) harbor the highest faunal densities, since more surface area per unit of area is available for the adherence of nutrient-rich organic carbon (Gray, 1981). Larger particles (gravel, rock) are associated with high current flow or wave action, suspending and transporting the smaller, finer particles away from the area (Gray, 1981). Sediment grain sizes are distinguished by phi size classes (the negative logarithm to the base 2 of the

particle size; Krumbein, 1934). Increasing phi size (ϕ) indicates decreasing particle size in millimeters, where $\phi \leq 1$ is very coarse sand to gravel, $\phi = 2$ is medium sand, $\phi = 3$ is fine sand, $\phi = 4$ is very fine sand, and $\phi \geq 5$ is silt and clay (Krumbein, 1934).

Total organic carbon: Sediment total organic carbon measurements (TOC) indicate the sum of organic carbon deposited per unit area. Sediment total organic nitrogen measurements indicate the sum of organic nitrogen deposited per unit area, which can indicate limits to primary productivity (Gray, 1981).

Carbon to nitrogen ratios: Ratios of surface sediment total organic carbon to total organic nitrogen (C/N) are measures of “food quality” deposited on the sea floor (Grebmeier et al., 1988). A larger amount of total organic carbon in the sediment in proportion to the amount of total organic nitrogen in the sediment can indicate the relative amount of terrestrial versus marine organic matter contributions to that sediment. Recently deposited, nutritious benthic organic matter is indicated by low C/N ratios typically within the 6-8 weight/weight ratio range, whereas older, less nutritious organic matter of either marine or terrestrial origin is indicated by a higher C/N ratio, typically greater than 10, which is evidence of nitrogen utilization (Grebmeier et al., 1988).

Sediment chlorophyll *a* content: The quantity of chlorophyll *a* deposited on the benthos is an indicator of overlying water column primary production, and provides benthic communities with a nourishing carbon source (Grebmeier, 1993). In the polar regions, a large percentage of surface-derived primary production reaches the benthos in shallow areas without being consumed by zooplankton (Petersen and Curtis, 1980).

The composition of regional macroinfaunal communities is influenced by the regional characteristics of both overlying water masses and sea floor sediments, since

macroinfaunal species vary in their temperature, salinity, and carbon supply requirements, in addition to requiring different grain sizes in order to construct appropriate tubes and burrows for shelter. Changes in these aforementioned environmental parameters could thus change the diversities and distributions of the benthic communities, which can also be a long-term, integrated indicator of carbon deposition to the benthos (Grebmeier and Dunton, 2000) where there is tight coupling with many of the regional sediment and overlying water column processes.

Several studies have utilized statistical numeric clustering programs based on species abundance to determine regional benthic community structure in the Bering and Chukchi Seas (Grebmeier, 1987; Feder et al., 1994; Grebmeier and Cooper, 1995; Grebmeier and Cooper, in press). Using this methodology, stations may be grouped into regional communities according to similarity level, and taxa dominating the stations' macroinfaunal abundances, total wet weights, and organic carbon weights may be assessed. As a proxy for biodiversity, the Shannon-Weaver species diversity index (H') is used, which takes into account species richness and the proportion of that species within the community. A high level of diversity is indicated by a high value of H' (Shannon-Weaver, 1963). The evenness of this diversity is measured by the Shannon-Weaver evenness index (J), which is a measure of the relative abundance of a species in a community with regard to Shannon-Weaver diversity H' , and can range from 0 to 1. The differences in the diversities (measured by H') and compositions of these communities (determined by the three most abundant taxa in abundance and weight) can then be compared to environmental factors in order to determine environmental influences.

Regional benthic parameters

Gulf of Alaska (GOA): A variable benthic topography exists on the GOA shelf: the eastern GOA is characterized by strong tidal currents with variable bottom topography, low suspended sediment load, and low quantities of organic carbon in both suspended particulate form and in the sediment (Feder and Jewett, 1986). Benthic biomass is similarly low, and dominated by deposit feeders (Feder and Jewett, 1986). The northeastern GOA is characterized by a wide shelf (up to 100 km), with shallow banks and grounds (less than 200 m) intersecting canyons and troughs (Feder and Jewett, 1986). Annual POC in the water column is also low; however, sediment organic matter content ranges from low to high levels (Feder and Jewett, 1986). Infaunal communities in the NE GOA are dominated by deposit feeders (bivalves (F. Nuculidae, F. Nuculanidae) polychaetes (F. Lumbrineriidae, F. Maldanidae, F. Oweniidae, F. Spionidae, F. Sternaspidae,), brittle stars (F. Ophiuridae), and cumaceans (F. Leuconidae). By comparison, suspension feeders dominated on banks, such as ectoprocts, brachiopods, polychaetes (F. Polyodontidae), and bivalves (F. Mytilidae). Measurements of benthic biomass average 5 gC m^{-2} (Feder and Jewett, 1986).

The western gulf is a combination of steep slopes, flat, shallow banks, reefs, patchy bottom sediments, and rocky substrate (Feder and Jewett, 1986) indicative of higher current flow. Suspended particulate organic carbon load is high, with low levels of suspended sediment (Feder and Jewett, 1986). Bottom sediments exhibit low organic carbon values, and communities are dominated by suspension feeders, except in troughs where deposit feeders dominated. Higher benthic standing stocks have been measured in

the western study areas, and have been attributed to swift bottom currents and winter storms preventing deposition in the northeast, whereas gyre activity traps this westward-moving water near Kayak Island, facilitating sediment deposition. The sediment that is deposited in the northeast is largely of glacial origin, which typically has a low organic carbon concentration; therefore, a lack of high quality organic carbon supply may limit infaunal organisms in these areas (Feder and Jewett, 1986). In contrast, the north-central GOA's gyre activity concentrates suspended particulate organic carbon for benthic populations, which originates from glacial, fluvial, and detritus from regional algal beds, providing a higher-quality organic carbon supply (Feder and Jewett, 1986).

Bering and Chukchi Seas: The Bering and Chukchi Seas have historically been known as extremely high areas of primary and secondary production, drawing large mammals such as walruses, diving sea birds, seals, and whales to feed in "hot spots" of production, such as the intensive gray whale feeding areas of the northern Bering Sea (Highsmith and Coyle, 1992; Grebmeier and Harrison, 1992). Benthic biomass has been observed to increase from east to west in the northern Bering Sea, as well as increasing from south to north (Grebmeier and Cooper, 1994). The southeastern Bering Sea exhibit average benthic biomass values of below 10 gC m^{-2} , compared to 60 gC m^{-2} in the southern Chukchi (Grebmeier and Cooper, 1994). Recent studies through the Western Arctic Shelf-Basin Interactions (SBI) project (<http://www.utmsi.utexas.edu/people/staff/dunton/SBI/index.htm>) have focused in part on the compilation of available benthic biomass and integrated chlorophyll *a* measurements for the Bering, Chukchi, and Beaufort Seas (Dunton et al., 2002). GIS results for the Bering and Chukchi historical data sets have included data sources spanning the 1970's-

2000. Bering Sea benthic biomass shows a clear trend of lowest mean biomass in the southeast, increasing in the mid-Bering Sea, and exhibiting maxima both southwest of St. Lawrence Island (Grebmeier and Cooper 1995; Grebmeier and Dunton, 2000; Dunton et al., 2002) and in the middle of the Chirikov Basin in the northern Bering Sea (Grebmeier et al. 1988; Grebmeier and Dunton, 2000). These maxima values are also seen in the southern Chukchi Sea (Grebmeier and Cooper, 1994; Grebmeier and Dunton, 2000; Dunton et al., 2002; Grebmeier and Cooper, in press). The average benthic biomass shows a north-easterly decrease in the northern Chukchi and Beaufort Seas, but a higher mean biomass is maintained along the Russian Federation coastline (Reed, 1998; Dunton et al., 2002). This may be due to higher nutrient and productive water observed along this coastline, as discussed previously in the Chukchi hydrodynamic characteristics section (Weingartner et al., 2001).

Beaufort Sea: The SBI benthic biomass and integrated chlorophyll *a* compilation efforts (Dunton et al., 2002) indicate that benthic organisms attain a biomass of no greater than 125 g wet weight m⁻² along the entire coast of the Beaufort Sea. Integrated chlorophyll *a* values of 0.1 to 50 mg m⁻² are observed along the coast, although areas of higher chlorophyll *a* are observed in summer near Point Barrow (100 to 200 mg m⁻²) and near a region of upwelling near Barter Island, exhibiting values of 50 to 200 mg m⁻² (Dunton et al., 2002). Dunton et al. (2002) also suggest that the western Beaufort Sea benthic infaunal communities are closely coupled with an advected Bering Sea carbon supply, while eastern Beaufort Sea benthic communities are dependent on regionally derived carbon production, and do not exhibit as tight a coupling with overlying primary production as does the western Beaufort Sea.

Canadian Archipelago (CA): CA benthic standing stock has been characterized as variable, and on average, lower in mass than Bering and Chukchi Sea measurements (Grebmeier et al., 1995). Grebmeier et al. (1995) suggest that this mosaic of productivity is caused by a reduced seasonal growing period stemming from extended ice coverage. George and Paul (1970) observed relatively low benthic standing stock, and large amounts of ice-rafted rocks based upon benthic photographs taken near Ellesmere Island, off of Ice Island T-3. Ophiuroids, the sponge *Thenaea* sp., and the holothurian *Elpidia glacialis* were observed to be dominant detectable benthic macroinfauna. Lancaster Sound and Baffin Bay by comparison had standing stock with high variability, ranging from 40-500 g wet weight m⁻² (Thomson, 1982). Atkinson and Wacasey (1987) calculated that as much of 30-50% of primary production, also reaches the Frobisher Bay benthos in the eastern Canadian Arctic. This variability in both primary and secondary production may be due to North Water polynya upwelling events (Dunbar, 1981).

Materials and methods: Macroinfaunal and sediment tracer parameters

Macroinfaunal biomass and abundance: Four van Veen grabs (0.1m²) weighted with 32 kg of lead were taken at each station for replicate quantitative infaunal sampling. The sediment sample was then washed through 1 mm sieve screened boxes and transferred to plastic storage containers and preserved with 10% hexamethylenetetramine buffered formalin until land-based laboratory identification to family taxonomic level could be completed. Taxonomic groups were then both counted for the abundance of total individuals and weighed to determine wet weight biomass. Results were converted

to carbon values using previously determined carbon conversion values (Stoker 1978, 1981; Grebmeier, 1987).

Sediment total organic carbon and carbon to nitrogen ratios: Surface sediment (1 g) was processed by acidifying with 2 ml of 1N HCl, and homogenizing after being dried overnight at 105 °C to ensure carbonate-free sediments. A CHN elemental analyzer at University of California, Santa Barbara measured for carbon and nitrogen content, and carbon to nitrogen ratios were calculated (weight to weight).

Sediment grain-sizing: Sediment samples were processed using the techniques outlined in Reed (1998). Sediments were dried and ground into a heterogeneous mixture using a mortar and pestle. Aliquots (20g) were then treated with 30 ml of 30% hydrogen peroxide, stirred, and heated to 60 °C in order to dissolve organic material and to remove the remaining excess hydrogen peroxide. Iron oxides were removed from the sediments by adding sodium citrate buffer (90 ml) and sodium bicarbonate (2.0 g) to the sediment aliquots and placing them in a hot water bath (60°C) for five minutes before centrifuging for 5 minutes at 1500 rpm. The supernatant was decanted, and the iron oxide removal steps were repeated. After the second iron oxide treatment, distilled water (250 ml volume, including sediment volume) and 10% sodium hexametaphosphate (50ml) were added to the sediment aliquots. Sediments were wet sieved through a size 4 phi geological sieve to separate the $\phi \geq 5$ fraction from the larger grain sizes. The $\phi \geq 5$ fraction was treated with magnesium chloride to flocculate the material. After flocculation, this $\phi \geq 5$ fraction was placed into aluminum weigh boats, dried at 60°C in an oven before weighing. The larger grain sizes (still heterogeneous) were dried on the

geological sieve in an oven (60°C) before the dry weight was recorded prior to dry sieving.

Dried sediment aliquots were sieved through a nested sieve stack, utilizing a sieve shaker, in order to obtain sediment grain-size values. Sand and gravel fractions are separated from the silt/clay fractions, depending on mesh sieve phi size. Phi size categories were: $\phi \leq 1$ consisting of coarse sand, gravel, and cobbles, $\phi=2$ consisting of medium sand, $\phi=3$ consisting of fine sand, $\phi=4$ =very fine sand and $\phi \geq 5$ consisting of silt and clay (Gray, 1981). Individual phi size category weights were recorded, and the weight of the $\phi \geq 5$ fraction from the wet sieving step was added to the $\phi \geq 5$ fraction remaining after dry sieving in order to determine the total $\phi \geq 5$ fraction. Grain size percentage composition for each phi size class was determined from these weights for the complete sample. Modal sediment size was determined by the dominant percent composition phi size.

Sediment chlorophyll a content: Duplicate 2 cm³ samples of surface sediment were obtained from the first of five van Veen benthic grab samples taken at each station. Sediment samples were collected using a modified syringe and placed in 15 ml polypropylene centrifuge tubes (Falcon®, BD Biosciences, Bedford, MA) with 90% acetone for extraction and mixed. After a twelve-hour dark incubation (4°C), the acetone was decanted off of the sediment into a clean glass test tube and chlorophyll *a* readings were determined as above for the water column (Cooper et al., 2001). Sediment chlorophyll *a* values (mg m⁻²) were calculated using conversion values.

Cluster analysis: A numerical clustering program was used to calculate station groupings according to faunal similarity, using methods of Grebmeier et al. (1989). A

dendrogram was constructed from these values, and the number of clusters was determined by examining station similarity levels and knowledge of regional geography and oceanographic processes. In addition, the Shannon-Weaver diversity index was used as a measure of family diversity within these clusters (Shannon and Weaver, 1963).

Results

Macroinfaunal parameters: wet weight, biomass, abundance, diversity, and evenness

Gulf of Alaska (GOA): Macroinfaunal organic carbon biomass ranged from 2.8 to 7.2 gC m⁻² (Figure 8a; see Appendix D for individual station macroinfaunal values).

Macroinfaunal abundance ranged from 1045 to 7723 individuals m⁻² (Figure 9a).

Bivalves (F. Veneridae, *Yoldia sp.*) and sand dollars (F. Echinarachniidae) dominated station total organic biomass values (Figure 10a). GOA stations had the second lowest mean diversity of the 4 regions and also possessed the lowest mean evenness (Table 3).

Bering and Chukchi Seas: Macroinfaunal organic carbon biomass was low (2 gC m⁻²) at both the southernmost Bering Sea station and the northernmost Chukchi Sea station (Figure 8b). The highest biomasses were found in the St. Lawrence Island region (61 gC m⁻²), with the southern Chukchi Sea stations also showing high values (58 gC m⁻²) (Figure 8b). With respect to macroinfaunal abundance, again the southernmost Bering Sea and the northernmost Chukchi Sea stations showed the lowest abundances (1210 individuals m⁻² and 883 individuals m⁻², respectively) (Figure 9b). The highest macroinfaunal abundance (12,278 individuals m⁻²) was found in the southern Chukchi Sea (Figure 9b). Near the Aleutian Islands station total organic biomass was dominated

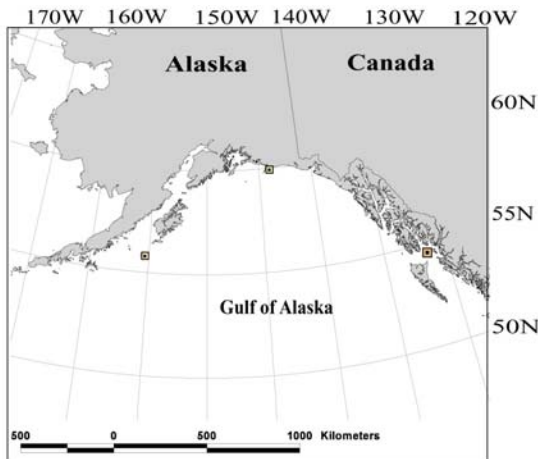


Figure 8a. Gulf of Alaska

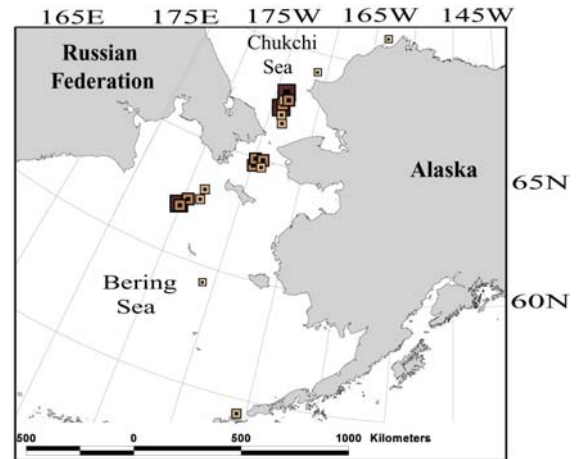


Figure 8b. Bering and Chukchi Seas

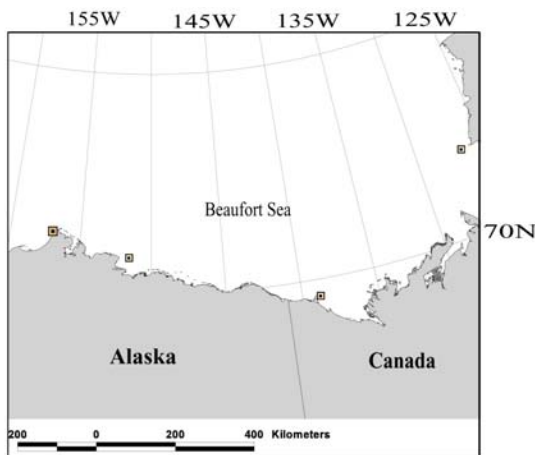


Figure 8c. Beaufort Sea

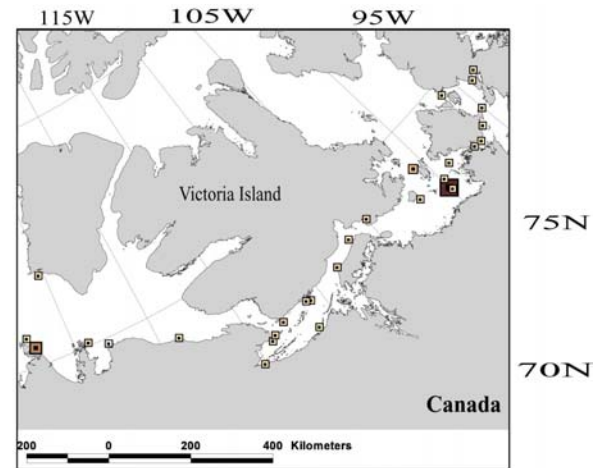


Figure 8d. Canadian Archipelago

Macroinfaunal organic carbon mass legend

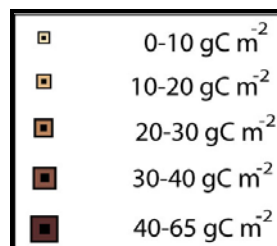


Figure 8. Macroinfaunal organic carbon mass for the four study regions: (a) Gulf of Alaska, (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago.

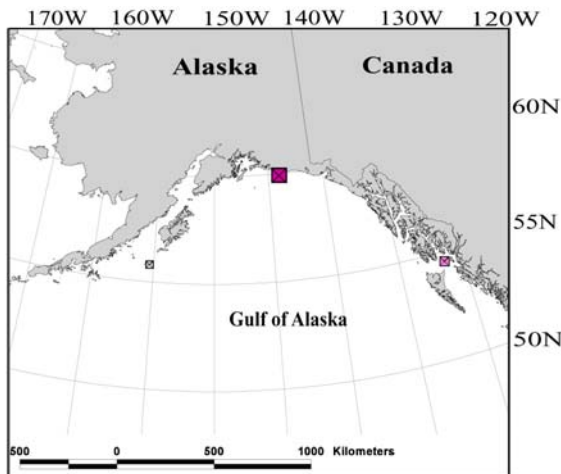


Figure 9a. Gulf of Alaska

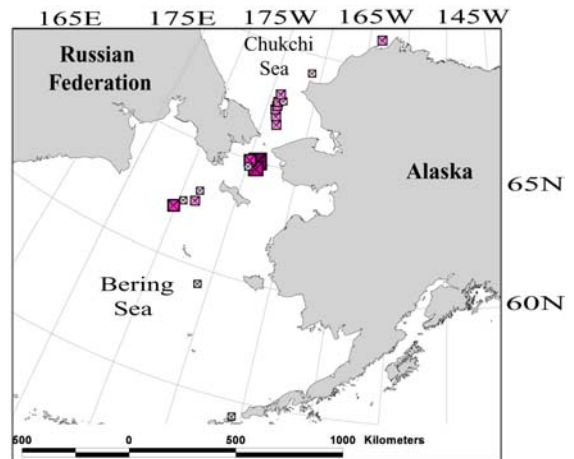


Figure 9b. Bering and Chukchi Seas

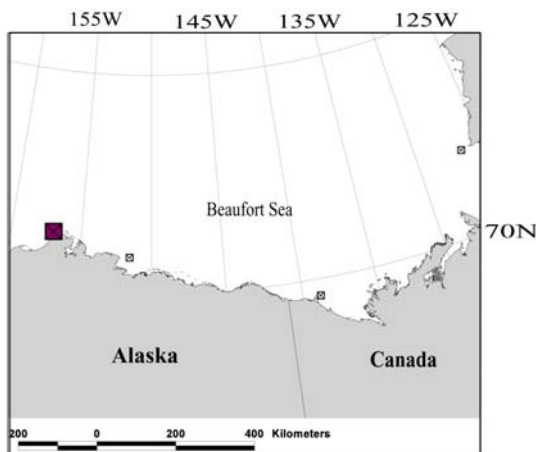


Figure 9c. Beaufort Sea

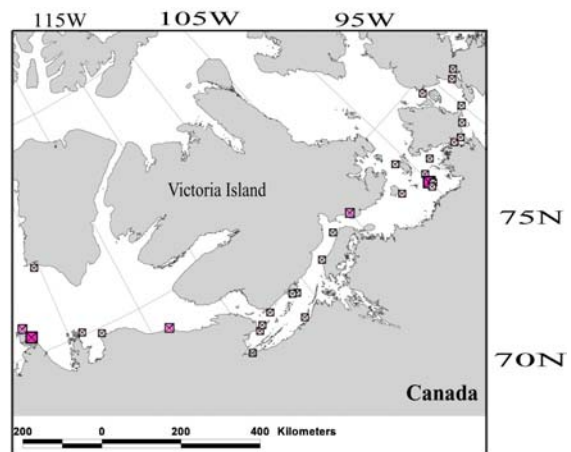


Figure 9d. Canadian Archipelago

Macroinfaunal abundance legend

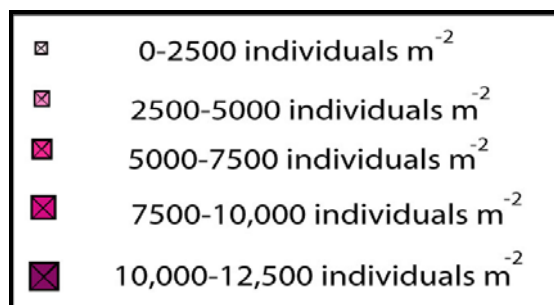


Figure 9. Macroinfaunal abundance for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

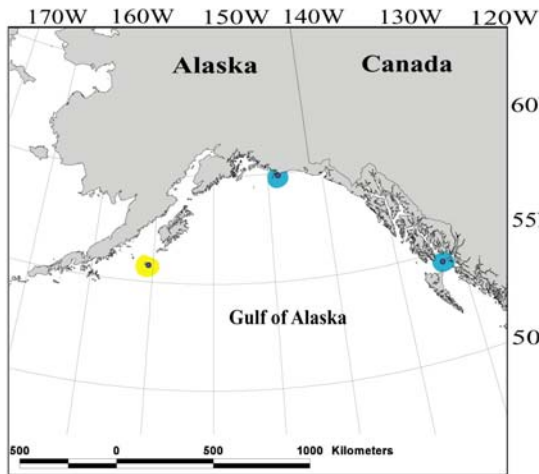


Figure 10a. Gulf of Alaska

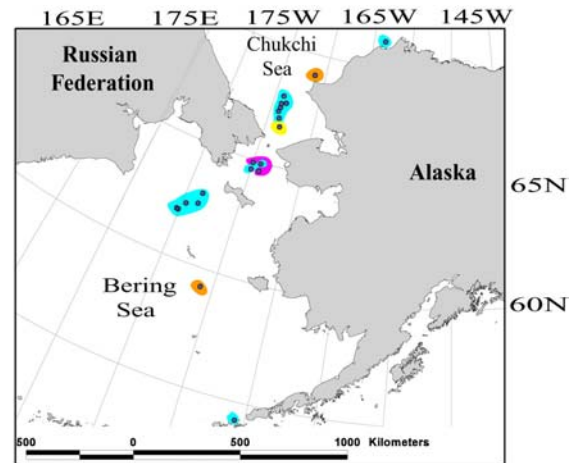


Figure 10b. Bering and Chukchi Seas

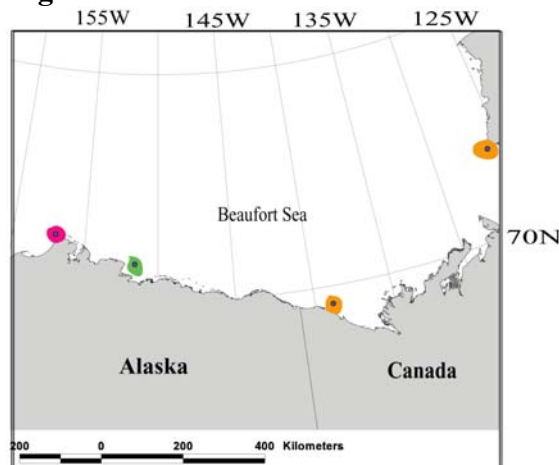


Figure 10c. Beaufort Sea

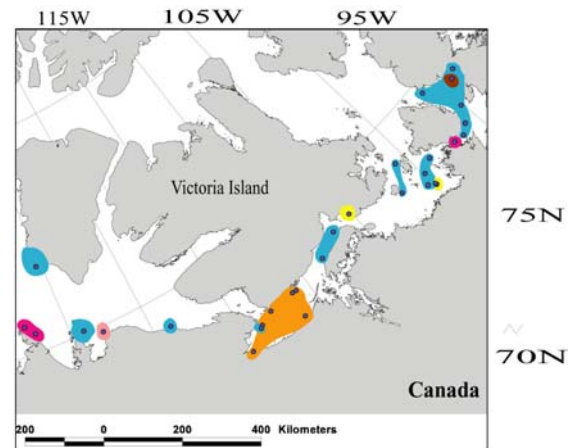


Figure 10d. Canadian Archipelago

Dominant station animal legend

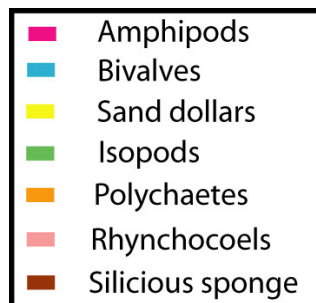


Figure 10. Dominant station animal by total organic biomass for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

Table 3. Regional mean values for macroinfaunal parameters. Standard deviations are in parentheses.

Region	Mean macroinfaunal abundance (no. individuals m ⁻²)	Mean macroinfaunal biomass (g carbon m ⁻²)	Mean community diversity (H')	Mean community evenness (J)
Gulf of Alaska	4055.0 (3387.0)	6.9 (3.8)	2.0 (0.9)	0.5 (0.206)
Bering/Chukchi	3846.4 (3023.8)	21.6 (15.9)	2.3 (0.5)	0.7 (0.1)
Beaufort	3048.1 (4952.9)	4.6 (7.5)	1.9 (0.8)	0.6 (0.2)
Canadian Archipelago	1712.9 (1856.0)	6.9 (13.0)	2.2 (0.4)	0.7 (0.1)

by bivalves (F. Tellinidae, *Macoma calcaria*) and polychaetes (F. Nephtyidae). Bivalves dominated macroinfaunal abundance near St. Lawrence Island (*Nuculana radiata* and *Nucula belloti*) and amphipods (*Ampelisca sp.*) dominated macroinfaunal abundance in the Bering Strait region (Figure 10b). In the Chukchi Sea, bivalves and polychaetes dominated macroinfaunal biomass in the northeast (*Macoma calcaria*, *Nucula belloti* and F. Sternaspidae). In the southern Chukchi Sea, sand dollars (F. Echinarachniidae; *Echinarachnius parma*) dominated macroinfaunal biomass (Figure 10b) (See Appendix E for dominant animal station listings). Bering/Chukchi stations exhibited the highest mean diversity and the second to highest mean species evenness values (Table 3).

Beaufort Sea: Macroinfaunal organic carbon biomass ranged from 1-16 gC m⁻² (Figure 8c). Macro-infaunal abundance ranged from 707-10,470 individuals m⁻² (Figure 9c). Station total organic biomass values were dominated by amphipods (*Byblis sp.*) in the western station, by isopods (F. Idotheidae) in the central station, and by polychaetes (F. Nephtyidae) in the two eastern stations (Figure 10c). Beaufort stations exhibited the lowest mean diversity value and the second to lowest mean evenness value (Table 3).

Canadian Archipelago (CA): Macroinfaunal organic carbon biomass ranged from 0 to 30 GC m⁻², with a maximum occurring near Hat Island in Queen Maud Gulf, where 43 gC m⁻² was observed (Figure 8d). Faunal abundance consistently ranged from 0-2,500 individuals m⁻² throughout the study region, with the Hat Island and WB-5 (Bathurst Inlet) stations exhibiting 5,547 and 6,770 individuals m⁻², respectively (Figure 9d). Station total organic carbon biomass was dominated by bivalves (*Yoldia sp.*), Rhynchocoela, and amphipods (*Ampelisca sp.*) in western stations. In central CA stations, macroinfaunal organic carbon biomass was dominated by bivalves (F. Astartidae, *Yoldia sp.*), sand dollars (F. Echinarachniidae), and polychaetes (F. Maldanidae, F. Oweniidae, F. Nephytidae, and F. Magelonidae). In northeastern CA stations, macroinfaunal organic carbon biomass was dominated by bivalves (F. Astartidae, *Yoldia sp.*, F. Mytilidae), silicious sponge, polychaetes (F. Sabellidae, F. Maldanidae), amphipods (*Ampelisca sp.*), and sand dollars (F. Echinarachniidae (Figure 10d). CA stations exhibited the second highest mean diversity and the highest mean species evenness values (Table 3).

Stations from all four geographic localities combined: Mean macroinfaunal biomass attains the highest average maximum in the Bering/Chukchi, decreasing in the Beaufort Sea, and becoming highly variable in the CA, as does faunal abundance (Table 3). Mean species diversity, the total number of taxa a community may possess, and species evenness, the distribution of taxa within the existing community diversity (Shannon and Weaver, 1963) appear to increase with movement from the GOA into the Bering/Chukchi Seas, decreasing again to low levels in the Beaufort Sea before increasing once again in the CA.

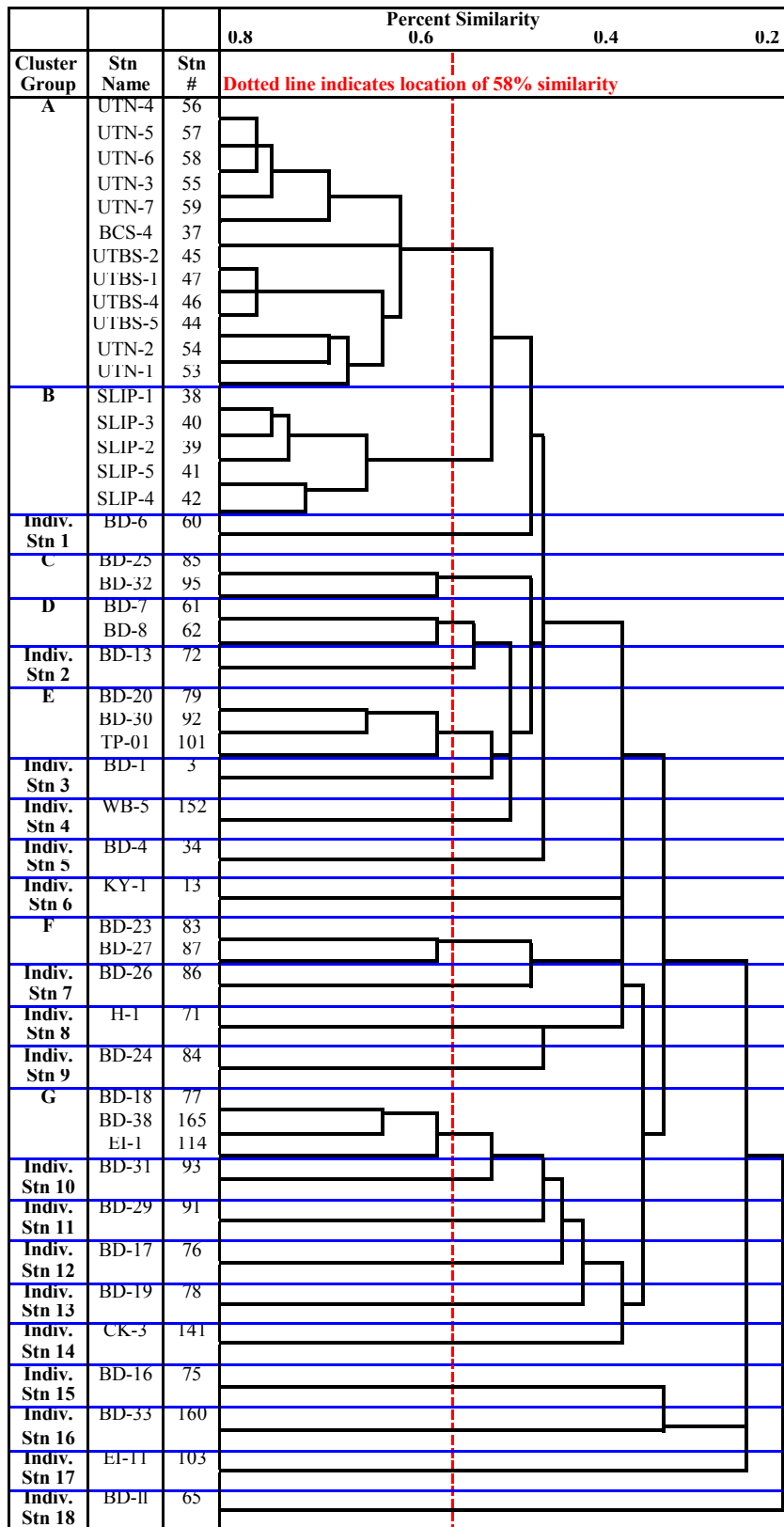
Cluster analysis

Forty-seven stations were grouped into 7 clusters (labeled A through G) and 18 individual stations at the 58% similarity level, based on hierarchical clustering of macroinfaunal abundance per square meter (Figure 11). Cluster similarity level was chosen based on regional oceanography and other environmental data parameters. The seven cluster groups are: (A) UTN and UTBS northern Bering Sea stations and southern Bering Sea BCS-4 (Figure 12b), (B) St. Lawrence Island Polynya (SLIP) stations (Figure 12b), (C) CA stations BD-25 and BD-32 (Figure 12d), (D) Near-shore Beaufort Sea BD-7 and BD-8 (Figure 12c), (E) CA stations BD-20, BD-30, and TP-01 (Figure 12d), (F) CA stations BD-23 and BD-27 (Figure 12d), and (G) CA stations BD-18 BD-38, and EI-1 (Figure 12d).

The stations that were classified as individually distinct at the 58% similarity level were (1) BD-6, (2) BD-13, (3) BD-1, (4) WB-5, (5) BD-4, (6) KY-1, (7) BD-26, (8) H-1, (9) BD-24, (10) BD-31, (11) BD-29, (12) BD-17, (13) BD-19, (14) CK-3, (15) BD-16, (16) BD-33, (17) EI-11, and (18) BD-11. These individual stations were excluded from further community composition analysis.

Cluster Group A is comprised of 12 stations, all occurring within the Bering and Chukchi Seas, consisting of the UTN group, the UTBS group, and the southern Bering BCS-4 (Figure 12b). It had a mean abundance of 4795.23 individuals m⁻², a mean diversity of H'=2.43, and a mean evenness of J=0.67 (Table 4). Total cluster abundance was dominated by amphipods (*Ampelisca sp.*, F. Haustoriidae, and F. Phoxocephalidae), and total cluster organic carbon biomass was dominated by bivalves (*Macoma calcare*

Figure 11. Cluster analysis grouped by macroinfaunal abundance. The red dotted line indicates 58% similarity level; the blue line indicates the separation of stations into clusters.



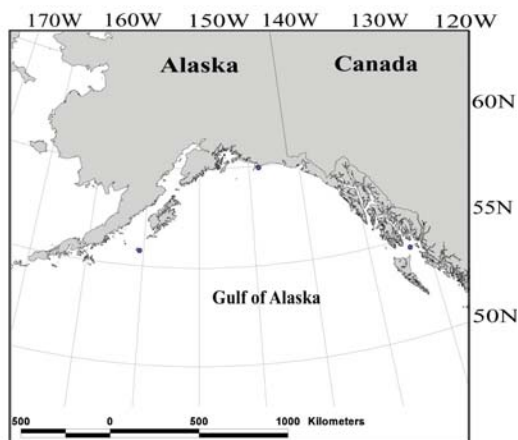


Figure 12a. Gulf of Alaska

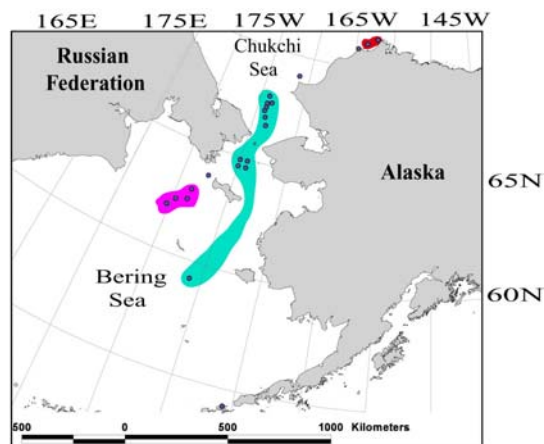


Figure 12b. Bering and Chukchi Seas

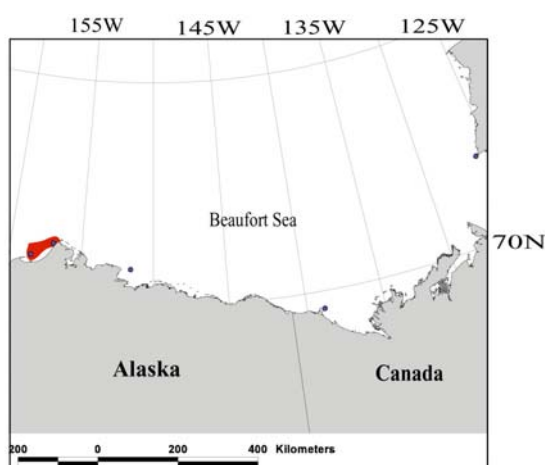


Figure 12c. Beaufort Sea

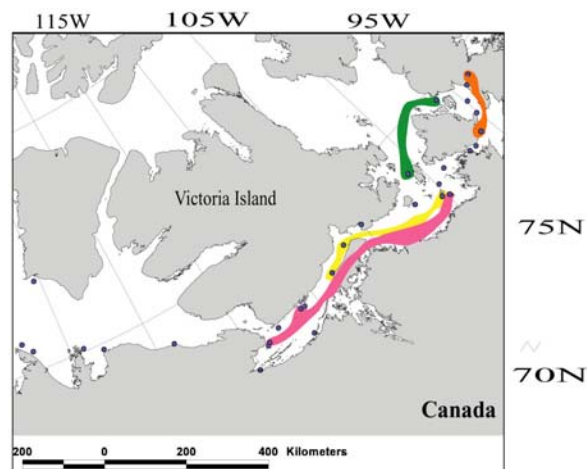


Figure 12d. Canadian Archipelago

Cluster group legend

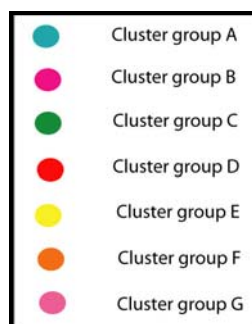


Figure 12. Locations of cluster groups based on abundance, for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA). Note: no cluster groups were observed in the GOA stations.

Table 4. Mean values for cluster group macroinfaunal parameters. Standard deviations are in parentheses. Negative signs (-) indicate standard deviation could not be computed because only one measurement was available.

Cluster Group	Station Name	Dominant taxa (no. indiv. m ⁻²)	Dominant taxa (gC m ⁻²)	Mean TOC (%)	Mean sed chl <i>a</i> (mg m ⁻²)	Mean C/N (wt./wt.)	Mean modal grain size (Ø)	Mean macro-infaunal abundance (no. indiv. m ⁻²)	Mean macro-infaunal biomass (gC m ⁻²)	Mean diversity (H')	Mean evenness (J)
A	UTN-4	<i>Ampelisca sp.</i>	<i>M. calcarea</i>	0.7 (0.4)	20.6 (5.2)	6.2 (0.5)	4.4 (0.8)	4795.2 (3387.9)	22.8 (14.8)	2.4(0.5)	0.7 (0.1)
	UTN-5	Haustoriidae	<i>N. belloti</i>								
	UTN-6	Phoxocephalidae	<i>Yoldia sp.</i>								
	UTN-3										
	UTN-7										
	BCS-4										
	UTBS-2										
	UTBS-1										
	UTBS-4										
	UTBS-5										
	UTN-2										
	UTN-1										
B	SLIP-1	<i>N. radiata</i>	<i>N. radiata</i>	1.0 (0.2)	19.5 (3.5)	6.3 (0.3)	5.0 (0)	2388.0 (1641.8)	27.6 (19.5)	2.4 (0.4)	0.7 (0.1)
	SLIP-3	<i>N. belloti</i>	<i>N. belloti</i>								
	SLIP-2	Maldanidae	Maldanidae								
	SLIP-5										
	SLIP-4										
C	BD-25	Sabellidae	Sabellidae	0.4 (0.2)	11.1 (9.3)	4.5 (0.1)	2.5 (3.5)	1453.8 (903.3)	9.1 (5.6)	2.9 (0.2)	0.8 (0.1)
	BD-32	Ostracoda Ophiuridae	<i>Yoldia sp.</i> Astartidae								

Table 4. Continued.

Cluster Group	Station Name	Dominant taxa (no. indiv. m ⁻²)	Dominant taxa (gC m ⁻²)	Mean TOC (%)	Mean sed chl <i>a</i> (mg m ⁻²)	Mean C/N (wt./wt.)	Mean modal grain size (ϕ)	Mean macro-infaunal abundance (no. indiv. m ⁻²)	Mean macro-infaunal biomass (gC m ⁻²)	Mean diversity (H')	Mean evenness (J)
D	BD-7 BD-8	Isaeidae <i>Byblis sp.</i> Foraminifera	<i>Byblis sp.</i> Anthozoa <i>Clinocardium sp.</i>	0.5 (0.2)	11.8 (1.2)	8.6 (2.5)	1.5 (2.1)	7728.9 (3876.5)	11.0 (6.8)	1.6 (0.6)	0.4 (0.1)
E	BD-20 BD-30 TP-1	Lampropidae Thyasiridae Astartidae	Astartidae <i>M. calcarea</i> Hiatellidae	0.6 (0)	9.5 (1.7)	5.9 (0.6)	4.7 (0.6)	4042.5 (1725.0)	19.6 (20.0)	2.7 (0.2)	0.7 (0)
F	BD-23 BD-27	Haustoriidae Lampropidae <i>P. arctica</i>	Astartidae <i>P. arctica</i> Rhynchocoela	0.8 (-)	10.1 (14.3)	5.8 (-)	5.0 (0)	1621.3 (1005.9)	3.0 (2.1)	2.1 (0.2)	0.6 (0)
G	BD-18 BD-38 EI-1	Thyasiridae <i>N. belloti</i> Oweniidae	Oweniidae Lumbrineridae Mytilidae	0.6 (0.2)	5.4 (6.0)	5.1 (0.5)	5.0 (0)	885.8 (246.6)	1.1 (0.3)	1.9 (0.3)	0.6 (0.1)

Nucula belloti, and *Yoldia sp.*) (Table 4).

Cluster Group B contained 5 stations, consisting of the SLIP group of stations (Figure 12b). The mean abundance of this cluster group was 2388 individuals m⁻², the mean diversity (H') was 2.42, and mean evenness (J) was 0.69. The mean diversity values for Clusters A and B are almost equal, differing by only 0.01; the evenness values differ only by 0.02. Total cluster abundance was dominated by bivalves (*Nuculana radiata* and *Nucula belloti*) and by polychaete worms (F. Maldanidae) (Table 4). Total cluster organic carbon biomass was dominated by the same organisms (Table 4).

Cluster Group C contained 2 stations (BD-25 and BD-32), both located in the CA (Figure 12d). The mean abundance for this cluster group was 2092.5 individuals m⁻², the mean diversity (H') was 2.87, and the mean evenness (J) was 0.77 (Table 4). This cluster exhibited the highest mean diversity value as well as the highest mean evenness value. Total cluster abundance was dominated by polychaete worms (F. Sabellidae), ostracods, and brittle stars (F. Ophiuridae) (Table 4). Total cluster organic carbon biomass was dominated by polychaete worms (F. Sabellidae), bivalves (*Yoldia sp.* and F. Astartidae) (Table 4).

Cluster Group D contained 2 stations (BD-7 and BD-8), both located in the Beaufort Sea (Figure 12c). The mean abundance for this cluster group was 7729 individuals m⁻², the mean diversity (H') was 1.55, and the mean evenness (J) was 0.40 (Table 4). This cluster exhibited the highest mean abundance value, and both the lowest mean diversity and evenness values. Total cluster abundance was dominated by amphipods (F. Isaeidae and *Byblis sp.*) and foraminifera (Table 4). Total cluster organic

carbon biomass was dominated by amphipods (*Byblis sp.*), sea anemones (Cl. Anthozoa), and bivalves (*Clinocardium sp.*) (Table 4).

Cluster Group E contained 3 stations (BD-20, BD-30, TP-01); all located in the Canadian Archipelago (Figure 12d). The mean abundance for this cluster group was 4043 individuals m^{-2} , the mean diversity (H') was 2.71, and the mean evenness (J) was 0.72 (Table 4). Total cluster abundance was dominated by cumaceans (F. Lampropidae) and bivalves (F. Thyasiridae and F. Astartidae) (Table 4). Total cluster organic carbon biomass was dominated by bivalves (F. Astartidae, *Macoma calcarea*, and F. Hiatellidae) (Table 4).

Cluster Group F contained 2 stations (BD-23 and BD-27), both located in the Canadian Archipelago (Figure 11d). The mean abundance for this cluster group was 1621 individuals m^{-2} , the mean diversity (H') was 2.05, and the mean evenness (J) was 0.64 (Table 4). Total cluster abundance was dominated by amphipods (F. Haustoriidae), cumaceans (F. Lampropidae), and bivalves (*Portlandia arctica*). Total cluster organic carbon biomass was dominated by bivalves (F. Astartidae and *Portlandia arctica*) and rhynchocoels (Table 4).

Cluster Group G contained 3 stations (BD-18, BD-38, and EI-1); all located in the Canadian Archipelago (Figure 12d). The mean abundance for this cluster group was 886 individuals m^{-2} , the mean diversity (H') was 1.89, and the mean evenness (J) was 0.58 (Table 4). This cluster had the lowest mean abundance value. Total cluster abundance was dominated by bivalves (F. Thyasiridae and *Nucula belloti*) and polychaete worms (F. Oweniidae) (Table 4). Total cluster organic carbon biomass was dominated by

polychaete worms (F. Oweniidae and F. Lumbrineridae), and bivalves (F. Mytilidae) (Table 4).

Sediment chlorophyll *a* content

Gulf of Alaska (GOA): Although 8 stations were occupied in the GOA, benthic collections were successful at only 3 because of glacial and current-scoured bed rock encountered. For soft bottom sediments, sediment chlorophyll *a* values ranged from 10.7 to 43.0 mg m⁻² (Figure 13a; see Appendix F for individual station sediment values).

Bering and Chukchi Seas: Sediment chlorophyll *a* concentrations ranged from 97-373 mg m⁻². The highest concentration occurred in the northern Bering Sea St. Lawrence Island Polynya region, and the lowest concentration occurred in the Bering Strait region (Figure 13b).

Beaufort Sea: Sediment chlorophyll *a* concentrations ranged from 28 to 257 mg m⁻². The highest concentration occurred to the east of Point Barrow, and the lowest concentration occurred near the Mackenzie River (Figure 13c).

Canadian Archipelago (CA): Sediment chlorophyll *a* showed a wide range of concentrations (0-500 mg m⁻²). The lowest concentrations occurred mostly in Coronation Gulf and at the western-most edge of Amundsen Gulf. Intermediate concentrations (50-150 mg m⁻²) were found near-shore islands and coastlines. The highest concentrations occurred in Queen Maud Gulf and St. Roch Basin (Figure 13d).

Stations from all four geographic localities combined: Along the entire cruise track, sediment chlorophyll *a* concentrations show the highest average value in the Bering and Chukchi Seas, decreasing in the Beaufort, and becoming highly variable in

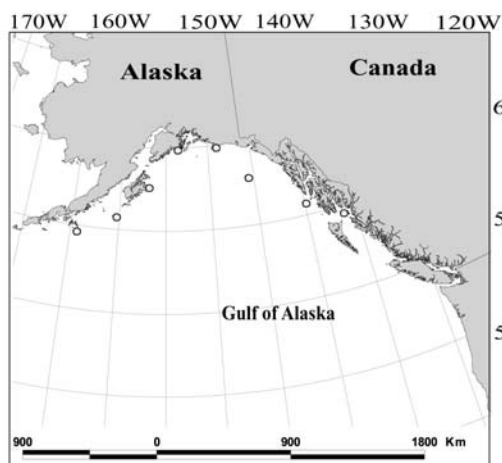


Figure 13a. Gulf of Alaska

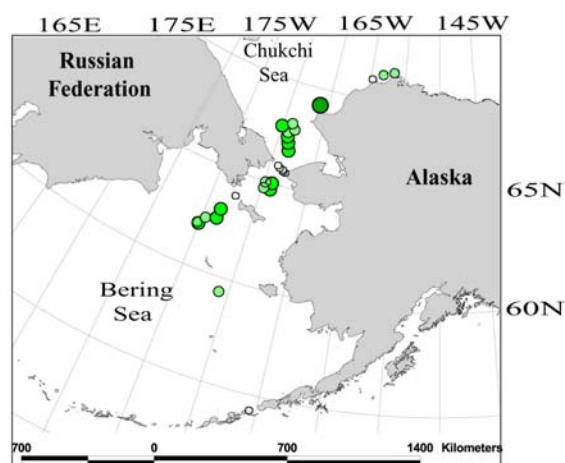


Figure 13b. Bering and Chukchi Seas

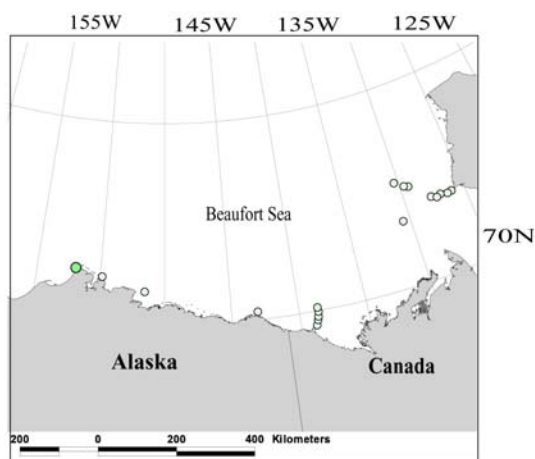


Figure 13c. Beaufort Sea

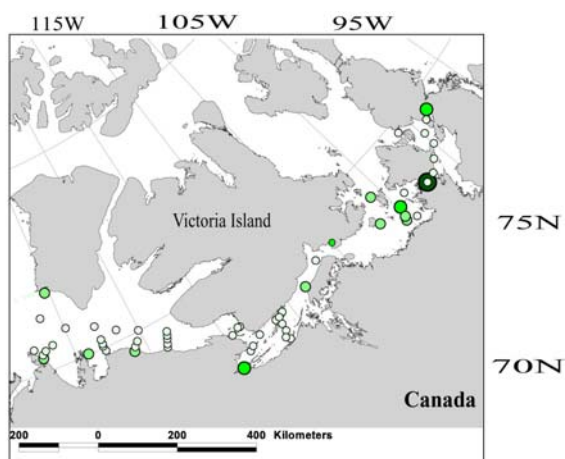


Figure 13d. Canadian Archipelago

Sediment chlorophyll *a* concentration legend

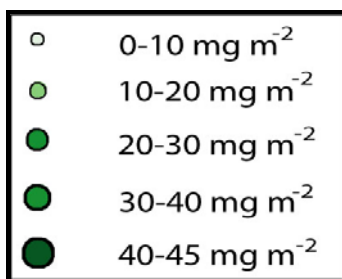


Figure 13. Sediment chlorophyll *a* concentrations for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

the Canadian Archipelago, where both the lowest (0.08 mg m⁻²; BD-23) and highest concentrations (394 mg m⁻²; BD-27) overall were found (see Table 5 for average values; see Appendix F for individual station sediment values).

Sediment TOC, C/N ratio, and modal grain size

Gulf of Alaska (GOA): Total organic carbon in surface sediments ranged from 0-1% (Figure 14a). The lowest of the three C/N ratios occurred at BD-1, which was in the Inside Passage (Figure 15a). A sediment modal grain size of $\phi \geq 5$ was found near-shore in the GOA, and a modal size of 3 ϕ was found south of Kodiak Island. Grain size overall was closely correlated with TOC content (Spearman's $\rho=0.352$, $p<0.005$, $n=62$; see Appendix I) and will not be illustrated on a separate map.

Table 5. Regional mean values for sediment parameters. Standard deviations are in parentheses.

Region	Mean sediment chlorophyll <i>a</i> (mg m ⁻²)	Mean modal grain size (ϕ)	Mean TOC (%)	Mean C/N (weight/weight)
Gulf of Alaska	27.16 (23.28)	4.00 (1.00)	0.46 (0.14)	8.59 (2.67)
Bering/Chukchi	219.89 (108.81)	4.42 (0.84)	0.78(0.38)	6.99 (2.05)
Beaufort	82.96 (99.50)	4.00 (1.92)	0.96 (0.60)	8.18 (1.32)
Canadian Archipelago	100.22 (107.93)	4.50 (1.38)	0.60 (0.26)	5.49 (1.32)

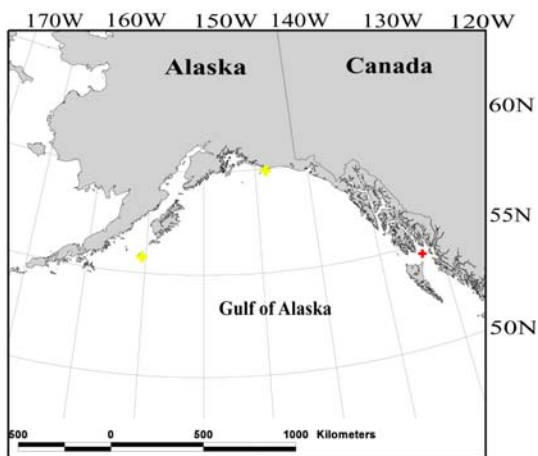


Figure 14a. Gulf of Alaska

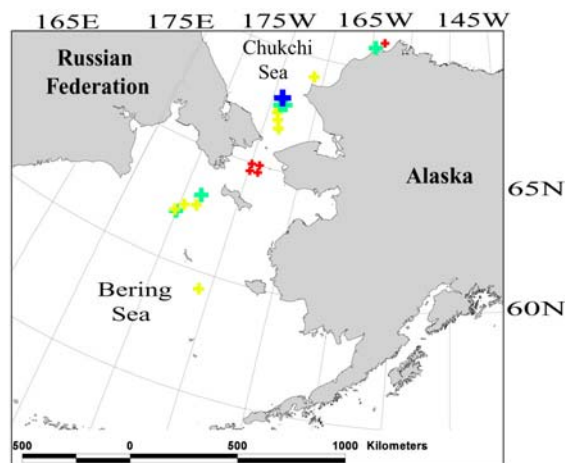


Figure 14b. Bering and Chukchi Seas

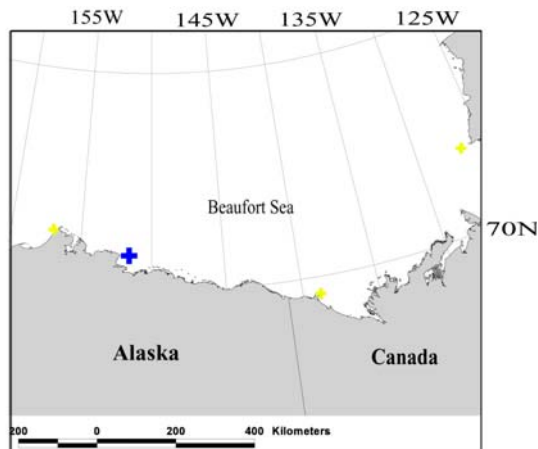


Figure 14c. Beaufort Sea

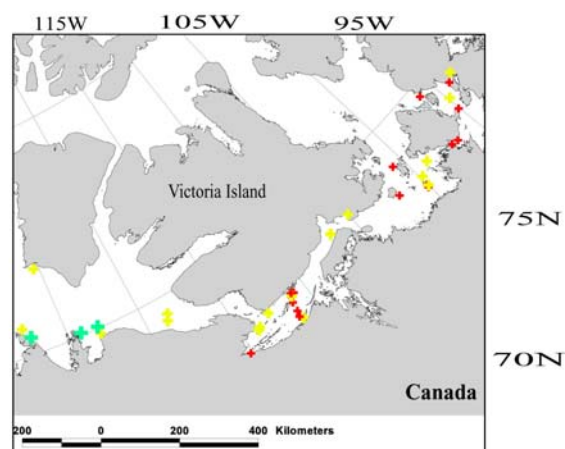


Figure 14d. Canadian Archipelago

**Sediment total organic carbon
content legend**

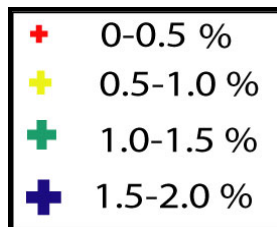


Figure 14. Sediment total organic carbon (TOC) content for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

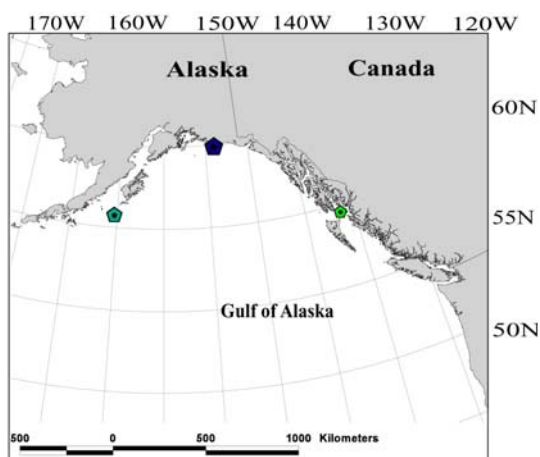


Figure 15a. Gulf of Alaska

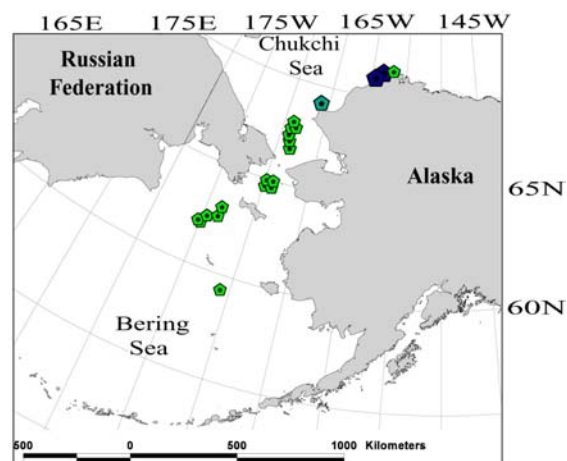


Figure 15b. Bering and Chukchi Sea

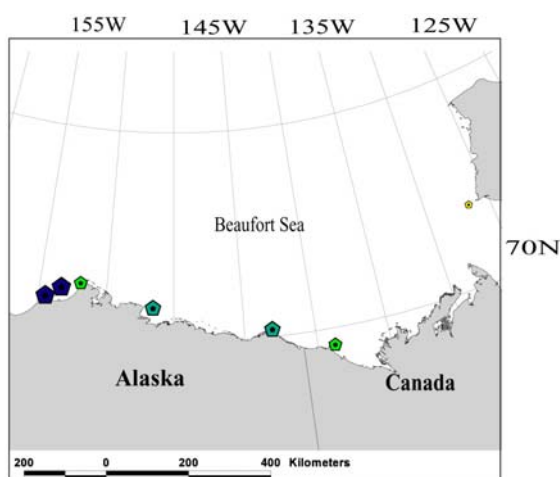


Figure 15c. Beaufort Sea

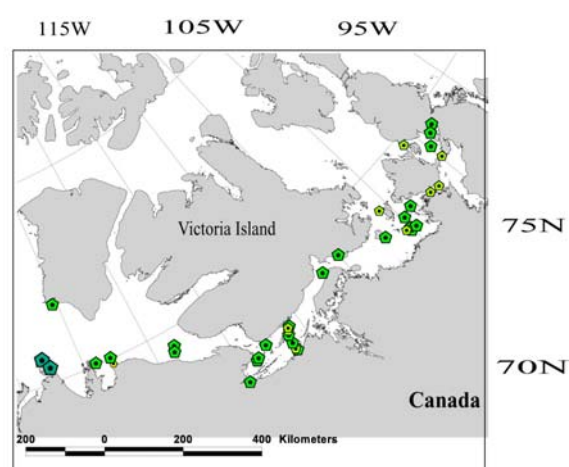


Figure 15d. Canadian Archipelago

Sediment C/N ratio legend

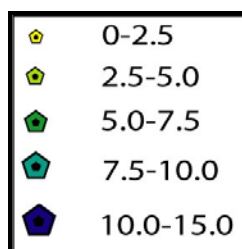


Figure 15. Sediment total organic carbon to total organic nitrogen ratios (weight/weight) for the four study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

Bering and Chukchi Seas: The four Bering Sea (UTBS) stations possessed the lowest TOC, ranging from 0.2-0.4 %. Other stations averaged 0.5-1, with the highest value (1.6 %) occurring in the southern Chukchi (Figure 14b). C/N ratios ranged from 5.1 to 9.7 wt./wt. The lowest ratio occurred in the southern Chukchi and the highest ratio occurred in the northernmost Chukchi Sea station (Figure 15b). Modal size was predominantly $\phi \geq 5$, with $\phi = 3$ and $\phi = 4$ occurring in the Bering Strait, and $\phi = 3$ again in the northernmost Chukchi station.

Beaufort Sea: Total organic carbon ranged from 0.3 to 1.9 %, with no discernable pattern between stations (Figure 14c). C/N ratios ranged from 7.3 to 13.9 wt./wt.; the lowest ratios occurring in the eastern region and the highest ratios occurring in the western region (Figure 15c). To the west of Point Barrow, stations had a modal size of ≥ 1 and 3. To the east of Point Barrow, all stations had a ϕ size of 5.

Canadian Archipelago (CA): Total organic carbon ranged from 0 to 1.5 % (Figure 14d). The lowest TOC occurred in the center of straits and gulfs. The highest values occurred near-shore in southern Amundsen Gulf. The majority of stations had C/N ratios between 5 and 7.5 wt./wt. (Figure 15d). The highest ratios (7.5-10 wt./wt.) occurred at the western-most edge of Amundsen Gulf. The lowest values (2.5-5 wt./wt.) occurred in Franklin Strait and St. Roch Basin. Modal size was predominantly $\phi 5$ (fine silt and clay). Smaller ϕ sizes occurred at stations in the centers of straits.

Stations from all four geographic localities combined: Mean surface sediment chlorophyll *a* concentrations were by far the highest in the Bering and Chukchi Seas, followed by the CA with about half of the Bering and Chukchi Sea concentration observed (Table 5). The Beaufort Sea had moderate mean sediment chlorophyll *a*

concentration (82.96 mg m^{-2}), and the GOA had the lowest sediment chlorophyll *a* mean concentration (27.16 mg m^{-2} ; Table 5). Total organic carbon appeared as minimum values in the Inside Passage, the Bering Strait, at Point Barrow, Coronation Gulf, and Queen Maud Gulf (Figure 14). Maximum mean total organic carbon occurred in the Beaufort Sea, followed by the Bering and Chukchi Seas (Table 5). The lowest mean TOC occurred in the Gulf of Alaska (Table 5). Mean C/N ratios range were highest in the GOA and Beaufort Sea. The Bering/Chukchi Seas had moderate mean C/N, and the lowest mean C/N ratio occurred in the CA (Table 5). Modal phi size 4 predominated throughout the cruise track (Table 5).

Statistical relationships between macroinfaunal and sediment tracer parameters

A Spearman's rho non-parametric test was used to examine correlations among parameters having a sample size <50 . This test assumes non-normal distribution of values and was used for relationships involving benthic, bottom water, and integrated water column parameters.

The GOA and Beaufort Sea regions did not contain an adequate number of benthic stations to be discussed in regional statistical analyses; however, their values are included in the overall statistical analysis.

Bering and Chukchi Seas: Sediment chlorophyll *a* concentration was significantly positively correlated with sediment TOC (Spearman's $\rho=0.491$, $p<0.033$, $n=19$; Figure 16). Bottom water salinity was significantly and positively correlated with integrated water column chlorophyll *a* concentration (Spearman's $\rho=0.742$, $p<0.0001$, $n=26$). Significant negative correlations were observed between bottom water

	Depth			Bot Sal			Bot Temp			Int Chl			Sed Chl			Abund.			Bio. gC			Modal			TOC			C/N			Diversity			Evenness		
	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O			
Depth																																				
Bot Sal	ns	+	+																																	
Bot Temp	-	ns	ns	ns	-	ns																														
Int Chl	ns	ns	+	+	ns	+	ns	ns	ns																											
Sed Chl	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	+																								
Abund.	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns																					
Bio. gC	ns	ns	ns	ns	ns	+	-	ns	ns	ns	ns	ns	ns	ns	+	ns	+	+																		
Modal	+	ns	+	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns																
TOC	ns	ns	ns	ns	+	+	ns	ns	ns	ns	ns	ns	+	ns	+	ns	ns	ns	ns	ns	ns	+	ns	+												
C/N	ns	ns	ns	-	ns	+	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	+	ns	ns	+	ns	+	ns	ns	+	+										
Diversity	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns						
Evenness	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	+	+	+					

Figure 16. Regional comparisons between macroinfaunal and sediment tracer statistical Spearman's rho relationships for Bering Sea and Chukchi Sea stations (BC), Canadian Archipelago stations (CA), and cruise stations combined overall (O). Please see List of Abbreviations and Definitions for parameters and units. Positive significant correlations are indicated by '+' in yellow and negative significant correlations are indicated by '-' in magenta. 'ns' indicates no significance.

temperature and macroinfaunal organic carbon biomass (Spearman's $\rho=-0.535$, $p<0.018$, $n=19$).

Canadian Archipelago (CA): Faunal abundance was significantly and positively correlated with organic carbon biomass (Spearman's $\rho=0.806$, $p<0.0001$, $n=32$; Figure 16).

Stations from all four geographical regions combined: Bottom water salinity showed significant positive correlations with integrated water column chlorophyll *a* concentration (Spearman's $\rho=0.378$, $p<0.0001$, $n=96$), surface sediment chlorophyll *a* content (Spearman's $\rho=0.397$, $p<0.002$, $n=56$), faunal abundance (Spearman's $\rho=0.412$, $p<0.002$, $n=53$), and macroinfaunal organic carbon biomass (Spearman's $\rho=0.488$, $p<0.0001$, $n=53$). Integrated water column chlorophyll *a* concentration and sediment chlorophyll *a* content were positively and significantly correlated (Spearman's $\rho=0.290$, $p<0.028$, $n=57$); and surface sediment chlorophyll *a* concentration showed positive and significant correlations with macroinfaunal organic carbon biomass (Spearman's $\rho=0.390$, $p<0.003$, $n=55$). Macroinfaunal abundance was correlated positively and significantly with macroinfaunal organic carbon biomass (Spearman's $\rho=0.802$, $p<0.0001$, $n=59$) as well as with sediment C/N ratio (Spearman's $\rho=0.355$, $p<0.009$, $n=53$). Significant positive correlations were also observed between macroinfaunal organic carbon biomass and both sediment C/N ratio (Spearman's $\rho=0.273$, $p<0.048$, $n=53$; Figure 16) and species diversity (Spearman's $\rho=0.404$, $p<0.001$, $n=46$; Figure 16).

A significant negative correlation was observed between faunal abundance and sediment grain modal size (Spearman's $\rho=-0.262$, $p<0.049$, $n=57$; Figure 16).

Discussion

The diversity of macroinfaunal communities within each of the 4 study regions did not show significant correlations ($P < 0.05$) with any of the sediment or hydrographic parameters. However, this result may reflect small sample size, because when the stations from the entire cruise track were combined, a significant positive Spearman's ρ non-parametric correlation were observed between macroinfaunal diversity and macroinfaunal carbon biomass, and also between macroinfaunal diversity and the sediment C/N ratio. This indicates that greater macroinfaunal biomass may be associated with larger numbers of species types. It also indicates that the quality of available carbon, measured by the C/N ratio, is also important to the number of species that can survive within a given area.

Similarity cluster analysis indicates seven groupings of stations that clustered in ways that may be related to current flow. This current flow is important in carrying advected carbon sources and controlling sediment deposition (and grain size) patterns, which have been stated previously as important determinants of where different species may survive.

The patterns of sediment variables (sediment chlorophyll *a* content, TOC, C/N, sediment modal grain size) ranged widely among the four study regions. The GOA showed the lowest mean among surface sediment chlorophyll *a* concentration, the lowest mean TOC, the highest mean C/N ratios, the highest mean macroinfaunal abundances, the lowest species evenness, the second to lowest species diversity, and a low mean total organic biomass, similar to that observed in the CA region (6.87 gC m^{-2}) (Tables 4 and 5). An elevated benthic biomass at KY-1 (Kayak Island) is consistent with the previous

findings that a gyre in the vicinity of Kayak Island has a productive influence on the benthos (Jewett and Feder, 1986). Low sediment chlorophyll *a* concentration and low sediment TOC indicate a reduced availability of carbon as compared to the other study regions. This may be due to swift bottom currents. Low sediment chlorophyll *a* concentration may also be the result of warmer water temperatures which allow increased pelagic zooplankton grazing activity (Feder and Jewett, 1986). Higher sediment C/N ratios indicate a poorer food quality either from terrigenous material accumulating in sediments or greater degradation rates of carbon descending to the benthos (Gray, 1981; Grebmeier et al., 1989).

By comparison, the Bering and Chukchi Seas exhibited the highest mean sediment chlorophyll *a* content, the second highest sediment TOC, the second lowest C/N ratio, the highest total benthic carbon biomass, the second highest benthic abundance, the highest benthic species diversity, and the second highest benthic species evenness (Tables 4 and 5). These high sediment chlorophyll *a*, macroinfaunal organic carbon biomass, and diversity values are consistent with maxima previously reported (Stoker, 1978; Grebmeier, 1987; Grebmeier et al., 1989; Grebmeier and Cooper, in press). Low sediment C/N ratios and high sediment TOC indicate food of high quality is reaching the sediments (Gray, 1981; Grebmeier et al., 1989).

The Beaufort Sea stations had the second lowest mean sediment chlorophyll *a* content, the highest mean sediment TOC content, the second highest mean C/N ratio, the second lowest mean macroinfaunal abundance, the lowest mean benthic carbon biomass, the lowest mean species diversity, and the second lowest mean species evenness (Tables 4 and 5). High total organic carbon values may result from advection of carbon from

BSAW water (Feder et al., 1996; Dunton et al., 2002), or from fluvial output (Carmack and Macdonald, 2002). High mean sediment C/N ratios indicate a poor quality food source accumulating in the sediments, and ratios of 8-12 may indicate terrestrial sediment run-off (Grebmeier et al., 1987 and references therein). The lowest total benthic carbon biomass and lowest benthic species diversity may be a consequence of seasonal ice scouring, which has been estimated to rework coastal Beaufort Sea sediment down to a depth 20 centimeters approximately every fifty years (Reimnitz et al., 1987).

The CA exhibited the second highest mean chlorophyll *a* concentrations (although only half of the Bering/Chukchi Sea mean value), the second lowest mean sediment TOC content, the lowest mean sediment C/N ratio, the lowest mean macroinfaunal abundance, mean total organic carbon biomass equivalent to the GOA, the second highest mean species diversity, and the highest mean species evenness (Tables 4 and 5). The high surface sediment chlorophyll *a* concentrations and low sediment C/N ratios indicate high quality food reaching the benthos. The high variation of most parameters within the CA is consistent with the Grebmeier et al. (1995) description of the CA as a mosaic of varying interactions.

When all geographical regions are combined for statistical analysis, benthic carbon biomass is significantly correlated with bottom salinity, integrated water column chlorophyll *a* concentration, surface sediment chlorophyll *a* concentration, and sediment C/N ratio. Differences observed among the statistical relationships of Bering Sea/Chukchi Sea station parameters and CA station parameters (i.e. significant correlations among several parameters (surface sediment chlorophyll *a* concentration and sediment TOC; bottom water chlorophyll *a* concentration and sediment C/N; integrated

water column chlorophyll *a* concentration and sediment C/N) were observed in the Bering/Chukchi Seas. By comparison there were no significant relationships among these parameters in the CA (Figure 16), which likely indicates varying primary production and deposition to the benthos between these two systems.

Sediment parameters, including modal grain size, C/N ratios, and chlorophyll *a* content, have been established previously as tracers of macroinfaunal organic carbon in the system (Gray, 1981 and references therein; Grebmeier, 1987), as discussed earlier. These measurements differ in the magnitude of their relationships based on geographical areas (this study). In addition to these sediment tracer/macroinfaunal biomass relationships, an overall significant positive relationship between species diversity and macroinfaunal organic carbon biomass (Spearman's $\rho=0.404$, $p<0.005$, $n=46$) and between species diversity and sediment C/N ratio (Spearman's $\rho=0.440$ $p<0.048$, $n=45$) should be emphasized (this study).

Possible alterations in oceanic circulation and water mass characteristics resulting from projected global warming could have far-reaching consequences for benthic macroinfaunal communities. Increased water temperatures could alter regional salinity and density parameters, and changes in the corresponding current flow could alter sediment grain size distribution and organic matter deposition patterns. A result would be altering regional benthic community diversities because of species variation in habitat requirements. Since many of these benthic species not only differ in their functional groups, but also in their organic carbon content (see Grebmeier, 1987 for benthic Arctic macroinfaunal feeding strategies and carbon conversions), changes in macroinfaunal

diversity could also alter the benthic carbon food source available to higher trophic levels that depend on these benthic communities.

Chapter summary

The GOA stations had the lowest mean surface sediment chlorophyll *a* concentrations, followed by the Beaufort Sea, and the Canadian Archipelago (Table 6). The Bering and Chukchi Sea stations had the highest mean surface sediment chlorophyll *a* concentrations (Table 6). This reflects previously determined patterns of high productivity in the Bering and Chukchi Seas, highly variable productivity in the CA, and low productivity in the freshwater-influenced near-shore GOA and Beaufort Sea.

The CA had the lowest C/N ratios, followed by the Bering and Chukchi Sea stations, then the Beaufort Sea, and lastly, the GOA stations had the highest C/N ratios (Table 6). This indicates that the carbon supply is of poorest nutritive quality in the GOA and the Beaufort Sea, and of higher quality in the Bering and Chukchi Seas and in the CA.

Table 6. A comparison of mean sediment tracer parameter values between study regions.

Region	Mean sediment chlorophyll <i>a</i> (mg m ⁻²)	Mean modal grain size (Ø)	Mean TOC (%)	Mean C/N (weight/weight)
Gulf of Alaska	Lowest	4	Lowest	Highest
Bering/Chukchi	Highest	4	Moderate	Moderate
Beaufort	Moderate	4	Highest	Highest
Canadian Archipelago	Moderate	4	Low	Low

The GOA had the lowest TOC, followed, in ascending order, by the CA, the Bering/Chukchi, and the Beaufort Sea stations, which had the highest TOC (Table 6). This may have indicated recent deposition of ice algae in the Beaufort Sea area after summer ice melt. The quantity of this material may remain low (reflected in low sediment chlorophyll *a* values) because it is quickly consumed by biota or advected out of the area.

Sediment modal grain size was silt and clay near-shore in the GOA, with very fine sand present farther offshore and into the Bering and Chukchi Seas. Very coarse sand and gravel was present in the western Beaufort Sea and in the middle of straits in the CA; the eastern Beaufort Sea and near-shore CA stations had clay and silt. These patterns are consistent with previously established current flow patterns that would influence sediment characteristics.

Throughout all of the study regions, bivalves dominated in areas of high clay and silt or fine sand, sand dollars and amphipods dominated in areas of fine sand; polychaetes dominated in stations of both high clay and silt or fine sand. The families of polychaetes and amphipods appeared universally throughout the study regions, however, dominance of bivalves shifted from *Macoma calcaria*, *Nuculana radiata*, and *Nucula belloti* in the southern stations (GOA and Bering/Chukchi) to F. Mytilidae and F. Astartidae in more northern stations (CA). It is of interest to note that isopods were dominant in the Beaufort Sea and not elsewhere, as was silicious sponge in the most northeastern CA station. This could be due to these animals having limits to colder temperatures in the northeastern CA than for animals found in the more southern stations.

The Beaufort Sea stations had the lowest average species diversity, followed by the GOA stations, the CA stations, and lastly, the Bering and Chukchi Sea stations which possessed the highest average species diversity (Table 7). This is consistent with previously known patterns of high biomass in the Bering and Chukchi Sea maxima, while the heterogeneous CA probably supports high levels of diversity because of many available environmental niches. Higher levels of diversity may support higher levels of biomass because of functional group redundancy and compensatory growth (Naeem and Li, 1997). Increases in community diversity have also been observed in other environments to increase community stability and increase production (Tilman, 1996; Naeem and Li, 1997). An increase in macroinfaunal production and growth could explain higher levels of biomass. The Beaufort Sea is known to have low diversity because of its seasonal exposure to ice scour, and the GOA's high current regime may also scour sediment from the benthos, preventing high levels of diversity to persist.

Table 7. A comparison of mean macroinfaunal parameter values between study regions.

Region	Mean macroinfaunal abundance (no. individuals m⁻²)	Mean macroinfaunal biomass (g carbon m⁻²)	Mean community diversity (H')	Mean community evenness (J)
Gulf of Alaska	Highest	Low	Low	Moderate
Bering/Chukchi	High	Highest	Highest	High
Beaufort	High	Lowest	Lowest	Lowest
Canadian Archipelago	Lowest	Low	High	Highest

IV. BACTERIAL AND VIRAL ABUNDANCES AND DISTRIBUTION

Introduction

The study of bacterial and viral abundances aids in the understanding of macroinfaunal community diversity because of their recognized contributions to carbon cycling dynamics. Carbon cycling is vital to the macroinfaunal communities that depend on the quantity, quality, and the availability of carbon supplied from surface production as their primary food source. If bacteria do not recycle detritus into bioavailable nutrients, these nutrients cannot be re-used within the food web. In addition, many deposit-feeding and filter-feeding organisms can utilize bacteria as a food source directly. Because of this, the abundance of bacteria (and the viral abundance that is thought to control bacterial abundance) is of interest when attempting to elucidate relationships between microbial communities and macroinfaunal communities. The diversities of microbial and viral communities are beyond the scope of this study, and only their abundances will be used as a relative measure of their contribution (functioning both as nutrition and as nutrient processors) to the regional carbon supply. Pelagic bacterial and viral abundances will be discussed in terms of particles L^{-1} , and also in integrated water column measurements of particles m^{-2} to indicate the estimated amount of bacteria and viruses in the overlying water column (and therefore the abundance of possible competitors for the carbon supply settling down to the bottom). Sediment bacterial and viral abundances will be discussed in terms of particles g^{-1} of dry sediment. These abundances include pore water abundance as well.

The influence of bacteria on mineral nutrient availability has been well documented since the observation of the importance of this process in the early 1970's

(Pomeroy, 1974). Bacterial importance was further highlighted in Azam et al.'s (1983) work, which illustrated the microbial loop concept, highlighting the interactions of bacteria with phytoplankton and flagellates as important pathways of nutrient availability in marine systems. (Figure 17). The dissolved organic matter (DOM) released from phytoplankton blooms can serve as a carbon source for heterotrophic bacteria, which in turn can be consumed by predatory ciliates and flagellates that act as controlling factors of water-column bacterial abundances (Azam et al., 1983; Bernard and Fenchel, 1995). Up to 70% of the total marine biotic carbon pool is made up of photic zone heterotrophic bacteria populations (Fuhrman et al., 1989). Wilhelm and Suttle (1999) estimated that this percentage could increase to as much as 90% of marine biotic carbon biomass if autotrophic bacteria are also included in the calculations. This percentage reflects the extremely large pool of stored energy potentially available for microbial grazers.

Data has demonstrated significant correlations between bacterial and viral abundance (Rinta-Kanto, 2001), bacterial abundance and primary production (Van Es and Meyer-Reil, 1982), as well as a relationship between bacterial growth rates and diurnal cycles in the marine photic zone (Azam et al., 1983). However, in the polar environment, where ice pack-related seasonal phytoplankton blooms and periods of continuous daylight and darkness affect primary production rates, these relationships that are observed in temperate climates may not hold constant with polar seasonal microbial dynamics. The understanding of these potential seasonal differences in microbial carbon processing. Future studies could contribute to the further understanding of microbial dynamics and their role in biogeochemical cycling on a comparative ecosystem level.

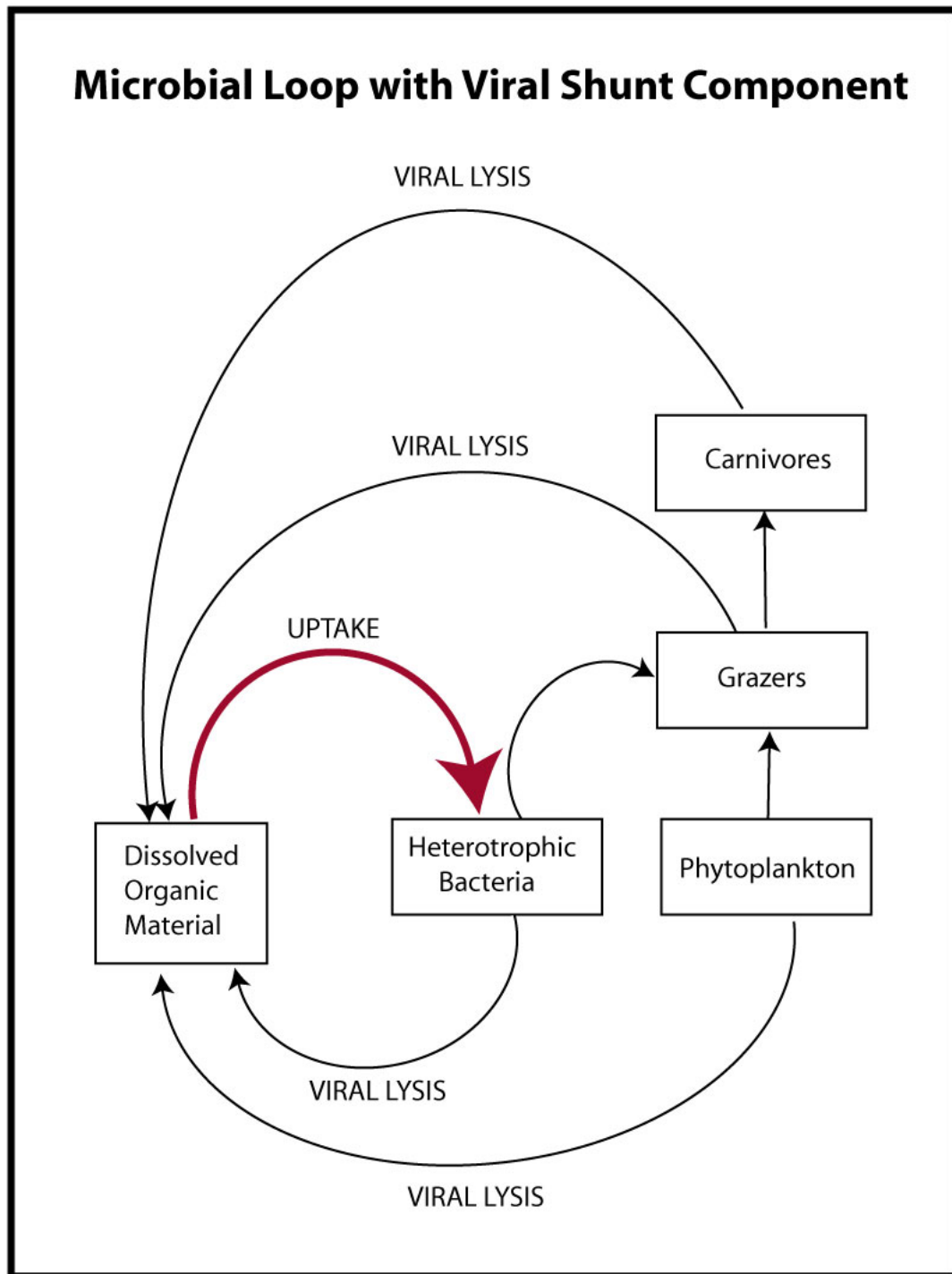


Figure 17. An illustration of the microbial loop including the viral shunt component, modified from Wilhelm and Suttle (1999).

Until the 1980's, it was thought that since temperature acts as a major limiting factor in many marine microbial metabolism processes and growth rates (Eppley, 1972), polar environments may not have extensive microbial life (Bano and Holligbaugh, 2000). However, recent studies have shown that Arctic microbial communities exhibit high production rates and abundances, suggesting that temperature may in fact not be entirely limiting (Horriggan, 1981; Maranger et al., 1994; Voytek and Ward, 1995). These polar microbial communities, if dominated by psychrotolerant bacteria rather than psychrophiles, would function at suboptimal temperatures for growth and assimilation, showing decreased DOC assimilation efficiency as compared to temperate microbial communities (Pomeroy and Wiebe, 2001 and references therein). Pelagic psychrotolerant and psychrophilic microbial communities are coupled with the overlying seasonal ice cover.

Notably, portions of the water column viral and bacterial communities near the ice-water interface become entrained annually within ice pack brine pockets and veins during winter, and are released back into the water column during summer to reseed the ocean water column populations (Deming, 2002 and references contained therein). Therefore, a reduction in ice pack cover from the effects of global warming could affect arctic viral and bacterial populations by reducing the surface area available for microbial refuge, conceivably resulting in alterations to microbial biogeochemical cycling regimes.

Over the past decade it has been demonstrated that viruses can cause a significant proportion of bacterial mortality in marine systems (Wilhelm and Suttle, 1999). This mortality can be an important factor affecting microbial community composition, nutrient cycling, and mineralization rates (Weinbauer and Suttle, 1997; Fuhrman, 1999). By

inducing the mortality of bacteria, viral activity directly impacts the availability of carbon to microbial grazers by reducing bacterial abundances (Wilhelm and Suttle, 1999). However, Proctor and Fuhrman (1992) observed that the bacterial mortality due to viruses actually increased overall bacterial production rates by releasing materials into the water that could be used for growth. This release of dissolved organic matter and nutrients from within the ruptured cells back into the water column has been shown to increase bacterial growth in many different aquatic systems (Middelboe et al., 1996; Gobler et al., 1997; Noble et al., 1999; Middelboe and Lyck, 2002). Wilhelm and Suttle (1999) further specify the importance of iron, nitrogen and phosphorus releases for these increased production rates of phytoplankton. Wilhelm and Suttle have estimated that viral lysis is responsible for the release of between 6 and 26 percent of fixed organic carbon back to the dissolved organic material pool in their “viral shunt” model (Wilhelm and Suttle, 1999; Figure 17). It is expected from these observations that an increase in bacterial abundance can result in an increase in viral abundance, but not necessarily vice versa.

It is thought that viruses may act as a top-down (predator-driven) control on bacterial growth (Middelboe and Lyck, 2002). This viral top-down control may serve to limit bacterial community composition by host-specific infectivity (Wommack and Colwell, 2000) and increased bacterial respiration (Middelboe et al., 1996). A reduced amount of organic matter is available to higher trophic levels because it recycles within the bacterial cell size class (Fuhrman, 1999). Viruses are susceptible to UV-damage (Weinbauer et al., 1999) and decreases in salinity (Wommack and Colwell, 2000). Decreased ice cover would allow increased UV-light penetration as well as result in

decreased salinity levels due to ice melt, which could have impacts on viral mortality, and subsequent impacts on global bacterial community dynamics and nutrient cycling.

Initial viral studies utilizing transmission electron microscopy (TEM) observed surface marine water concentrations ranging from 10^5 to 10^8 virus-like particles (VLP) per milliliter (Bergh et al., 1989; Borsheim et al., 1990; Proctor and Fuhrman, 1990). As enumeration protocols continue to improve, it has been suggested that these TEM numbers may be significant underestimates (Weinbauer and Suttle, 1997). In all cases, these viral abundances are defined as numbers of VLP because of the possibility that other stain-susceptible particles in natural seawater samples cannot be differentiated from viruses. Nagata and Kirchman (1992) suggested that these particles might include flagellate-produced particles of stainable DNA bound by membranes, formed during bacterial grazing. Weinbauer and Suttle (1997) argue that this possible overestimate is unlikely to be significantly different, because TEM methods have not observed large numbers of non-viral particles that interfere in VLP counts.

An increasing interest in bacterial and viral dynamics has led to an improved understanding of bacterial production, growth, and abundances in polar regions (Maranger et al., 1994; Steward et al., 1996; Rowe et al., 1997; Pomeroy and Wiebe, 2001 and references therein; Davidson and Belbin, 2002; Lovejoy et al., 2002; Thingstad et al., 2002; Vaque et al., 2002). However, in spite of an increased understanding of both water column and benthic bacterial populations in the Arctic, the number of Arctic water column viral studies remains scarce (Maranger et al., 1994; Steward et al., 1996). At the present time, only one study reports arctic sediment viral abundance, and that enumeration resulted from only one pore water sediment sample (Steward et al., 1996).

The available work has revealed a large abundance of microbes living in what were previously considered as inhabitable conditions. Psychrophilic or psychrotolerant bacteria are capable of surviving in subzero conditions, maintaining considerable numbers within ice formations (Skidmore et al., 2000; Deming, 2002 and references therein). Psychrophiles have been shown to sustain replication and respiration rates comparable to temperate populations (Pomeroy and Wiebe, 2001), and serve as theoretical models for exobiology (Deming, 2002). The contribution of these ice and sediment entrained bacteria and viruses to water column abundances remains currently unquantified.

Water column abundances and distribution

Bano and Holligbaugh (2000) show evidence of a highly diverse community of ammonia-oxidizing bacteria in the western Arctic Ocean, influenced by nutrient-rich Bering and Chukchi Sea waters. Maximum abundance of these ammonia-oxidizers occurred at the pycnocline, suggesting vertical stratification, possibly due to an accumulation of organic matter in this region that could cause an elevation of decomposition rates, thus sustaining higher abundances of nitrifiers. Bacterial surface abundances may also be limited by UV damage (Bano and Holligbaugh, 2000; Davidson and Belbin, 2002) or by competition for nutrient uptake with shallow water phytoplankton and ice algal populations (Bano and Holligbaugh, 2000). Water column bacterial abundances ranged from 10^8 to 10^9 bacteria-like particles (BLP) L^{-1} in the Bering and

Chukchi Seas (Steward et al., 1996) and from 1.5×10^6 BLP L⁻¹ in early spring to 1×10^8 BLP L⁻¹ in late spring in the High Arctic (Maranger et al., 1994).

The polar sea pack ice cover is an extensive area of habitat for many microfaunal organisms in both the Arctic and the Antarctic (Helmke and Weyland, 1995). These organisms have been observed within pockets of brine that permeate the ice pack, and may include protozoans, flagellates, bacteria, diatoms (Helmke and Weyland, 1995) and viruses (Maranger et al., 1994). Bacteria have also been observed within the solid ice matrix (Helmke and Weyland, 1995). These flora and fauna must be tolerant of large changes in salinity, and consequently large changes in osmotic pressure, during seasonal periods of ice melt and formation (Helmke and Weyland, 1995; Deming, 2002). Most polar studies have demonstrated a relatively uniform vertical but horizontally patchy distribution of bacteria in midwinter, reaching a maximum abundance within the bottom ice edge in some studies (Helmke and Weyland, 1995; Maranger et al., 1994), but not in others Gradinger and Zhang (1997). Marginal ice zone bacterial abundances far surpassed young ice bacterial abundances, with the greatest microbial abundances within ice observed in older ice formations (Helmke and Weyland, 1995). Viral abundance in ice was also observed to be 10 to 100 fold higher than in the underlying water column, coincident with some of the highest virus to bacteria ratios (VBR) reported from natural samples (Maranger et al., 1994). Underlying water column abundances averaged 1.1×10^7 VLP L⁻¹ in the High Arctic (Maranger et al., 1994), and 10^9 - 10^{10} VLP L⁻¹ in open water of the Bering and Chukchi Seas (Steward et al., 1996).

Sediment bacterial and viral abundances and distribution

It has long been understood that the organic matter content of sediments, as well as the size of the particles that comprise the sediment, appear to affect microbial abundances more than depth or latitude (ZoBell, 1942). The relationships between sediment traits and bacterial populations are complex, and it remains somewhat unclear whether bacterial abundance controls sediment surface area through mucus-sediment grain agglutination, or whether sediment surface area controls bacterial abundances (DeFlaun and Mayer, 1983).

Helmke and Weyland (1991) separated psychrophilic bacterial communities taxonomically in sea ice, and in the underlying water column and in Antarctic sediments. This may be evidence of heterogeneous habitat optimization by various temperature-adapted bacterial assemblages. Bacteria may also create their own distinct habitat for other organisms to colonize. Bernard and Fenchel (1995) described shallow-water sediment bacterial mats containing meiofauna, macroinfauna, and protozoan grazers (ciliates, flagellates, and amoebae). The bacteria composing these mats were determined to be an important food web base, due to their association with oxygen consumption, although the process of species succession within these sedimentary mats remains largely unknown.

Surface sediment viral abundances range from approximately 10 to 1000 times greater than water column abundances (Maranger and Bird, 1996; Steward et al., 1996; Danovaro and Serresi, 2000, Hewson et al., 2001b). These viruses may be bacteriophages (Fuhrman 1999; Wommack and Colwell, 2000; Pomeroy and Wiebe, 2001) or infect benthic microalgae (Suttle et al., 1991; Hewson et al., 2001a). The large

numbers of these viruses indicate the possibility of their “potential to play a significant role in benthic microbial communities” (Hewson et al., 2001a).

Materials and methods

Bacterial enumeration

Water column: A 50 ml sample of seawater was collected at each of the designated depths into sterile polypropylene centrifuge tubes and preserved with a final concentration of 2.5% glutaraldehyde. Samples were stored in the dark at 4°C for processing after the cruise. Duplicates for each depth were processed and individually filtered through 0.2 µm pore-size, 25 mm diameter black polycarbonate (Millipore ®) filters after being stained with Acridine Orange (Hobbie et al., 1977). A Leica ® DMRXA epifluorescent microscope equipped with a blue light filter (ex_{λ} =450-490 nm; em_{λ} =510 nm; suppression filter $_{\lambda}$ =510 nm) was used to enumerate up to twenty ocular grids or 200 bacterial-like particles for each sample. Counts were converted to cells L⁻¹ values using filter grid area conversion values.

Sediment: Two cubic centimeters of sediment were obtained using a modified syringe as described previously for sediment chlorophyll, and placed into a sterile polypropylene centrifuge tube. The sediment aliquot was preserved using 2.5% glutaraldehyde (final concentration) in 3 ml of sterile water. Samples were sealed and stored in the dark at 4°C. Duplicates of each sediment plug were processed for each station using techniques modified from Danovaro et al. (2001). MilliQ water (4 ml) and 1.0 ml of sodium pyrophosphate solution (10-mM final concentration) were added to

each sediment sample and incubated for fifteen minutes at 4°C before shaking manually for one minute. After manually shaking, the sediment-containing centrifuge tube was placed in a sonic bath for 3 minutes. Although Danovaro et al. (2001) centrifuged for only 1 minute after sonication was enough to reduce the suspended particle load, silty sediments from the majority of stations required up to 5 minutes of centrifuging to reduce suspended particle concentration in the supernatant (from opaque to translucent liquid) before filtering 0.25 µL aliquots of the supernatant (containing cells released from pore water and sediment particles) through a 0.02 µm-pore-size Anodisc filter (Whatman ®) and staining with SYBR Green I (Noble and Fuhrman, 1998). Epifluorescent microscopy was used to enumerate twenty field view grids or 200 bacteria-like particles. Due to heavy concentrations of cells in these sediments, a minimum of ten fields was always counted, even if the 200-cell count was reached at a lower number. Cell counts were normalized to volume (cells L⁻¹) using predetermined conversion values. Sediment samples were dried and weighed after the cruise to determine bacterial per dry weight of sediment.

Virus-like particle enumeration

Water column: Replicates for each station depth were processed from the seawater samples collected and preserved for bacterial counts. Seawater (0.25 µL aliquots diluted in 775 µL of MilliQ water) was filtered through 0.02-µm nominal pore-size Anodisc filters and stained with SYBR Green I (Noble and Fuhrman, 1998). Epifluorescent microscopy was then used to enumerate twenty fields of view or 200

virus-like particles. Counts were again converted into VLP L⁻¹ using predetermined conversion values.

Sediment: Replicates for each sediment sample were processed from the sediment samples collected and preserved for sediment bacterial enumeration (described in the previous section). Supernatant (0.25 µL aliquots diluted in 775 µL of MilliQ water) were filtered and stained with SYBR Green I using previously described methods for sediment processing and enumeration. These counts were then converted into VLP L⁻¹ values using predetermined filter grid area conversion values. Sediment samples were dried and weighed after the cruise for the determination of per gram of sediment VLP values.

Results

Water column bacterial and virus-like particle abundances

Gulf of Alaska (GOA): All stations exhibited a surface water bacterial abundance [bacterial-like particles (BLP)] ranging from 1.4×10^8 to 5.1×10^8 BLP L⁻¹ (Figure 18a). Bottom water BLP abundance ranged from 7×10^7 to 3×10^8 BLP L⁻¹ (Figure 19a; see Appendix J for individual station bacterial and viral measurements). Surface water VLP abundance ranged from 1.9×10^9 to 2.3×10^{11} VLP L⁻¹ (Figure 20a). The highest abundance of bottom water VLP was found near Kodiak Island (5.4×10^6 VLP L⁻¹) and the lowest abundance (1.9×10^9 VLP L⁻¹) was found near-shore Kayak Island (Figure 21a). Mean bottom water viral and bacterial abundances were higher than the Beaufort Sea and CA, but lower than the Bering/Chukchi Seas (Table 8). Significant positive Spearman's rho correlations (used for $n < 50$) were observed between chlorophyll *a* concentration L⁻¹ and

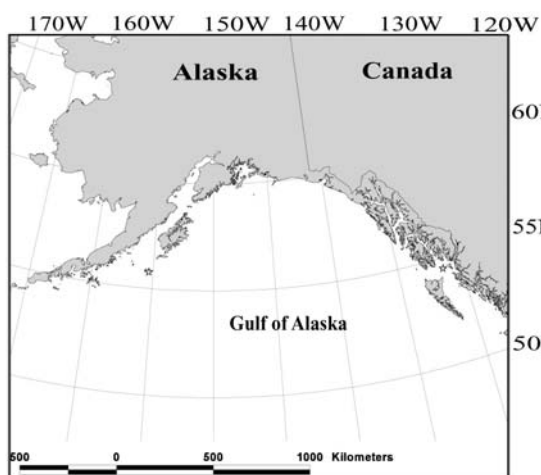


Figure 18a. Gulf of Alaska



Figure 18b. Bering and Chukchi Seas

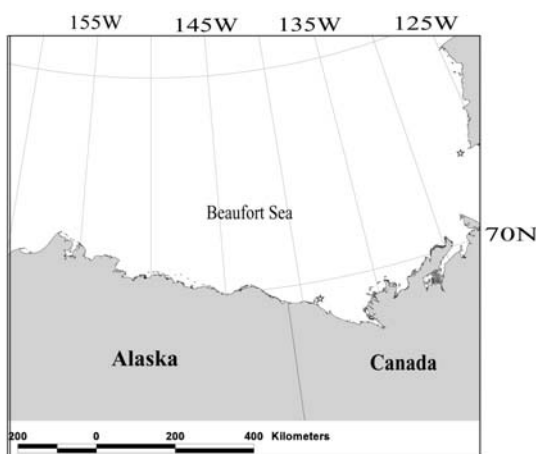


Figure 18c. Beaufort Sea

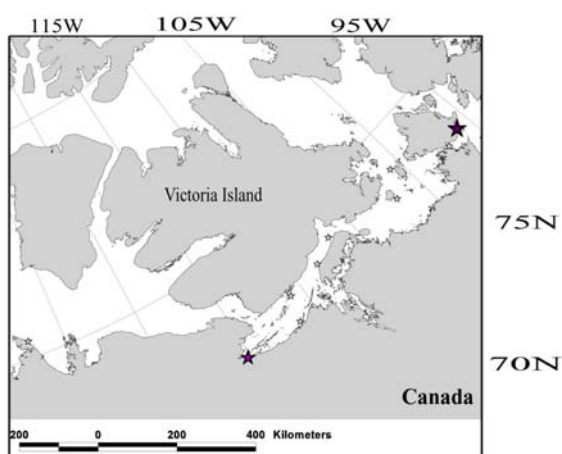


Figure 18d. Canadian Archipelago

Surface water bacterial abundance legend

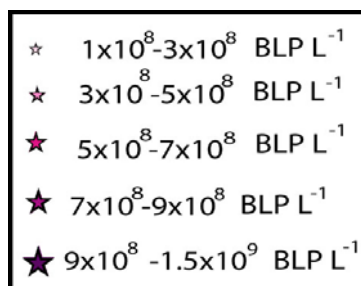


Figure 18. Surface water bacterial (bacterial-like particle) abundances for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

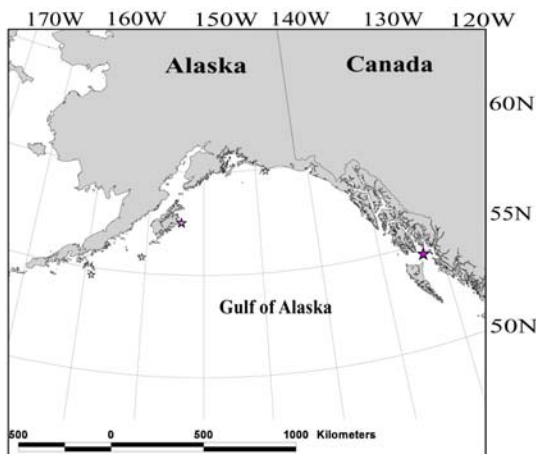


Figure 19a. Gulf of Alaska

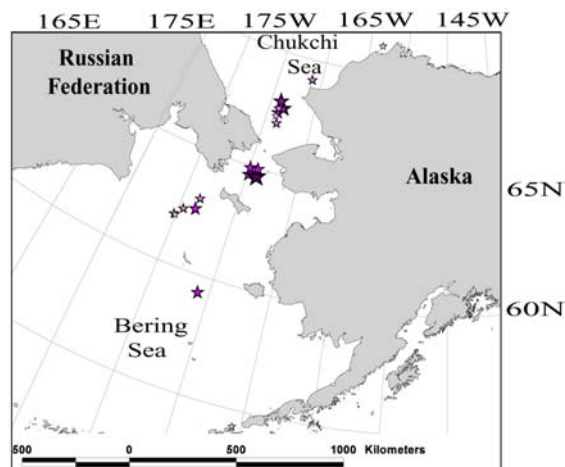


Figure 19b. Bering and Chukchi Seas

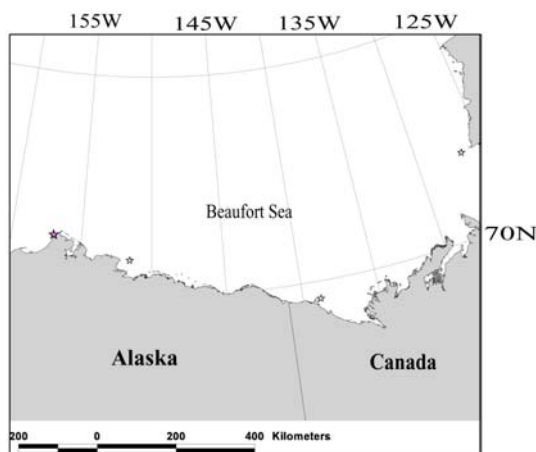


Figure 19c. Beaufort Sea

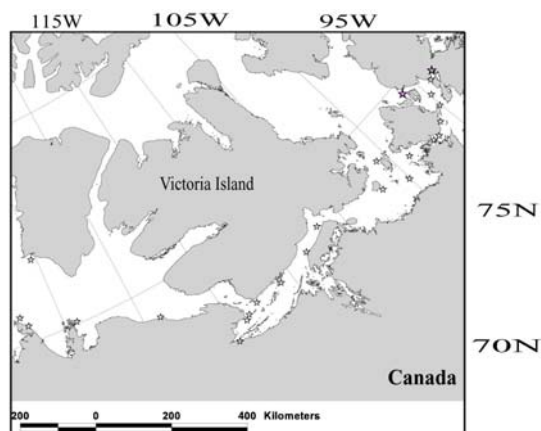


Figure 19d. Canadian Archipelago

Bottom water bacterial abundance legend

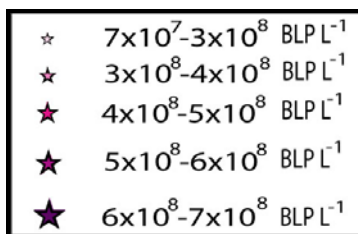


Figure 19. Bottom water bacterial (bacterial-like particle) concentrations for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

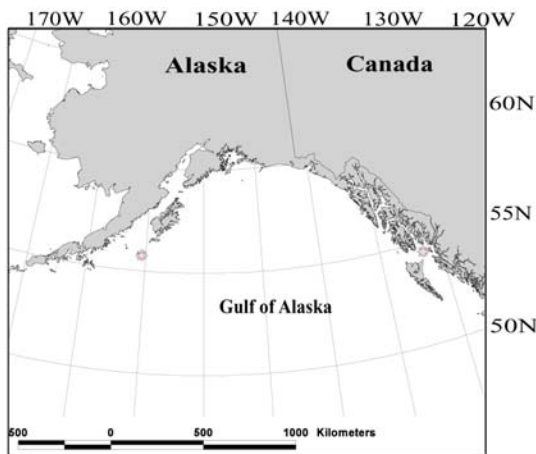


Figure 20a. Gulf of Alaska

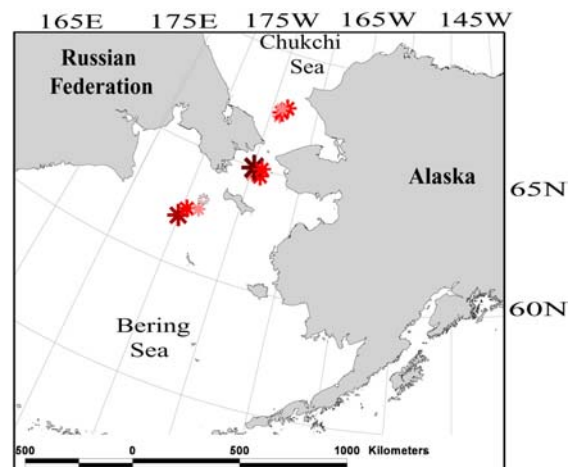


Figure 20b. Bering and Chukchi Seas

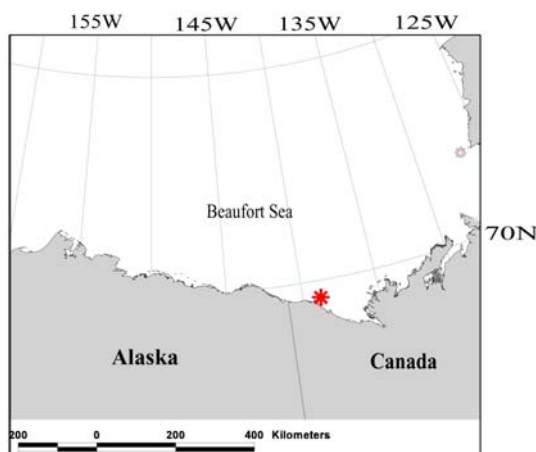


Figure 20c. Beaufort Sea

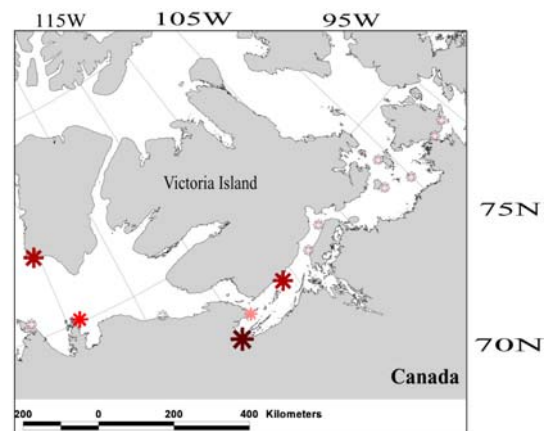


Figure 20d. Canadian Archipelago

Surface water viral abundance legend

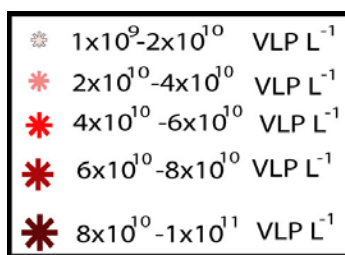


Figure 20. Surface water virus (virus-like particle) abundances for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

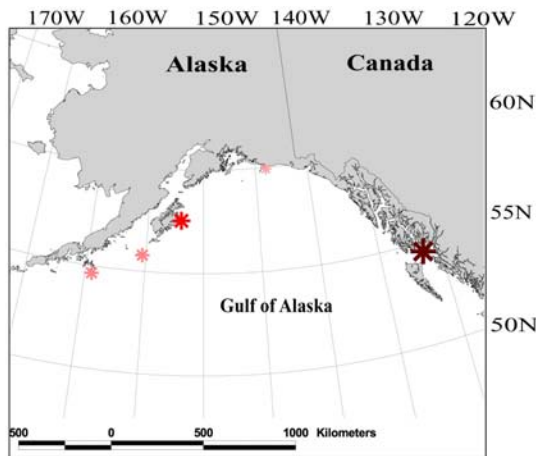


Figure 21a. Gulf of Alaska

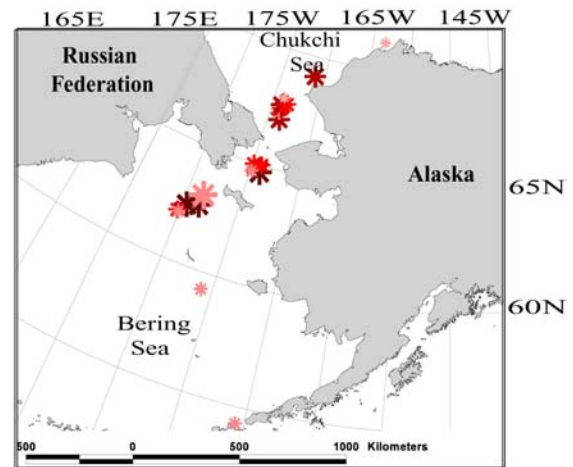


Figure 21b. Bering and Chukchi Seas

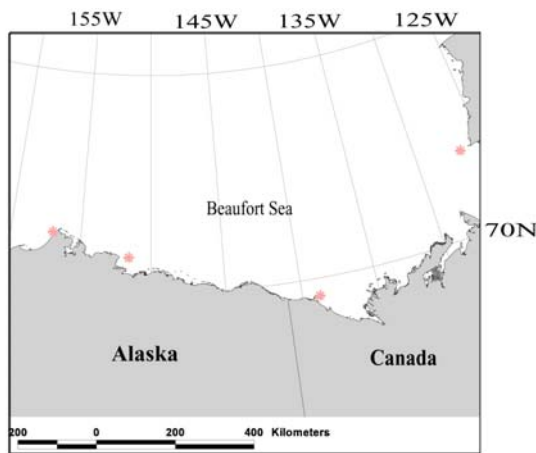


Figure 21c. Beaufort Sea

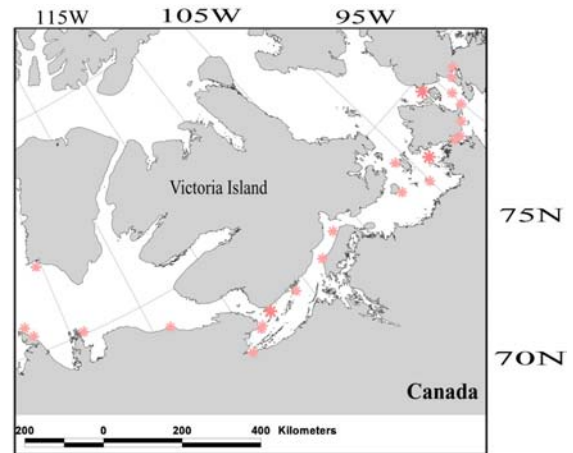


Figure 21d. Canadian Archipelago

Bottom water viral abundance legend

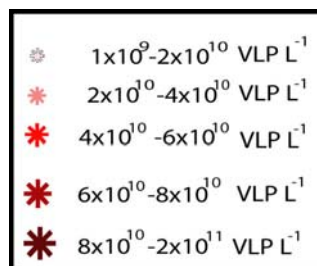


Figure 21. Bottom water viral (virus-like particle) abundances for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

Table 8. Regional means for bacterial and viral abundance (surface and bottom water) values. Standard deviations are in parentheses.

Region	Mean surface water bacterial abundance (BLP L⁻¹)	Mean surface water viral abundance (VLP L⁻¹)	Mean bottom water bacterial abundance (BLP L⁻¹)	Mean bottom water viral abundance (BLP L⁻¹)
Gulf of Alaska	3.10x10 ⁸ (1.85x10 ⁸)	4.76x10 ¹⁰ (7.05x10 ¹⁰)	2.69x10 ⁸ (1.47x10 ⁸)	4.66x10 ¹⁰ (4.92x10 ¹⁰)
Bering/Chukchi Sea	4.11x10 ⁸ (2.30x10 ⁸)	5.54x10 ¹⁰ (3.47x10 ¹⁰)	3.92x10 ⁸ (1.40x10 ⁸)	5.15x10 ¹⁰ (2.81x10 ¹⁰)
Beaufort Sea	2.21x10 ⁸ (7.44x10 ⁷)	3.55x10 ¹⁰ (3.19x10 ¹⁰)	1.61x10 ⁸ (1.18x10 ⁸)	1.08x10 ¹⁰ (1.63x10 ⁹)
Canadian Archipelago	4.18x10 ⁸ (3.45x10 ⁸)	3.82x10 ¹⁰ (4.33x10 ¹⁰)	1.70x10 ⁸ (8.40x10 ⁷)	1.40x10 ¹⁰ (5.65x10 ⁹)

both bacterial (Spearman's $\rho=0.722$, $p<0.001$, $n=30$) and viral abundances L^{-1} (Spearman's $\rho=0.553$, $p<0.002$, $n=30$; see Appendix K for correlation matrix values); and between bacterial and viral abundances L^{-1} (Spearman's $\rho=0.798$, $p<0.001$, $n=30$; Figure 22).

Bering and Chukchi Seas: Surface water bacterial abundance showed a minimum concentration (1.2×10^8 BLP L^{-1}) in the Bering Strait region, and a maximum concentration (8.7×10^8 BLP L^{-1}) in the St. Lawrence Island Polynya (SLIP) region (Figure 18b). Bottom water bacterial abundance exhibited a minimum concentration (1.6×10^8 BLP L^{-1}) in the southern Chukchi Sea, and a maximum (6.9×10^8 BLP L^{-1}) concentration in the Bering Strait (Figure 19b). Surface water VLP abundances ranged 2×10^{10} to 6×10^{10} VLP L^{-1} throughout the region, exhibiting the highest concentration in the SLIP (7.5×10^{10} VLP L^{-1}) and Bering Strait (8.9×10^{10} VLP L^{-1}) regions (Figure 20b). Bottom water VLP concentrations ranged widely (1×10^9 to 2×10^{11} VLP L^{-1}), with no obvious pattern (Figure 21b). Significant positive Pearson's product-moment correlations (used for $n>50$) were observed between bacterial abundance L^{-1} and salinity ($r=0.239$, $p<0.011$, $n=112$; see Appendix L for correlation matrix values); between bacterial abundance L^{-1} and chlorophyll *a* concentrations ($r=0.191$, $p<0.043$, $n=112$); and between bacterial abundance L^{-1} and viral abundance L^{-1} ($r=0.228$, $p<0.015$, $n=112$). Significant negative correlation was observed between temperature and both bacterial abundance L^{-1} ($r=-0.229$, $p<0.015$, $n=112$).

Beaufort Sea: Surface water bacterial abundance ranged from 1.7×10^8 to 2.7×10^8 BLP L^{-1} (Figure 18c). Bottom water bacterial abundance ranged from 7×10^7 to 3×10^8 BLP L^{-1} (Figure 19c). Surface water VLP abundance ranged from 1.3×10^{10} to

	Depth						Temp					Salinity					Chl <i>a</i>					Bact L ⁻¹					VLP L ⁻¹				
	GOA	BC	B	CA	O		GOA	BC	B	CA	O	GOA	BC	B	CA	O	GOA	BC	B	CA	O	GOA	BC	B	CA	O	GOA	BC	B	CA	O
Depth																															
Temp	-	-	-	-	-																										
Salinity	+	+	+	+	+	-	-	-	-	-																					
Chl <i>a</i>	-	ns	-	ns	ns	ns	-	+	-	+	-	+	-	+	+																
Bact L ⁻¹	-	ns	-	-	ns	ns	-	+	+	+	ns	+	ns	-	+	+	+	ns	ns	+											
VLP L ⁻¹	-	ns	ns	ns	ns	ns	-	+	ns	+	ns	ns	ns	-	+	+	ns	-	ns	+	+	+	+	+	+	+	+	+	+	+	+

Figure 22. Regional statistical Pearson’s product-moment relationships of discrete depth water column bacterial and viral abundances versus hydrographic parameters; Gulf of Alaska stations (GOA), Bering/Chukchi Sea stations (BC), Beaufort Sea stations (B), Canadian Archipelago stations (CA), and stations combined overall (O). See List of Definitions and Abbreviations for parameter units. Positive ‘+’ signs in yellow indicate significant positive correlations, negative ‘-’ signs in magenta indicate significant negative correlation, and “ns” indicates no significance.

5.8×10^{10} VLP L⁻¹ (Figure 20c). Bottom water VLP abundance ranged from 1×10^9 to 2×10^{10} VLP L⁻¹ (Figure 21c). Mean bottom water bacterial and viral abundances were lowest in the Beaufort Sea region (Table 8). Significant positive correlations were observed between temperature and both bacterial (Spearman's $\rho=0.506$, $p<0.008$, $n=26$; see Appendix M for correlation matrix values) and viral abundances L⁻¹ (Spearman's $\rho=0.653$, $p<0.0001$, $n=26$); as well as between bacterial abundance L⁻¹ and viral abundance L⁻¹ (Spearman's $\rho=0.403$, $p<0.041$, $n=26$). Significant negative correlations were observed between bacterial abundance L⁻¹ and depth (Spearman's $\rho=-0.419$, $p<0.033$, $n=26$); and between viral abundance L⁻¹ and chlorophyll *a* concentration (Spearman's $\rho=-0.450$, $p<0.021$, $n=26$; Figure 22).

Canadian Archipelago (CA): Surface water bacterial abundance ranged from 1 - 3×10^8 BLP L⁻¹ (Figure 18d). Bottom water bacterial abundances ranged from 7×10^7 - 3×10^8 BLP L⁻¹ for all stations (Figure 19d). Surface VLP abundance showed a greater range of variance than did bacterial abundance: numbers ranged from 8×10^8 to 1×10^9 VLP L⁻¹ (Figure 20d). Bottom water VLP values ranged from 1×10^9 to 4×10^{10} VLP L⁻¹ (Figure 21d). Mean bottom water bacterial and viral abundances were higher in the CA than in the Beaufort Sea, but lower than the Bering/Chukchi Seas and the GOA (Table 8). A significant positive Pearson's product moment correlation was observed between bacterial abundance L⁻¹ and temperature ($r=0.217$, $p<0.016$, $n=123$; see Appendix N for correlation matrix values; Figure 22). Significant negative Pearson's product-moment correlations were observed between bacterial abundance L⁻¹ and depth ($r=-0.184$, $p<0.041$, $n=123$); between salinity and both bacterial ($r=-0.367$, $p<0.0001$, $n=123$) and viral abundances L⁻¹ ($r=-0.198$, $p<0.024$, $n=129$); Figure 22).

Stations from all four geographic localities combined: The highest mean bacterial surface water abundance was seen in the CA, followed by the Bering/Chukchi Seas, and the GOA; the Beaufort Sea had the lowest mean bacterial surface water abundance (Table 8). The highest mean surface water viral abundance occurred in the Bering/Chukchi Seas, followed by the GOA, and the CA; again, the Beaufort Sea had the lowest mean abundance (Table 8). The Bering/Chukchi Seas had the highest bottom water bacterial and viral abundances, followed by the GOA and the CA; the Beaufort Sea again had the lowest mean abundances (Table 8).

The highest surface water bacterial abundance was found in the SLIP region of the northern Bering Sea (Figure 18); surface water VLP abundance showed the highest average values in the Bering/Chukchi region, decreasing in the Beaufort Sea, and then was variable in the CA (Figure 20). Bottom water bacterial abundance was highest in the Bering Strait and southern Chukchi Sea regions (Figure 19), as were bottom water VLP abundances, which remained at low values in both the Beaufort Sea and the CA (Figure 21). Significant positive Pearson's product-moment correlations were observed between temperature and both bacterial ($r=0.164$, $p<0.005$, $n=293$; see Appendix O for correlation matrix values) and viral abundances L^{-1} ($r=0.150$, $p<0.009$, $n=305$); between salinity and both bacterial ($r=0.206$, $p<0.0001$, $n=293$) and viral abundances L^{-1} ($r=0.431$, $p<0.0001$, $n=305$); between chlorophyll *a* concentration and both bacterial ($r=0.292$, $p<0.0001$, $n=292$) and viral abundances L^{-1} ($r=0.354$, $p<0.0001$, $n=304$); and between viral and bacterial abundance L^{-1} ($r=0.610$, $p<0.0001$, $n=292$; Figure 22).

Sediment virus-like particle and bacterial abundance

Gulf of Alaska (GOA): Although eight stations were occupied in the GOA, sediments were collected at only three stations. Sediment bacterial abundance ranged from 1×10^6 to 6×10^6 BLP g^{-1} for all stations averaging 8×10^6 BLP g^{-1} (Figure 23a; see Appendix I for individual station bacterial and viral measurements; Table 9). Sediment viral abundance ranged from 1×10^7 to 6×10^7 VLP g^{-1} for all stations (Figure 24a), averaging 4×10^7 VLP g^{-1} (Table 9). These stations were included in the overall combined statistical analysis, although the comparisons with other regions are limited by small sample size.

Bering and Chukchi Seas: Sediment bacterial abundance ranged from 8.2×10^6 BLP g^{-1} in the southernmost Bering Sea station to 9.8×10^8 BLP g^{-1} in the southern Chukchi Sea (Figure 23b), averaging 8×10^7 BLP g^{-1} (Table 9). Stations predominantly ranged from 1×10^8 to 6×10^8 VLP g^{-1} . The highest value (1×10^9 VLP g^{-1}) was found in the SLIP region (Figure 24b), averaging 4×10^8 VLP g^{-1} (Table 9). No significant relationships were observed between bacterial and viral abundances and the hydrographic and sediment parameters, but they were observed between sediment bacterial and viral abundances (Spearman's $\rho=0.659$, $p<0.0001$, $n=20$; Figure 25).

Beaufort Sea: Sediment bacterial abundance ranged from 7×10^6 to 1×10^8 BLP g^{-1} averaging 2×10^7 BLP g^{-1} (Table 9), of which the highest values occurred in the western region (Figure 23c). Sediment viral abundance ranged from 8.9×10^8 to 1.7×10^9 VLP g^{-1} for the 4 stations enumerated (Figure 24c), averaging 2×10^8 VLP g^{-1} (Table 9). These stations were included in the combined overall statistical analysis.

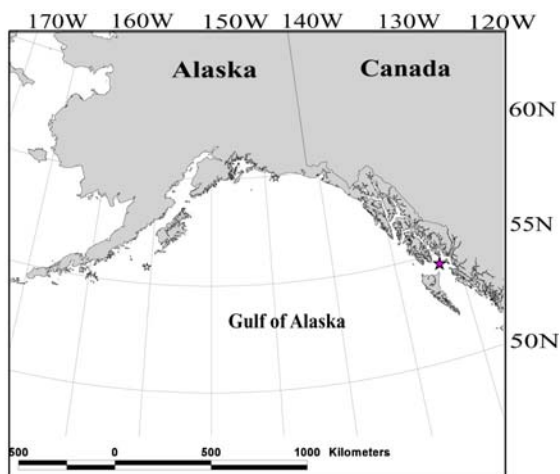


Figure 23a. Gulf of Alaska

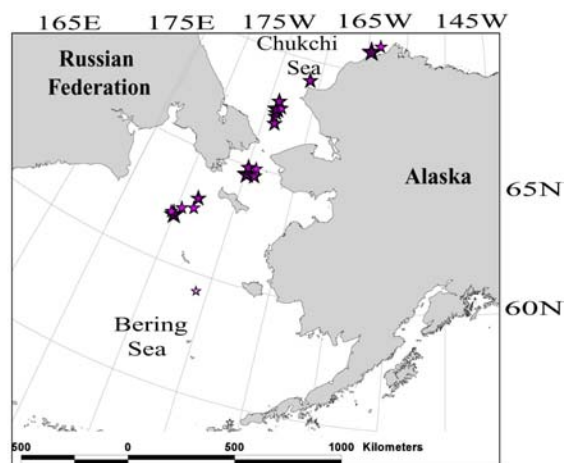


Figure 23b. Bering and Chukchi Seas

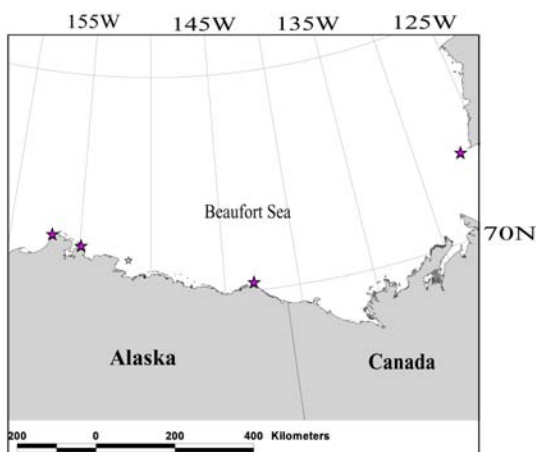


Figure 23c. Beaufort Sea

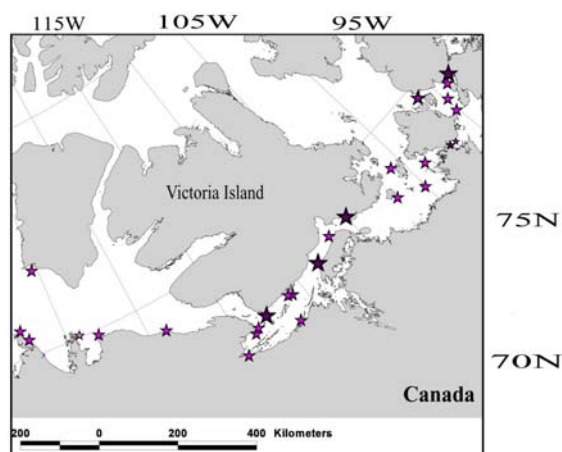


Figure 23d. Canadian Archipelago

Sediment bacterial abundance legend

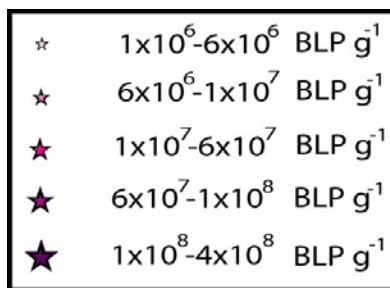


Figure 23. Sediment bacterial (bacteria-like particle) abundances for the 4 study regions; see legend above for values (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

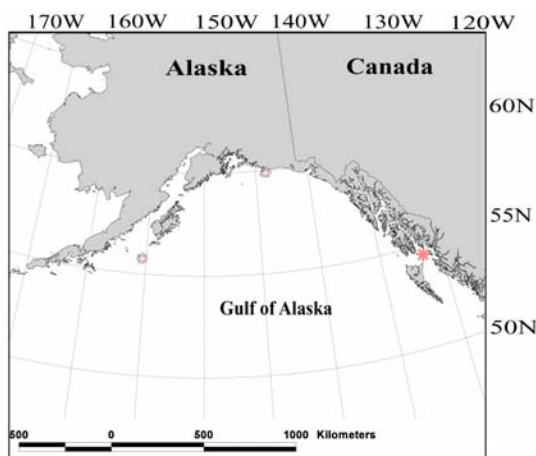


Figure 24a. Gulf of Alaska

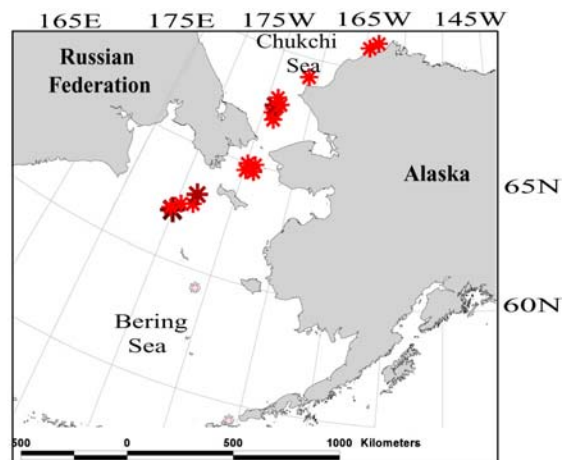


Figure 24b. Bering and Chukchi Seas

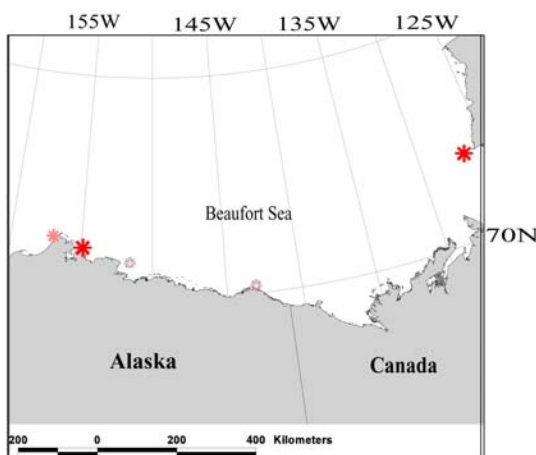


Figure 24c. Beaufort Sea

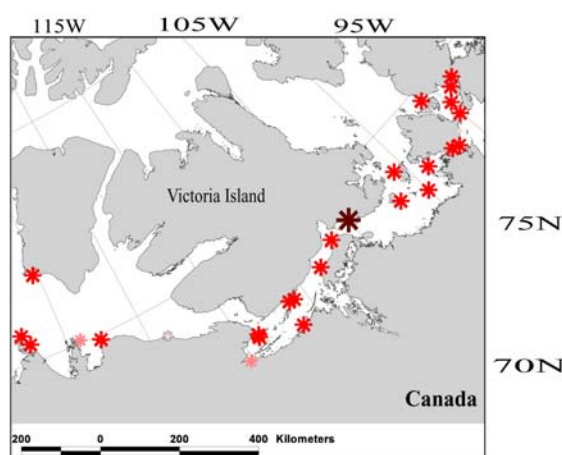


Figure 24d. Canadian Archipelago

Sediment viral abundance legend

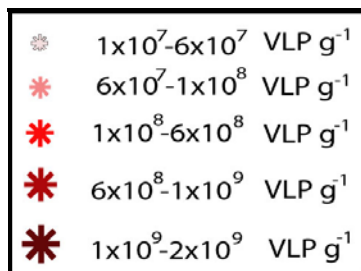


Figure 24. Sediment virus (virus-like particle) concentrations for the 4 study regions: (a) Gulf of Alaska (GOA), (b) Bering/Chukchi Seas, (c) Beaufort Sea, and (d) Canadian Archipelago (CA).

	Depth			Bot Sal			Bot Temp			Bot Virus			Bot Bact			Int Chl			Sed Chl			Sed Bact			Sed Virus			Modal			TOC			C/N		
	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O			
Depth																																				
Bot Sal	ns	+	+																																	
Bot Temp	-	ns	ns	ns	-	ns																														
Bot Virus	ns	ns	ns	ns	ns	+	ns	ns	ns																											
Bot Bact	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	+	+																								
Int Chl	ns	+	+	+	+	+	ns	ns	ns	ns	ns	+	ns	ns	ns																					
Sed Chl	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	+	ns	ns	+	ns	ns	ns																		
Sed Bact	ns	ns	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	ns	ns	+															
Sed Virus	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	ns	ns	+	ns	ns	ns	ns	ns	+	+	+	+												
Modal	+	ns	+	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns			
TOC	+	ns	ns	ns	+	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	ns	+	ns	ns	ns	ns	ns	ns	+	ns	+						
C/N	ns	ns	ns	-	ns	+	ns	ns	ns	ns	-	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	+				

Figure 25. Regional comparisons between bacterial, viral, and sediment tracer values. Please see List of Abbreviations and Definitions for parameter units. Positive ‘+’ signs in **yellow** indicate significant Spearman’s rho non-parametric positive correlations, negative ‘-’ signs in **magenta** indicate significant Spearman’s rho non-parametric negative correlations, and “ns” indicates no significance.

Table 9. Regional means for sediment bacterial and viral parameters. Standard deviations are in parentheses.

Region	Mean sediment bacteria (BLP g ⁻¹)	Mean sediment viruses (VLP g ⁻¹)
Gulf of Alaska	8.04x10 ⁶ (5.68x10 ⁶)	4.35x10 ⁷ (2.77x10 ⁷)
Bering/Chukchi Seas	8.03x10 ⁷ (7.49x10 ⁷)	4.28x10 ⁸ (3.02x10 ⁸)
Beaufort Sea	2.28x10 ⁷ (1.89x10 ⁷)	8.02x10 ⁷ (4.90x10 ⁷)
Canadian Archipelago	5.83x10 ⁷ (5.69x10 ⁷)	2.33x10 ⁸ (2.25x10 ⁸)

Canadian Archipelago (CA): Sediment bacterial abundance ranged from 1x10⁶ to 2x10⁸ BLP g⁻¹; the lowest numbers occurred in Amundsen Gulf and Queen Maud Gulf. The maximum value (2.0x10⁸ BLP g⁻¹) occurred at BD-27 in Spence Bay (Figure 23d). Mean regional abundance was 6x10⁷ BLP g⁻¹ (Table 9). Sediment VLP abundance ranged consistently between 1x10⁸ and 6x10⁸ VLP g⁻¹; the maximum abundance (1.2x10⁹ VLP g⁻¹) occurred at BD-20, near-shore in Dease Strait and the minimum abundance (7.0x10⁷ VLP g⁻¹) was found at BD-15, on the southern shore of Amundsen Gulf (Figure 24d). Mean regional abundance was 2x10⁸ VLP g⁻¹ (Table 9). A significant positive relationship was observed between sediment bacterial abundance and bottom water temperature (Spearman's rho=0.536, p<0.004, n=27; see Appendix Q for correlation matrix values). Positive significant correlations were observed between sediment bacterial and viral abundances (Spearman's rho=0.567, p<0.0001, n=36; Figure 25).

Stations from all four geographic localities combined: Both sediment bacterial and VLP abundance are highest on average in the Bering and Chukchi Seas, decreasing in the Beaufort Sea, and becoming highly variable again in the CA. Significant positive correlations were observed between bottom water viral abundance and sediment viral abundance (Spearman's $\rho=0.507$, $p<0.0001$, $n=48$; see Appendix R for correlation matrix values); between bottom water bacterial abundance and sediment viral abundance (Spearman's $\rho=0.434$, $p<0.002$, $n=48$); between sediment chlorophyll *a* content and sediment bacterial (Spearman's $\rho=0.338$, $p<0.015$, $n=51$) and viral abundances (Spearman's $\rho=0.463$, $p<0.001$, $n=50$); and between sediment bacterial and viral abundances (Spearman's $\rho=0.784$, $p<0.0001$, $n=55$) (Figure 25).

Discussion

Water column bacterial abundances in the Bering and Chukchi Seas are consistent with observations of bacterial abundance within the 10^8 L^{-1} range and viral abundance within the 10^{10} L^{-1} range (Steward et al., 1996). CA bacterial abundances are consistent with Maranger et al. (1994) in the 10^8 range; however, surface water viral values were two to three magnitudes higher (10^9 L^{-1} and 10^{10} L^{-1} opposed to 10^7 L^{-1}) than reported by Maranger et al. (1994). However, Maranger et al. (1994) results were enumerated from under-ice water column abundances, and the water column abundances in this study were for samples collected in open water, in mid-summer rather than spring. The GOA exhibited intermediate viral and bacterial values, the Bering and Chukchi Seas possessed the highest abundances of both water column and sediment viral and bacterial numbers, the Beaufort Sea stations had low viral and intermediate bacterial values, and the CA stations showed intermediate viral and low bacterial abundances. These bacterial and

viral abundances were strongly correlated with the highest regional average of chlorophyll *a* concentration. A tight coupling has been shown previously in polar waters between heterotrophic bacteria and phytoplankton concentrations (Fuhrman and Azam, 1980; Cota et al., 1990) and is thought to be controlled by phytoplankton-released DOC and its usage by bacterioplankton (Baines and Pace, 1991).

Bacterial and viral abundances were also significantly correlated with each other in both the water column and in the sediment, consistent with the observations of earlier studies that viruses exist in abundances several magnitudes greater than the corresponding bacterial abundances (Womack and Colwell, 2000 and references contained therein). Significant correlations between water column and sediment viral abundances (Figure 25) may indicate pelagic-benthic coupling between viral populations (the importation of pelagic viruses to the benthos is suggested by Hewson et al., 2001a). Specifically, since higher numbers of bottom water viruses correlate well with sediment virus abundance, the sediment viral community may be contributing to the pelagic viral community abundance by resuspension of viruses, or the bottom water viral abundance may be contributing to sediment viral abundance as viral particles settle out of the water column onto the benthos. However, no significant correlations were observed between water column and sediment bacterial abundances (Figure 25), indicating that these populations may be less tightly coupled than viral populations or that their numbers may be largely controlled by the existing viral abundance.

Sediment bacterial abundances ranged from 10^6 to 10^7 BLP g^{-1} , with sediment viral abundances typically a magnitude higher in the 10^7 - 10^8 VLP g^{-1} range for all

geographic regions (Table 9). A constancy of bacterial sediment abundances has been observed for widely ranging marine habitats. This may involve self-limitation of cell growth in density-dependent situations, where substrate surface area is limited (Schmidt et al., 1998 and references therein).

Bacterial and viral enumeration conducted here did not distinguish between cyanobacteria and heterotrophic bacteria. Acridine Orange does not necessarily distinguish between dead, starving, and active cells, which may result in over-estimation of live bacterial cells (Helmke and Weyland, 1995). There may also be substantial resuspension of sediment load into the water-column, which would bias water-column versus sediment bacterial and viral numbers. For example, Whitman et al. (1998) did not distinguish between the water column and the first ten centimeters of sediment in their estimates of prokaryote abundances in various environments. However, depending on sediment type, sea-floor depth and storm conditions, this upper ten centimeters is not necessarily in constant free-exchange with the water column, so non-motile populations within sediments could still be distinct from those in the overlying water column.

The presence of VLP could have been overestimated due to free RNA and DNA fragments existing in the samples (Bettarel et al., 2000), or because of the inclusion of fluorescent non-viral particles; free mitochondria, ribosomes, or nucleic acids, or very small bacteria (Fuhrman, 1999; Bettarel et al., 2000). Underestimation could have occurred, due to SYBR-Green I's rapid fade rate.

The large number of both bacteria and viruses present in the water column and in the sediment indicate that these may be important components in Arctic pelagic-benthic carbon cycling regimes, since these abundances are comparable to other marine systems

(10^7 - 10^9 VLP cm³ sediment and 10^7 - 10^8 BLP cm³ in Australian sediment where they have already been cited as important contributors to carbon cycling rates (Hewson et al., 2001a).

It is important to point out that the diversities of both marine bacteria and viruses are just beginning to be elucidated. Many viruses are host-specific, only infecting particular species of algae and bacteria (Wilhelm and Suttle, 1999; Fuhrman, 1999). Many bacteria occurring in natural samples remain unculturable in laboratory settings, and therefore their associated viruses remain unidentified. These bacteria and their host-specific viruses also have the potential to be impacted by global warming. Reductions in sea ice cover could increase the likelihood of viral UV radiation damage, decreasing infectivity rates and thereby also decreasing amounts of bioavailable nutrients released by lysed bacterial cells. Other environmental changes, including alterations of temperature, salinity, and carbon deposition patterns could affect Arctic viral and bacterial diversities in both the pelagic and benthic environments by reducing the heterogeneity of available substrates (sediment, ice, planktonic algae) for colonization, in addition to changing under-ice irradiance levels (Laurion et al., 1995 and references therein).

The decrease of sediment viral and bacterial abundances from the Bering/Chukchi Seas relative to the Beaufort Sea region is likely to be associated with the transition from a productive eutrophic system (Bering and Chukchi Seas) to oligotrophic waters (Beaufort Sea). Weinbauer and Suttle (1997) enumerated greater numbers of detectably infected bacteria in eutrophic water samples than in oligotrophic water samples, which has been observed in several other marine systems (Steward et al. 1996; Weinbauer et al. 1993). Environmental changes associated with global warming could have a large impact

on differences in both bacterial and viral abundances and their distributions observed between Arctic regions. Changes in the diversity, abundances and distributions of bacteria and viruses have the potential to alter nutrient cycling in both the pelagic and benthic environments, which could have consequences for the ecosystem food web.

Chapter summary

Both water column bacterial and viral abundances were lowest in the Beaufort Sea, with increasing values in the GOA, the CA, and lastly, the Bering and Chukchi Seas had the highest abundances (Table 10). Sediment bacterial and viral abundances were lowest in the GOA, with increasing values in the Beaufort Sea, the CA, and again, the Bering and Chukchi Seas had the highest abundances (Table 11).

Table 10. A comparison of mean water column bacteria and viral parameter values among study regions.

Region	Mean surface water bacterial abundance (BLP L ⁻¹)	Mean surface water viral abundance (VLP L ⁻¹)	Mean bottom water bacterial abundance (BLP L ⁻¹)	Mean bottom water viral abundance (BLP L ⁻¹)
Gulf of Alaska	Low	High	High	High
Bering/Chukchi Sea	High	Highest	Highest	Highest
Beaufort Sea	Lowest	Lowest	Lowest	Lowest
Canadian Archipelago	Highest	Low	Low	Low

Table 11. A comparison of mean sediment bacteria and viral parameter values among study regions.

Region	Mean sediment bacteria (BLP g⁻¹)	Mean sediment viruses (VLP g⁻¹)
Gulf of Alaska	Lowest	Lowest
Bering/Chukchi Seas	Highest	Highest
Beaufort Sea	Moderate	Lowest
Canadian Archipelago	High	Moderate

In all study regions, the abundances of both bacteria and viruses were both significantly and positively correlated to chlorophyll *a* concentration as well as to each other. However, some variation exists in relationships among other parameters throughout the study regions (Figure 25).

In the Bering and Chukchi Seas, temperature was positively correlated with bacterial and viral water column abundances, and salinity was negatively correlated (Figure 25).

In the Beaufort Sea, temperature was again positive correlated with both bacterial and viral water column abundances; however, the relationship between salinity and bacterial and viral abundances was not significant (Figure 25). Depth was significantly negatively correlated to bacterial abundance, and water column chlorophyll *a* concentration was significantly negatively correlated to water column viral abundance (Figure 25).

In the CA, temperature was again significantly positively correlated to water column bacterial and viral abundance, as well as positively correlated to sediment

bacterial abundance (Figure 25). Significant negative correlations were seen again between depth and water column bacterial abundance, and between salinity and both bacterial and viral abundances (Figure 25). Here, too, chlorophyll *a* concentration was significantly negatively correlated to bottom water water column viral abundance (Figure 25).

Overall, both water column and sediment abundances of bacteria and viruses showed significant positive relationships with the parameters of temperature, salinity, chlorophyll *a* content, and each other, respectively (Figure 25). This may indicate that the bacterial and viral populations are dependent on the same carbon source (e.g. surface sediment chlorophyll *a* content) that the macroinfauna are dependent on, and may possibly be competitors for this food source. This competition could effect the abundance and diversity of the macroinfaunal communities if a regime shift alters the quantity of available carbon and the abundances of both bacteria and viruses in that same region.

V. RELATIONSHIPS AMONG INFAUNAL, BACTERIAL, AND VIRAL COMPONENTS

Introduction

The relationships among bacteria, viruses, and dissolved organic matter, and their effects on macroinfaunal community biomass and diversity remain largely undefined. No published studies have investigated the associations of viruses with benthic macroinfaunal communities, although viruses may be an important control mechanism regulating the abundances of bacterial populations (Wilhelm and Suttle, 1999; Wommack and Colwell, 2000) that can be important food sources for deposit-feeding invertebrates.

The production of fecal castings and the accumulation of unconsumed prey remains from macroinfauna may enhance local microbial growth (Soltwedel and Vopel, 2001). Bioturbation may increase microbial abundances by increasing nutrient exchange at the sediment-water interface (Huettel and Gust, 1992). Other nutrients such as polysaccharides and proteins found in gastropod mucus (Connor, 1986) can also be utilized directly by bacteria (Herndl and Peduzzi, 1989). Soltwedel and Vopel (2001) observed bacterial abundances three times higher under animal tracks than in visually undisturbed deep-sea sediments. Burrows, tubes, and sediment mound structures can function to alter local water flow patterns, consequently altering the local sediment erosion and deposition rates (Friedrichs et al., 2000). This can increase bacterial abundances (Aller and Aller, 1986) in the vicinity of these structures, in addition to providing habitat for “burrow microbial biofilm” communities (Marinelli et al., 2002) and ventilated chemical refuges from anoxic sediment conditions (Marinelli, 1994).

Marine detritivores consume and absorb bacterial carbon as it passes through the gut (Plante et al., 1990 and references therein), and some macroinfaunal organisms such as echinurians may even garden bacterial populations near their residences by moving and tending their fecal pellets (Smith et al., 1986) in order to maintain a bacterial food source for ingestion. Stuart et al. (1982), and Plante et al. (1990) provide evidence for macroinfaunal consumption of both motile and non-motile water-column bacteria by the filter-feeding of sponges and bivalves, but the significance of this macroinfaunal grazing has been debated due to the size difference between trophic levels, and hence the consumption efficiency of using microbes as a primary food source (Azam et al., 1983).

Bernard and Fenchel (1995) observed macroinfauna (oligochaetes and polychaetes) inhabiting sulphurous bacterial mats in Niva Bay, Denmark sediment core samples, suggesting that these bacterial mats provide an important food web base. These benthic macroinfauna and bacteria existing in close proximity may indicate important interactions in the context of trophic and biogeochemical associations.

Materials and methods

Macroinfaunal benthic carbon biomass and associated faunal species diversity and evenness values were obtained by the methods described in Chapter 3. Bacterial and viral abundance values were obtained by the methods described in Chapter 4. A Spearman's rho non-parametric test was used to examine correlations among parameters having a sample size <50 . This test assumes non-normal distribution of values and was used for relationships involving benthic, bottom water, and integrated water column parameters.

Results

Gulf of Alaska (GOA): There were not enough benthic stations in this area to discuss regional statistical relationships separately; however, this region's stations measurements were included in the combined overall statistical analysis.

Bering and Chukchi Seas: No significant relationships were observed among micro- and macroinfaunal parameters (Figure 26; see Appendix S for correlation matrix values).

Beaufort Sea: There were not enough benthic stations in this area to discuss regional statistical relationships separately; however, the regional station measurements were included in the combined overall statistical analysis.

Canadian Archipelago (CA): No significant positive relationships were observed among micro- and macroinfaunal parameters. Significant negative relationships were observed between integrated water column viral abundance and both macroinfaunal abundance (Spearman's $\rho = -0.503$, $p < 0.012$, $n = 24$; see Appendix T) and benthic carbon biomass (Spearman's $\rho = -0.555$, $p < 0.005$, $n = 24$); and between integrated water column bacterial abundance and both macroinfaunal abundance (Spearman's $\rho = -0.604$, $p < 0.002$, $n = 24$) and benthic carbon biomass (Spearman's $\rho = -0.703$, $p < 0.0001$, $n = 24$; Figure 26).

Stations from all four geographic localities combined: Significant positive relationships were observed between bottom water bacterial abundance and macroinfaunal abundance (Spearman's $\rho = 0.385$, $p < 0.006$, $n = 49$; Figure 26), between bottom water viral abundance and macroinfaunal total organic carbon biomass (Spearman's $\rho = 0.458$, $p < 0.001$, $n = 49$; see Appendix U and Figure 26) and benthic

	Bot Virus			Bot Bact			Sed Bact			Sed Virus			Faunal Abund			Biomass gC			Diversity			Evenness		
	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O	BC	CA	O
Bot Virus																								
Bot Bact	ns	+	+																					
Sed Bact	ns	ns	ns	ns	ns	ns																		
Sed Virus	ns	ns	+	ns	ns	+	+	+	+															
Faunal Abund	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns												
Biomass gC	ns	ns	+	ns	ns	+	ns	ns	ns	ns	ns	+	ns	+	+									
Diversity	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	ns	ns	ns	ns	+	+						
Evenness	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	-	ns	-	ns	ns	ns	+	+	+			

Figure 26. A regional comparison of bacterial, viral, and macroinfaunal correlations. Bering/Chukchi Sea stations (BC), Canadian Archipelago stations (CA), stations combined overall (O). Please see List of Abbreviations and Definitions for parameter units. Positive '+' signs in yellow indicate significant positive correlations, negative '-' signs in magenta indicate significant negative correlation, and "ns" indicates no significance.

macroinfaunal carbon biomass (Spearman's $\rho=0.541$, $p<0.0001$, $n=49$); between integrated water column viral abundance and macroinfaunal benthic carbon biomass (Spearman's $\rho=0.402$, $p<0.004$, $n=50$); and between sediment viral abundance and the parameters of macroinfaunal benthic carbon biomass (Spearman's $\rho=0.393$, $p<0.004$, $n=51$), species diversity (Spearman's $\rho=0.349$, $p<0.024$, $n=42$), and species evenness (Spearman's $\rho=0.327$, $p<0.034$, $n=42$) (Figure 26).

Discussion

The lack of significant relationships among micro- and macroinfaunal parameters in the Bering and Chukchi Seas could be in part due to a lower sample size than the CA region, or possibly because in an area of high primary productivity (Walsh et al., 1989; Grebmeier and Cooper, 1994) where a substantial portion of the primary productivity settles to the benthos (Grebmeier and Dunton, 2000), there may be a lag time in microbial processing of settling carbon. The absence of significant relationships may also result from a dominance of unmeasured microfaunal-meiofaunal relationships rather than microfaunal-macroinfaunal interactions in this area. It could also be caused by a possible uncoupling of dependent interactions (macroinfaunal filter and deposit-feeding) on bacteria. Another alternative is that bacteria utilize macroinfaunal fecal and sloppy feeding remains when the carbon supply reaching the benthos from pelagic-benthic coupling in high productivity regions is large enough for the trophic components to feed independently from each other during the surplus. This carbon surplus may result in high abundances of both pelagic bacteria and VLP in the Bering and Chukchi Seas

coincident with carbon supply reaching the benthos that support macroinfaunal communities. In low productivity areas such as the CA, less of a carbon surplus exists, and pelagic microbial processing of this limited resource may control how much benthic carbon can be deposited.

In the CA, significant negative correlations between integrated water column viral and bacterial numbers and the parameters of macroinfaunal abundance and benthic carbon biomass indicate that in a less productive area (Grebmeier et al., 1995; this study) there may be a greater influence of pelagic microbial activity on the benthos because of degradation of surface-derived carbon as it settles to the sea floor. Higher abundances of pelagic bacteria and viruses may indicate a greater microbial consumption of carbon settling through the water column, and therefore a lower amount of unprocessed, high quality food reaching the benthos, resulting in the lower abundances and biomass of CA benthic macroinfaunal communities.

Significant relationships between both bottom water and total integrated water column viral abundances may influence macroinfaunal benthic carbon biomass. Bottom water bacterial abundance also appears to be related to macroinfaunal benthic carbon biomass. Overall, sediment viral abundance is positively correlated to macroinfaunal benthic carbon biomass, as well as to station species diversity. A greater number of viruses in the overlying water column and/or sediment could therefore enhance benthic macroinfaunal growth by reducing the number of pelagic bacteria competing for the same surface water-derived food source. In addition, increasing the levels of bioavailable dissolved organic compounds could also stimulate increased bacterial growth, which

could then be used as a food source for filter or deposit feeding organisms, also enhancing benthic macroinfaunal growth and diversity.

Chapter summary

Relationships among bacterial and viral abundances and macroinfaunal biomass and diversity varied between study regions. In the Bering and Chukchi Seas, no significant statistical relationships were observed. In the CA, however, the abundance of bacteria and viruses in the overlying water column (integrated values) were significantly negatively correlated with macroinfaunal biomass and abundance, indicating that the carbon was possibly being consumed by competing pelagic bacterial populations and reducing the biomass of macroinfaunal communities because of reduced food supply to the benthos.

Overall, significant positive correlations were observed between sediment viral abundance and macroinfaunal biomass and diversity, which may indicate that sediment viruses suppress sediment bacterial populations which would normally compete for the benthic food supply. Positive significant correlations between bottom water bacterial and viral abundances and macroinfaunal biomass may indicate that in areas of high carbon deposition supporting high macroinfaunal biomass, bacteria and their controlling viral abundance can co-habitat since the carbon source is so large and can maintain supplies for both trophic levels. Increased macroinfaunal activity (inferred from increased macroinfaunal biomass and macroinfaunal abundance) could also enhance sediment bacterial and viral abundances through bioturbation.

VI. BENTHIC CARBON FLOW MODEL

Introduction

The relationships between biotic and abiotic parameters in the Arctic will not necessarily remain the same if global warming alters the hydrographic and sediment characteristics. Salinity, temperature, and chlorophyll *a* concentrations all appear to effect bacterial, viral, and macroinfaunal populations in this study.

- (1) What happens when salinity is reduced because of ice melt and increased freshwater run-off?
- (2) What happens when temperatures increase because of atmospheric warming?
- (3) What happens when chlorophyll *a* deposition is altered because of change in ice melt and the timing of corresponding phytoplankton blooms?
- (4) What if changes in ocean currents alter sediment grain size patterns?
- (5) How will all of these possible changes in environmental parameters affect the biodiversity of marine Arctic benthic communities?

Although these questions are too complex to be modeled within the scope of this study, calculations of the basic carbon flow through a high productivity trophic system and a low productivity trophic system can provide estimates of carbon usage in Arctic environments. These estimates can then be examined in the context of the two potential global warming scenarios: (1) global warming increases primary productivity and (2) global warming decreases primary productivity.

In order to examine carbon flow through the Arctic marine system, data on the annual particulate organic carbon flux and benthic carbon consumption were entered into a conceptual box model by modification of the model used by Grebmeier (1987). My goal was to compare estimates of faunal carbon consumption between a high-productivity area (Northern Bering Sea) and a low-productivity area (Beaufort Sea). Community benthic carbon consumption rates were calculated from respiration chamber experiments conducted on board the first leg of the Laurier 2000 cruise (J. Grebmeier, unpublished data), using sediment oxygen respiration data to estimate sediment carbon mineralization rates (Grebmeier, 1987). Bacterial respiration rate estimates were calculated from prior work in the Northeast Water Polynya, near Greenland (Rowe et al., 1997). Microbial loop component estimates were based on the review of Wilhelm and Suttle (1999).

Methods and assumptions

Particulate organic carbon (POC) flux values were obtained from sediment trap mooring measurements summarized in Wassmann et al. (2003) such as Northern Bering Sea ($168.6 \text{ gC m}^{-2} \text{ yr}^{-1}$) and Beaufort Sea ($4.0 \text{ gC m}^{-2} \text{ yr}^{-1}$) carbon fluxes. It was assumed that these data are representative of average regional annual carbon flux, although high interannual variability has been observed in these regions (Wassmann et al., 2003). Nine stations (SLIP 1-5 and UTBS 1, 2, 4, 5) were used to obtain a mean Northern Bering Sea macroinfaunal organic carbon biomass and respiration values, and six stations (BD-8, 10-12, H1, CK-3) were used to obtain mean Beaufort Sea macroinfaunal organic carbon biomass and respiration values. Beaufort Sea stations were assumed to possess benthic carbon consumption values equivalent to previously measured ACW values (10.0 mmol

$\text{C m}^{-2} \text{ d}^{-1}$; Grebmeier, 1987) since respiration measurements were not available for this portion of the Laurier 2000 cruise. This assumption was based on Beaufort Sea benthic biomasses similar to GOA station biomasses (this study), and the observation that ACW water is bathymetrically steered along the northern coast of Alaska (Weingartner et al., 2001), influencing Beaufort Sea water masses. Stations that did not have sediment oxygen measurements but had macroinfaunal biomass measurements (UTBS-2, UTBS-5, BD-8, BD-11, H-1, CK-3) were assumed to have sediment oxygen uptake measurements proportional to their biomass, using the average of sediment oxygen uptake measurements from Northern Bering Sea stations with similar biomass. Stations with 1-10 gC m^{-2} were presumed to have a respiratory demand of $10 \text{ mmol C m}^{-2} \text{ d}^{-1}$, stations with 10-20 gC m^{-2} were presumed to have a respiratory demand of $16 \text{ mmol C m}^{-2} \text{ d}^{-1}$, and stations with 20+ gC m^{-2} were presumed to have a respiratory demand of $21 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Table 12).

Total annual benthic carbon consumption was calculated using summer total sediment oxygen uptake values, assuming a respiratory quotient (RQ) = 1 and winter benthic carbon consumption values equaling 60% of summer benthic carbon consumption values (Grebmeier, 1987), a 150 day open water season for the Northern Bering Sea (Grebmeier et al., 1989), and a 25 day open water season for the Beaufort Sea (Carmack and Macdonald, 2002). Annual benthic carbon consumption (ABCC) estimates were calculated using the equation $\text{ABCC} = (\text{mean summer benthic carbon mineralization (mmol C m}^{-2} \text{ d}^{-1}) * \# \text{ open water days} * 0.12 \text{ gC/mmol C}) + (0.60 * \text{mean summer benthic carbon mineralization (mmol C m}^{-2} \text{ d}^{-1}) * 365 - \# \text{ open water days} * 0.12 \text{ gC/mmol C})$ according to the methods of Grebmeier (1987).

Table 12. Stations and mean sediment oxygen rates used for model assumptions.

Model location	Stations used	Mean macroinfaunal biomass (gC m ⁻²)	Sediment oxygen respiration rate (mmol C m ⁻² d ⁻¹)
Beaufort Sea	BD-8	15.8	16.1
	BD-11	0.6	10.0
	H-1	0.7	10.0
	CK-3	1.2	10.0
		Mean=4.6	Mean= 11.5
Northern Bering Sea	SLIP-1	22.6	9.6
	SLIP-2	61.1	10.3
	SLIP-3	25.1	11.8
	SLIP-4	17.6	14.1
	SLIP-5	11.4	16.9
	UTBS-1	24.2	29.7
	UTBS-2	14.6	16.1
	UTBS-4	21.8	26.8
	UTBS-5	22.2	28.9
		Mean=24.5	Mean=17.3

Mean macroinfaunal carbon consumptions were calculated using the equation $MCD \text{ (macroinfaunal carbon demand)} = \text{mean benthic biomass (gC m}^{-2}\text{)} * (P/B) / TE$, where P/B is an annual production to biomass ratio assumed to equal 0.1 and TE is the food web transfer efficiency (Grebmeier, 1987). The transfer efficiency for each station was estimated by the equation $TE = \text{Station biomass (gC m}^{-2}\text{)} * (0.1 P/B) / (ABCC * \text{macroinfaunal percentage of total benthic carbon mineralization})$ according to the methods of Grebmeier (1987). The Northern Bering Sea station macroinfauna were assumed to account for 56% of total station benthic carbon mineralization (based on the calculations of Blackburn and Henriksen (1986) as was used in the model by Grebmeier (1987). The Beaufort Sea station macroinfauna were assumed to account for 13% of total station benthic carbon mineralization [based on the ACW (Alaskan Coastal Water) estimate of total benthic organic carbon mineralization calculated by Blackburn and

Henricksen (1986) and used by Grebmeier (1987)]. A general invertebrate transfer efficiency of 0.1 P/B was used for trophic level transfer efficiency calculations (Grebmeier, 1987).

Regional allochthonous primary production and terrestrial runoff contributions were calculated as the difference between annual community benthic carbon consumption and POC flux to the detritus pool in order to “balance” model carbon consumption and model carbon availability (Grebmeier, 1987).

The sum total of meiofaunal, microfaunal, and microbial carbon consumption was calculated as the difference between annual community benthic carbon consumption and annual macroinfaunal carbon consumption (Grebmeier, 1987).

Heterotrophic bacterial carbon consumption was estimated using previously calculated carbon consumption values (Rowe et al., 1997), assuming no differences between Northern Bering Sea and Beaufort Sea values, and that benthic bacterial carbon consumption values are accurately represented by the proportion of dissolved free amino acid (DFAA) uptake (Rowe et al., 1997).

Meiofaunal and microfaunal annual benthic carbon consumption rates were then calculated by subtracting the estimated annual heterotrophic bacterial carbon consumption rate from the sum total of meiofaunal, microfaunal, and microbial benthic carbon consumption values.

Annual benthic macroinfaunal deposit feeding carbon consumption rates were modified from estimates in Rowe et al. (1997). This high latitude study estimated that bacteria consumed $0.00076 \text{ gC m}^{-2} \text{ d}^{-1}$ or $0.27704 \text{ gC m}^{-2} \text{ yr}^{-1}$. The difference between total bacterial carbon consumption and bacterial respiration estimates represents the net

carbon incorporation used for growth, which was assumed in their model to equal the total amount consumed by infauna (Rowe et al., 1997). This has been modified for this study to utilize bacterial biomass [(calculated by abundance of cells * 20 fg C per cell; Wilhelm and Suttle, 1999)] multiplied by a trophic level (P/B) =0.1, as used for macroinfauna.

The total benthic carbon available for apex predator consumption was estimated to be the sum of carbon consumed by macroinfauna from both detritus pool and deposit feeding estimates multiplied by a trophic level transfer efficiency of 10% (Grebmeier, 1987). Meiofauna and microfauna may also be consumed by macroinfauna, but were neglected in these calculations.

Wilhelm and Suttle (1999) estimated that between 3-15% of bacteria are lysed by viral activity and bacteria reabsorb between 18 to 52% of dissolved organic matter (DOM). Estimates of bacterial carbon lysed by viruses were calculated using the 3-15% range and bacterial biomass values (this study); but since data were not available regarding the amount of carbon within the DOM pool, no estimates of bacterial uptake were calculated.

Results

In the model, the Northern Bering Sea benthos consumed $58.1 \text{ gC m}^{-2} \text{ yr}^{-1}$ and Beaufort Sea benthos consumed $31.7 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Figure 27). This is an overestimation of Beaufort Sea carbon consumption; since it was calculated assuming that respiration was proportional to biomass and derived from actual N. Bering Sea data. $16.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ were consumed by macroinfauna, $0.2 \text{ gC m}^{-2} \text{ yr}^{-1}$ by heterotrophic

Figure 27. Conceptual box model of benthic carbon flow through a high productivity (Northern Bering Sea, top numbers) region and a low productivity (Beaufort Sea, bottom numbers) region.

¹ Data from Wassmann et al. (2003).

² Calculations based on equations in Grebmeier (1987). A single asterisk (*) indicates that data used for this calculation were measured on this cruise (Grebmeier, unpublished data).

³ Values based on calculations in Rowe et al. (1997). A double asterisk (**) indicates that data used for this calculation were based on bacterial abundance and biomass obtained from this study.

⁴ Values based on percentage estimates in Wilhelm and Suttle (1999). A triple asterisk (***) indicates that data used for this calculation were based on bacterial abundance and biomass obtained from this study.



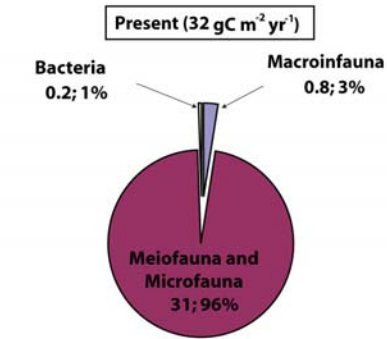
bacteria, and $41.2 \text{ gC m}^{-2} \text{ yr}^{-1}$ were consumed by meiofauna and microfauna in the Bering Sea. In the Beaufort Sea stations, only $0.8 \text{ gC m}^{-2} \text{ yr}^{-1}$ was consumed by macroinfauna, $0.2 \text{ gC m}^{-2} \text{ yr}^{-1}$ by heterotrophic bacteria, and $30.7 \text{ gC m}^{-2} \text{ yr}^{-1}$ by meiofauna and microfauna. The amounts of bacterial carbon consumed by deposit-feeding macroinfauna were very small in both regions— $0.0019 \text{ gC m}^{-2} \text{ yr}^{-1}$ in the Bering Sea and $0.0005 \text{ gC m}^{-2} \text{ yr}^{-1}$ in the Beaufort Sea.

The total amount of carbon available for apex predators such as predatory invertebrates, fish, birds, and marine mammals was estimated to be $2.1 \text{ gC m}^{-2} \text{ yr}^{-1}$ for the Bering Sea and $0.3 \text{ gC m}^{-2} \text{ yr}^{-1}$ for the Beaufort Sea. Viral lysis was assumed to release between 0.0069 and $0.0345 \text{ gC m}^{-2} \text{ yr}^{-1}$ of bacterial carbon into the DOM pool. To balance the model's carbon input with carbon consumption, the Beaufort Sea required an allochthonous input of $27.7 \text{ gC m}^{-2} \text{ yr}^{-1}$ although none was required for the Bering Sea. In the Bering Sea, $110.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ was available after benthic community consumption for burial or export out of the area. In the Beaufort Sea stations, no surplus of carbon was available after benthic community consumption.

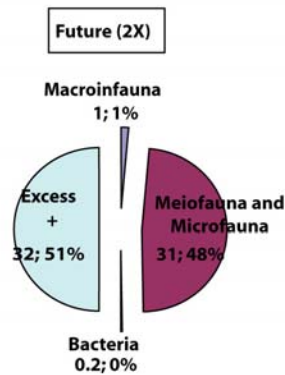
Global warming scenarios

Estimates of present day carbon usage can be taken from the conceptual box model and subjected to extremes of two global warming predictions in a low productivity Arctic marine system (the Beaufort Sea; Figure 28) and a high productivity Arctic marine system (the Northern Bering Sea; Figure 29), where (1) global warming increases primary productivity (for the sake of this exercise, a doubling of carbon deposition) and

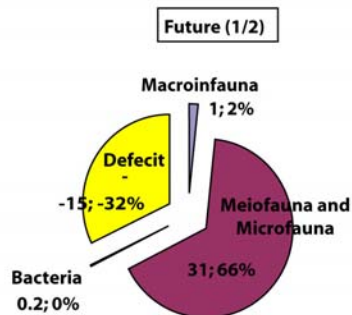
Annual Carbon Consumption Estimates A Low Productivity Arctic Area Example (Beaufort Sea)



NOTE: No excess carbon. 87% of estimated carbon demand required from allochthonous sources



.NOTE: Excess carbon now available. 75% of estimated carbon demand is required from allochthonous sources.

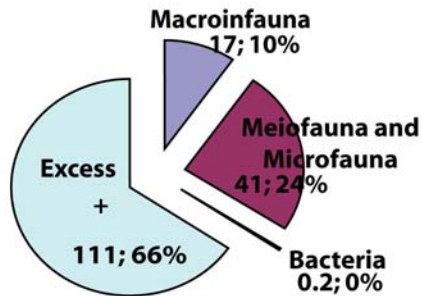


NOTE: Carbon demand cannot be met, even with input from allochthonous sources.

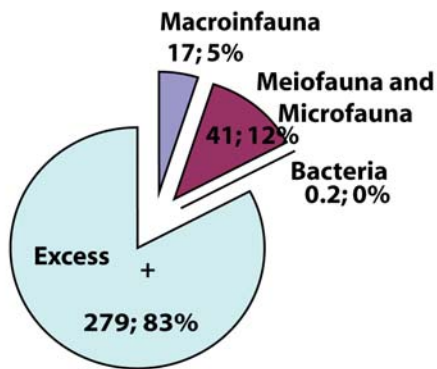
Figure 28. A graphical representation of global warming scenarios in a low productivity (Beaufort Sea) marine system.

Annual Carbon Consumption Estimates A High Productivity Arctic Area Example (Northern Bering Sea)

Present (169 gC m⁻²yr⁻¹)



Future (2X)



Future (1/2)

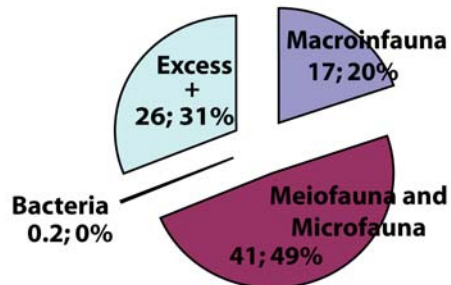


Figure 29. A graphical representation of global warming scenarios in a high productivity (Northern Bering Sea) marine system.

(2) where global warming decreases primary productivity (for the sake of this exercise, a halving of carbon deposition).

Discussion

The Northern Bering Sea stations were projected to have a much higher available source of carbon for benthic community consumption than the lower productivity Beaufort Sea stations. Local primary production in the Northern Bering Sea was adequate to sustain benthic community carbon demand, but the Beaufort Sea required 87% of its carbon to come from outside sources in order to sustain its benthic communities.

The assumption that benthic bacterial carbon consumption was equal in both regions is dubious, and this rate is based on the bacterial uptake of DFAA, which has been observed to occur without bacterial growth or production (Rowe et al., 1997). This may lead to inaccurate estimates of deposit feeding carbon supply and the amount of bacterial carbon released by viral lysis. Significant, one-order of magnitude differences between the bacterial biomass calculated in Rowe et al. (1997) and this study may be the result of the use of different carbon conversions. Rowe et al. (1997) used a conversion factor based on cell volume, and this study used a conversion factor based on carbon per cell.

The macroinfaunal carbon available for apex predator consumption in the northern Bering stations ($2.1 \text{ gC m}^{-2} \text{ yr}^{-1}$) was almost identical to the macroinfaunal carbon calculated for apex predators in Grebmeier's (1987) model ($2.0 \text{ gC m}^{-2} \text{ yr}^{-1}$), and the macroinfaunal carbon available for apex predator consumption in the low-

productivity Beaufort Sea stations ($0.38 \text{ gC m}^{-2} \text{ yr}^{-1}$) was only slightly lower than Grebmeier's (1987) calculations of $0.60 \text{ gC m}^{-2} \text{ yr}^{-1}$ for the hydrographically similar Alaskan Coastal Water of the northern Bering and southern Chukchi Seas.

When predictions of global warming effects on regional carbon deposition to the benthos are examined, it can be seen that in a low productivity system like the Beaufort Sea, increased primary productivity would allow for a surplus of carbon deposition such as is seen in the present day northern Bering Sea (assuming biotic carbon consumption remained constant and no carbon was lost from the system). A reduction in primary productivity would cause a large deficit of carbon that could not be balanced by allochthonous carbon sources (assuming biotic carbon consumption remained constant and no carbon was lost from the system). This deficit could very well cause mortality reduction in biomass of to macroinfaunal communities and a reduction of biodiversity.

In the high productivity northern Bering Sea, a doubling of primary productivity would result in an even larger surplus of carbon deposited to the benthos, in excess of benthic community carbon consumption demands (assuming biotic carbon consumption remained constant and carbon export did not change). If primary production was halved, carbon still remains in excess of benthic community carbon consumption demands (assuming biotic carbon consumption remained constant and carbon export did not change). From this exercise it can be seen that low productivity systems are far more susceptible to changes in carbon supply than high productivity systems, and depending on which way climate change will impact carbon fluxes, low productivity systems could either be bolstered to a higher productivity system or caused to crash.

VII. FINAL DISCUSSION AND CONCLUSIONS

The hypotheses pertaining to the thesis were:

1. “The macroinfaunal community diversity will be highest in the Bering and Chukchi Sea stations (previously documented productive stations), followed by the Gulf of Alaska (a well-known productive fishery), then the Canadian Archipelago (possessing a wide range of depths and environments), and lastly, the Beaufort Sea (known to have shallow depths, large freshwater inflow from the Mackenzie River, and seasonal ice scour).”

Result: Macroinfaunal community diversity was highest in the Bering and Chukchi Sea stations, followed by the CA, the GOA, and lastly, the Beaufort Sea stations with the lowest mean species diversity.

2. “Bacteria and viruses will both be significantly positively correlated to macroinfaunal biomass, abundance, and diversity, due to the utilization of the same carbon supply. “

Result: When all stations were grouped together, significant positive correlations occurred between sediment viral abundance and both macroinfaunal biomass and diversity. Positive significant correlations also occurred between bottom water bacterial and viral abundances and macroinfaunal biomass. Significant negative correlations occurred between integrated water column bacterial and viral abundances and both macroinfaunal biomass and macroinfaunal abundance in the CA.

3. “Significant pelagic-benthic coupling will exist throughout the study regions for both the macroinfaunal communities and bacterial and viral abundances since both groups of organisms should depend on pelagic food sources reaching the bottom.”

Result: In all study regions, significant positive relationships occurred between macroinfaunal communities (biomass and diversity) and the surface-derived chlorophyll *a* supply. This, in addition to the significant correlations of both bottom water salinity and temperature with macroinfaunal biomass and diversity, indicates that pelagic-benthic coupling existing throughout the study regions for macroinfauna. Both bacterial and viral abundances also showed evidence of pelagic-benthic coupling throughout the study regions, with sediment abundances significantly and positively correlated with temperature, salinity, and surface-derived chlorophyll *a* content.

The productivity, sediment tracer parameters, hydrographic parameters, and both biomass and biodiversity of macroinfaunal communities varied widely throughout the Arctic study regions. Biodiversity is an important component of ecosystem dynamics, providing various species the capacity to perform vital ecological functional roles, providing higher trophics with a selection of various prey items, and acting as a form of biological insurance against environmental disruptions. This biological insurance, however, can only buffer against so much environmental disruption (such as global warming regime shifts), and additional study is needed to discern how resilient the system is.

LIST OF REFERENCES

- Aagaard, K. & Carmack, E.C. (1989) The Role of Sea Ice and Other Fresh-Water in the Arctic Circulation. Journal of Geophysical Research-Oceans, 94, 14485-14498.
- Aagaard, K., Coachman, L.K., & Carmack, E.C. (1981) On the Halocline of the Arctic Ocean. Deep-Sea Research (A), 28, 529-545.
- Aller, R.C., Yingst, J.Y., & Ullman, W.J. (1983) Comparative biogeochemistry of water in intertidal Onuphis (Polychaeta) and Upogebia (Crustacea) burrows-temporal patterns and causes. Journal of Marine Research, 41 (3), 571-604.
- Aller, J.Y., & Aller, R.C. (1986) Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the Hebble Site, western North-Atlantic. Deep-Sea Research (A), 33 (6), 755-790.
- Aller, R. C., & Yingst, J. Y. (1978) Biogeochemistry of tube dwellings-study of sedentary polychaete *Amphitrite ornata* (Leidy). Journal of Marine Research, 36 (2), 201-258.
- Angel, M.V. (1997). Pelagic biodiversity. In Marine Biodiversity: Patterns and Processes (eds R.F.G. Ormond, John D. Gage, and Martin V. Angel). Cambridge University Press, Cambridge.
- Atkinson, E.G. & Wacasey, J.W. (1987) Sedimentation in Arctic Canada – Particulate Organic-Carbon Flux to a Shallow Marine Benthic Community in Frobisher Bay. Polar Biology, 8, 3-7.
- Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., & Thingstad, F. (1983) The Ecological Role of Water-Column Microbes in the Sea. Marine Ecology-Progress Series, 10, 257-263.
- Baines, S.B. & M.L. Pace (1991) The production of dissolved organic carbon by

- phytoplankton and its importance to bacteria—patterns across marine and fresh-water systems. Limnology and Oceanography, 36 (6), 1078-1090.
- Bano, N. & Hollibaugh, J.T. (2000) Diversity and distribution of DNA sequences with affinity to ammonia-oxidizing bacteria of the beta subdivision of the class Proteobacteria in the Arctic Ocean. Applied and Environmental Microbiology, 66, 1960-1969.
- Bergh, O., Borsheim, K.Y., Bratbak, G., & Heldal, M. (1989) High abundance of viruses found in aquatic environments. Nature, 340, 467-468.
- Bernard, C. & Fenchel, T. (1995) Mats of colourless sulphur bacteria 2. Structure, composition of biota and successional patterns. Marine Ecology-Progress Series, 128, 171-179.
- Bettarel, Y., Sime-Ngando, T., Amblard, C., & Laveran, H. (2000) A comparison of methods for counting viruses in aquatic systems. Applied and Environmental Microbiology, 66 (6), 2283-2289.
- Blanchard, G.F., Sauriau, P.G., Gall, V.C.L., Goulet, D., Olivier, F. (1997). Kinetics of tidal resuspension of microbiota: Testing the effects of sediment cohesiveness and bioturbation using flume experiments. Marine Ecology-Progress Series, 151, 17-25.
- Borsheim, K.Y., Bratbak, G., & Heldal, M. (1990) Enumeration and biomass estimation of planktonic bacteria and viruses by transmission electron-microscopy. Applied and Environmental Microbiology, 56, 352-356.
- Carey, A.G. (1991) Ecology of North-American Arctic Continental-Shelf Benthos – a Review. Continental Shelf Research, 11, 865-883.

- Carmack, E.C. (2000) St. Roch background. Unpublished report, Institute of Ocean Sciences, Sidney, BC.
- Carmack, E.C. & MacDonald, R.W. (2002) Oceanography of the Canadian shelf of the Beaufort Sea: A setting for marine life. Arctic, 55, 29-45.
- Carmack, E.C., Macdonald, R.W., & Papadakis, J.E. (1989) Water Mass Structure and Boundaries in the Mackenzie Shelf Estuary. Journal of Geophysical Research-Oceans, 94, 18043-18055.
- Coastal and Marine Geology InfoBank Atlas: Alaska region. USGS. 19 December 2002. < <http://walrus.wr.usgs.gov/infobank/gazette/html/regions/ak.html>>.
- Conlan, K.E., Lenihan, H.S., Kvitek, R.G., & Oliver, J.S. (1998) Ice scour disturbance to benthic communities in the Canadian High Arctic. Marine Ecology-Progress Series, 166, 1-16.
- Cooper, L.W., Grebmeier, J.M., Larsen, I.L., Egorov, V.G., Theodorakis, C., Kelly, H.P., & Lovvorn, J.R. (2002) Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Marine Ecology-Progress Series, 226, 13-26.
- Cooper, L.W., Larsen, I.L., Beasley, T.M., Dolvin, S.S., Grebmeier, J.M., Kelley, J.M., Scott, M., & Johnson-Pyrtle, A. (1998) The distribution of radiocesium and plutonium in sea ice- entrained Arctic sediments in relation to potential sources and sinks. Journal of Environmental Radioactivity, 39, 279-303.
- Cota, G.F., Kottmeier, S.T., Robinson, D.H., Smith, W.O., & Sullivan C.W. (1990) Bacterioplankton in the marginal ice-zone of the Weddell Sea—biomass, production, and metabolic activities during austral autumn. Deep-Sea Research

(A), 37, 1145-1167.

Danovaro, R., Dell'anno, A., Trucco, A., Serresi, M., & Vanucci, S. (2001)

Determination of virus abundance in marine sediments. Applied and Environmental Microbiology, 67, 1384-1387.

Danovaro, R. & Serresi, M. (2000) Viral density and virus-to-bacterium ratio in deep-sea

sediments of the Eastern Mediterranean. Applied and Environmental Microbiology, 66, 1857-1861.

Davidson, A. & Belbin, L. (2002) Exposure of natural Antarctic marine microbial

assemblages to ambient UV radiation: effects on the marine microbial community. Aquatic Microbial Ecology, 27, 159-174.

Deflaun, M.F. & Mayer, L.M. (1983) Relationships between bacteria and grain surfaces

in intertidal sediments. Limnology and Oceanography, 28 (5), 873-881.

Deming, J.W. (2002) Psychrophiles and polar regions. Current Opinion in Microbiology,

5, 301-309.

Dunbar, M.J. (1981). Physical causes and biological significance of polynyas and other

open water in sea ice. In Polynyas in the Canadian Arctic (eds. I. Stirling & H. Cleator). Canadian Wildlife Service, Ottawa, Canada.

Dunton, K. (1992) Arctic Biogeography - the Paradox of the Marine Benthic Fauna and

Flora. Trends in Ecology & Evolution, 7, 183-189.

Dunton, K.H., J.M. Grebmeier, D.R. Maidment, and S.V. Schonberg. (2002) Benthic

faunal processes in the western arctic: linkage to overlying water column

processes. EOS Trans. AGU, 83 (4), Ocean Sciences Meet. Suppl., Abstract

OS32M-06.

- Elmgren, R. & Hill, C. (1997) Ecosystem function at low diversity: The Baltic Example. In Marine Biodiversity: Patterns and Processes (eds. R.F.G. Ormond, John D. Gage, and Martin V. Angel),. Cambridge University Press, Cambridge.
- Environment Canada. (1972). Ice summary and analysis 1970 of the Canadian Arctic. Atmospheric Environment, Toronto, Ontario.
- Eppley, R.W. (1972) Temperature and Phytoplankton Growth in Sea. Fishery Bulletin, 70, 1063-1085.
- Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., & Whitledge, T.E. (1994) The Northeastern Chukchi Sea - Benthos-Environmental Interactions. Marine Ecology-Progress Series, 111, 171-190.
- Feder, H.M. & S. C. Jewett (1986). The Subtidal Benthos. In The Gulf of Alaska: Physical Environment and Biological Resources (eds. Hood, D.W. & S.T. Zimmerman). Alaska Office, Ocean Assessments Division, National Oceanic and Atmospheric Administration, U.S Department of Commerce.
- Fenchel, T. & Bernard, C. (1995) Mats of colourless sulphur bacteria .1. Major microbial processes. Marine Ecology-Progress Series, 128, 161-170.
- Fisheries-Oceanography Coordinated Investigations. NOAA. 19 December 2002. < <http://www.pmel.noaa.gov/foci/brochure/Map.html>>.
- Fortier, L., Martin Fortier, and 42 Canadian PIs and over 70 potential collaborators from 8 countries (2000) The Canadian Arctic Shelf Exchange Study (CASES). In Shelf-Basin Interactions Pan-Arctic Meeting (ed. J.M. Grebmeier). SBI Project Office, Callaway Gardens, GA, USA. 3 April 2003. <<http://arctic.bio.utk.edu>>.
- Friedrichs, M., Graf, G., & Springer, B. (2000) Skimming flow induced over a simulated

- polychate tube lawn at low population densities. Marine Ecology-Progress Series, 192, 219-228.
- Fuhrman, J.A., & Azam, F. (1980) Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. Applied Environmental Microbiology. 39, 1085-1095.
- Fuhrman, J.A. (1999) Marine viruses and their biogeochemical and ecological effects. Nature, 399, 541-548.
- Fuhrman, J.A. & Noble, R.T. (1995) Viruses and protists cause similar bacterial mortality in coastal seawater. Limnology and Oceanography, 40, 1236-1242.
- Fuhrman, J.A., Sleeter, T.D., Carlson, C.A., & Proctor, L.M. (1989) Dominance of Bacterial Biomass in the Sargasso Sea and Its Ecological Implications. Marine Ecology-Progress Series, 57, 207-217.
- George, R.Y. & .A. Z. Paul. (1970). USC-FSU biological investigations from the Fletcher's Ice Island T-3 on deep-sea and under-ice benthos of the Arctic Ocean. Technical Report #1. University of Southern California, Los Angeles, CA, USA.
- Gobler, C.J., Hutchins, D.A., Fisher, N.S., Cosper, E.M., & Sanudo-Wilhelmy, S.A. (1997) Release and bioavailability of C, N, P, Se, and Fe following viral lysis of a marine chrysophyte. Limnology and Oceanography, 42, 1492-1504.
- Gradinger, R. & Zhang, Q. (1997) Vertical distribution of bacteria in Arctic sea ice from the Barents and Laptev Seas. Polar Biology, 17, 448-454.
- Gray, J.S. (1981) The ecology of marine sediments. Cambridge University Press, Cambridge.
- Grebmeier, J.M. (1987) The Ecology of Benthic Carbon Cycling in the Northern Bering

- and Chukchi Seas. Ph.D. dissertation, University of Alaska, Fairbanks, Fairbanks, Alaska, USA.
- Grebmeier, J.M. (1993) Studies of Pelagic Benthic Coupling Extended onto the Soviet Continental-Shelf in the Northern Bering and Chukchi Seas. Continental Shelf Research, 13, 653-668.
- Grebmeier, J.M., Smith, W.O. Jr. & Conover, R.J. (1995). Biological Processes on Arctic Continental Shelves: Ice-Ocean-Biotic Interactions. In Arctic Oceanography: Marginal Ice Zones and Continental Shelves (eds. W.O. Smith, Jr. and J. M. Grebmeier). American Geophysical Union, Washington, D.C., USA.
- Grebmeier, J.M., & K.H. Dunton (2000) Benthic Processes in the Northern Bering/Chukchi Seas: Status and Global Change. In Impacts of Changes in Sea Ice and Other Environmental Parameters in the Arctic, Marine Mammal Commission Workshop (ed. H.P. Huntington), pp. 80-93, Girdwood, Alaska.
- Grebmeier, J.M. & Cooper, L.W. (1995) Influence of the St-Lawrence-Island Polynya Upon the Bering Sea Benthos. Journal of Geophysical Research-Oceans, 100, 4439-4460.
- Grebmeier, J.M., Feder, H.M., & McRoy, C.P. (1989) Pelagic-Benthic Coupling on the Shelf of the Northern Bering and Chukchi Seas .II. Benthic Community Structure. Marine Ecology-Progress Series, 51, 253-268.
- Grebmeier, J.M. & Harrison, N.M. (1992) Seabird Feeding on Benthic Amphipods Facilitated by Gray Whale Activity in the Northern Bering Sea. Marine Ecology-Progress Series, 80, 125-133.

- Grebmeier, J.M. & McRoy, C.P. (1989) Pelagic-Benthic Coupling on the Shelf of the Northern Bering and Chukchi Seas .III. Benthic Food-Supply and Carbon Cycling. Marine Ecology-Progress Series, 53, 79-91.
- Grebmeier, J.M., McRoy, C.P., & Feder, H.M. (1988) Pelagic-Benthic Coupling on the Shelf of the Northern Bering and Chukchi Seas .I. Food-Supply Source and Benthic Biomass. Marine Ecology-Progress Series, 48, 57-67.
- Grebmeier, J.M. & Cooper, L.W. (1994). A decade of benthic research on the continental shelves of the northern Bering and Chukchi Seas: Lessons learned. In Bridges of Science between North America and the Russian Far East (eds. R.H. Meehan, V. Sergienko, and G. Weller). Arctic Division, American Association for the Advancement of Science, Fairbanks, Alaska.
- Grebmeier, J.M. & Cooper, L.W. (In press) Sediment biogeochemical tracers and carbon cycling in the Bering and Chukchi seas during 1988 and 1993.
- Grotefendt, K., Logemann, K., Quadfasel, D., & Ronski, S. (1998) Is the Arctic Ocean warming? Journal of Geophysical Research-Oceans, 103, 27679-27687.
- Gutt, J. (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biology, 24, 55-564.
- Helmke, E. & Weyland, H. (1995) Bacteria in sea ice and underlying water of the Eastern Weddell Sea in Midwinter. Marine Ecology-Progress Series, 117, 269-287.
- Herndl, G.J., & Peduzzi, P. (1989) Potential microbial utilization rates of sublittoral gastropod mucus trails. Limnology and Oceanography, 34, 780-784.
- Hewson, I., O'Neil, J.M., Fuhrman, J.A., & Dennison, W.C. (2001a) Virus-like particle

- distribution and abundance in sediments and overlying waters along eutrophication gradients in two subtropical estuaries. Limnology and Oceanography, 46, 1734-1746.
- Hewson, I., O'Neil, J.M., Heil, C.A., Bratbak, G., & Dennison, W.C. (2001b) Effects of concentrated viral communities on photosynthesis and community composition of co-occurring benthic microalgae and phytoplankton. Aquatic Microbial Ecology, 25, 1-10.
- Highsmith, R.C. & Coyle, K.O. (1992) Productivity of arctic amphipods relative to gray whale energy requirements. Marine Ecology-Progress Series, 83, 141-150.
- Hobbie, J.E., Daley, R.J., & Jasper, S. (1977) Use of Nuclepore Filters for Counting Bacteria by Fluorescence Microscopy. Applied and Environmental Microbiology, 33, 1225-1228.
- Horrigan, S.G. (1981) Primary Production under the Ross Ice Shelf, Antarctica. Limnology and Oceanography, 26, 378-382.
- Huettel, M., & Gust, G. (1992) Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. Marine Ecology-Progress Series, 82, 187-197.
- Hunt, George L, Jr. (2002) Ecosystem studies of sub-arctic seas: results of a workshop held in Laguna Beach, California, September 4-6, 2002. 13 pp.
- Huston, A.L., Krieger-Brockett, B.B., & Deming, J.W. (2000) Remarkably low temperature optima for extracellular enzyme activity from Arctic bacteria and sea ice. Environmental Microbiology, 2, 383-388.

- Kristensen, E. (1984) Effect of natural concentrations on nutrient exchange between a polychaete burrow in estuarine sediment and the overlying water. Journal of Experimental Marine Biology and Ecology, 75, 171-190.
- Kristensen, E., Jensen, M.H., & Andersen, T. K. (1985) The impact of polychaete (*Nereis-Virens sars*) burrows on nitrification and nitrate reduction in estuarine sediments. Journal of Experimental Marine Biology and Ecology, 85, 75-91.
- Krumbein, W.C., 1934. Size frequency distributions of sediments, Journal of Sedimentary Petrology, 4, 65-77.
- Kvitek, R.G., Conlan, K.E., & Iampietro, P.J. (1998) Black pools of death: hypoxic, brine-filled ice gouge depressions become lethal traps for benthic organisms in a shallow Arctic embayment. Marine Ecology-Progress Series, 162, 1-10.
- Laurion, I., Demers, S., & Veznia, A.F. (1995) The microbial food-web associated with the ice algal assemblage-biomass and bacterivory of nanoflagellate protozoans in Resolute Passage (High Canadian Arctic). Marine Ecology-Progress Series, 120, 77-87.
- Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos, 9, 3-17.
- Lovejoy, C, Legendre, L, & Price, N.M. (2002) Prolonged diatom blooms and microbial food web dynamics: experimental results from an Arctic polynya. Aquatic Microbial Ecology, 29, 267-278.
- Maranger, R. & Bird, D.E. (1996) High concentrations of viruses in the sediments of Lac Gilbert, Quebec. Microbial Ecology, 31, 141-151.
- Maranger, R. & Bird, D.F. (1995) Viral abundance in aquatic systems - a comparison

- between marine and fresh-waters. Marine Ecology-Progress Series, 121, 217-226.
- Maranger, R., Bird, D.F., & Juniper, S.K. (1994) Viral and bacterial dynamics in arctic sea-ice during the spring algal bloom near Resolute, NWT, Canada. Marine Ecology-Progress Series, 111, 121-127.
- Marinelli, R.L. (1994) Effects of burrow ventilation on activities of a terebellid polychaete and silicate removal from sediment pore waters. Limnology and Oceanography, 39, 303-317.
- Marinelli, R.L., Lovell, C.R., Wakeham, S.G., Ringelberg, D.B., & White, D.C. (2002) Experimental investigation of the control of bacterial community composition in macroinfaunal burrows. Marine Ecology-Progress Series, 235, 1-13.
- Markham, W.E. (1981) Ice Atlas--Canadian arctic waterways. Environment Canada, Atmospheric Environment Service, Ottawa, Ontario.
- McGrady-Steed, J.P. Harris, & Morin, P.J. 1997. Biodiversity regulates ecosystem predictability. Nature, 390, 162-165.
- Melling, H. (1993) The formation of a haline shelf front in wintertime in an ice-covered arctic sea. Continental Shelf Research, 13, 1123-1147.
- Melling, H., Lake, R.A., Topham, D.R., & Fissel, D.B. (1984) Oceanic thermal structure in the western Canadian Arctic. Continental Shelf Research, 3, 233-258.
- Middelboe, M., Jorgensen, N.O.G., & Kroer, N. (1996) Effects of viruses on nutrient turnover and growth efficiency of noninfected marine bacterioplankton. Applied and Environmental Microbiology, 62, 1991-1997.
- Middelboe, M. & Lyck, P.G. (2002) Regeneration of dissolved organic matter by viral

- lysis in marine microbial communities. Aquatic Microbial Ecology, 27, 187-194.
- Munchow, A., Weingartner, T.J., & Cooper, L.W. (1999) The summer hydrography and surface circulation of the east Siberian shelf Sea. Journal of Physical Oceanography, 29, 2167-2182.
- Nagata, T. & Kirchman, D.L. (1992) Release of macromolecular organic-complexes by heterotrophic marine flagellates. Marine Ecology-Progress Series, 83, 233-240.
- Naeem, S., & Li, S. 1997. Biodiversity enhances ecosystem reliability. Nature, 390, 507-509.
- Naeem, S., Hahn, D.R., & Schuurman, G. (2000) Producer-decomposer co-dependency influences biodiversity effects. Nature, 403, 762-764.
- Niebauer, H.J., Alexander, V., & Henrichs, S.M. (1995) A time-series study of the spring bloom at the Bering Sea-ice edge I. Physical processes, chlorophyll and nutrient chemistry. Continental Shelf Research, 15, 1859-1877.
- Niebauer, H.J., Roberts, J., & Royer, T.C. (1981) Shelf break circulation in the northern Gulf of Alaska. Journal of Geophysical Research-Oceans and Atmospheres, 86, 4231-4242.
- Noble, R.T. & Fuhrman, J.A. (1998) Use of SYBR Green I for rapid epifluorescence counts of marine viruses and bacteria. Aquatic Microbial Ecology, 14, 113-118.
- Noble, R.T. & Fuhrman, J.A. (1999) Breakdown and microbial uptake of marine viruses and other lysis products. Aquatic Microbial Ecology, 20, 1-11.
- Oechel, W.C. & Vourlitis, G.L. (1994) The effects of climate-change on land atmosphere feedbacks in arctic tundra regions. Trends in Ecology & Evolution, 9, 324-329.

- Pacific Walrus Research: Bering and Chukchi Sea Databases—Bathymetry Coverage.
USGS. 19 December 2002.
<<http://www.absc.usgs.gov/research/walrus/bering/bathy/>>.
- Paul, A.Z. & Menzies, R.J. (1974) Benthic ecology of the high arctic deep sea. Marine Biology, 27, 251-262.
- Petersen, G.H. & Curtis, M.A. (1980) Differences in energy flow through major components of subarctic, temperate, and tropical marine shelf ecosystems. Dana, 1, 53-64.
- Peterson, B. J., R. M. Holmes, J.W. McClelland, C.J. Vörösmarty, R.B. Lammers, A.I. Shiklomanov, I.A. Shiklomanov, & Rahmstorf, S. Increasing river discharge to the Arctic Ocean. Science, vol. 298, Dec. 13, 2002, 2171-2173.
- Pimm, S.L. (1984) The complexity and stability of ecosystems. Nature, 307, 321-326.
- Plante, C.J., Jumars, P.A., & Baross, J.A. (1990) Digestive associations between marine detritivores and bacteria. Annual Review of Ecology and Systematics, 21, 93-127.
- Pomeroy, L.R. (1974) Oceans food web, a changing paradigm. Bioscience, 24, 499-504.
- Pomeroy, L.R. & Wiebe, W.J. (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquatic Microbial Ecology, 23, 187-204.
- Prinsenberg, S.J. & Bennett, E.B. (1987) Mixing and transports in Barrow Strait, the central part of the Northwest Passage. Continental Shelf Research, 7, 913-935.
- Proctor, L.M. & Fuhrman, J.A. (1990) Viral mortality of marine bacteria and

- cyanobacteria. Nature, 343, 60-62.
- Proctor, L.M. & Fuhrman, J.A. (1992) Mortality of marine bacteria in response to enrichments of the virus size fraction from seawater. Marine Ecology-Progress Series, 87, 283-293.
- Ray, G.C., Hayden, B.P, McCormick-Ray, M.G., & Smith, T.M. (1997). Land-seascape diversity of the USA East Coast coastal zone with particular reference to estuaries. In Marine biodiversity: Patterns and Processes (eds. R.F.G. Ormond, John D. Gage, and Martin V. Angel). Cambridge University Press, Cambridge.
- Reed, A.J. (1998) Benthic macroinfaunal invertebrates of the East Siberian and Chukchi Seas: Benthic biomass, community structure, and radionuclide contamination. M.S., University of Tennessee, Knoxville, Knoxville, TN, USA.
- Reed, R.K., J. D. Schumacher, & Incze, L.S. (1987) Circulation in Shelikof Strait, Alaska. Journal of Physical Oceanography, 17, 1546-1554.
- Reimnitz, E., Kempema, E.W., & Barnes, P.W. (1987) Anchor ice, seabed freezing, and sediment dynamics in shallow arctic seas. Journal of Geophysical Research-Oceans, 92, 14671-14678.
- Reimnitz, E., McCormick, M., Bischof, J., & Darby, D.A. (1998) Comparing sea-ice sediment load with Beaufort Sea shelf deposits: Is entrainment selective? Journal of Sedimentary Research, 68, 777-787.
- Rinta-Kanto, J. (2001) The effect of viral size class enrichments on microbial communities in marine systems. M.S., University of Kuopio, Finland, Kuopio, Finland, 56 pp.

- Rothrock, D.A., Yu, Y., & Maykut, G.A. (1999) Thinning of the Arctic sea-ice cover. Geophysical Research Letters, 26, 3469-3472.
- Rowe, G.T., Boland, G.S., Briones, E.G.E., CruzKaegi, M.E., Newton, A., Piepenburg, D., Walsh, I., & Deming, J.(1997) Sediment community biomass and respiration in the Northeast Water Polynya, Greenland: A numerical simulation of benthic lander and spade core data. Journal of Marine Systems, 10, 497-515.
- Royer, T.C. (1982) Coastal fresh water discharge in the northeast Pacific. Journal of Geophysical Research-Oceans, 87, 2017-2021.
- Schmidt, J.L., Deming, J.W., Jumars, P.A., & Keil, R.G. (1998) Constancy of bacterial abundance in surficial marine sediments. Limnology and Oceanography, 43, 976-982.
- Schottler, U., Wienhausen, G., & Zebe, E. (1983) The mode of energy-production in the lugworm *Arenicola marina* at different oxygen concentrations. Journal of Comparative Physiology, 14, 547-555.
- Schumacher, J.D. & Reed, R.K. (1986) On the Alaska Coastal Current in the Western Gulf of Alaska. Journal of Geophysical Research-Oceans, 91, 9655-9661.
- Shannon, C.E. & Weaver .W. (1963) The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois, USA.
- Skidmore, M.L., Foght, J.M., & Sharp, M.J. (2000) Microbial life beneath a high Arctic glacier. Applied and Environmental Microbiology, 66, 3214-3220.
- Smith, C.R., Jumars, P.A., & Demaster, D.J. (1986) In situ studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. Nature, 323(6085), 251-253.

- Soltwedel, T., & Vopel, K. (2001) Bacterial abundance and biomass in response to organism-generated habitat heterogeneity in deep-sea sediments. Marine Ecology-Progress Series, 219, 291-298.
- Stabeno, P.J., Reed, R.K., & Schumacher, J.D. (1995) The Alaska Coastal Current – continuity of transport and forcing. Journal of Geophysical Research-Oceans, 100, 2477-2485.
- Steward, G.F., Smith, D.C., & Azam, F. (1996) Abundance and production of bacteria and viruses in the Bering and Chukchi Seas. Marine Ecology-Progress Series, 131, 287-300.
- Stirling, I. (1997) The importance of polynyas, ice edges, and leads to marine mammals and birds. Journal of Marine Systems, 10, 9-21.
- Stoker, S.W. (1978) Benthic invertebrate macroinfauna of the eastern continental shelf of the Bering/Chukchi Seas. Ph. D., University of Alaska, Fairbanks, Fairbanks, Alaska, USA.
- Stoker, S.W. (1981). Benthic invertebrate macroinfauna of the eastern Bering/Chukchi continental shelf. In The Eastern Bering Sea Shelf: Oceanography and Resources (eds. D.W. Hood and J.A. Calder), Vol. 2. University of Washington Press, Seattle.
- Stuart, V., Field, J.G., & Newell, R.C. (1982) Evidence for absorption of kelp detritus by the ribbed mussel *Aulacomya ater* using a new CR-51 labeled microsphere technique. Marine Ecology-Progress Series, 9, 263-271.
- Suttle, C.A. (1991) Use of ultrafiltration to isolate viruses from seawater which are pathogens of marine phytoplankton. Applied Environmental Microbiology. 57,

721-726.

- Suttle, C.A. (1994) The significance of viruses to mortality in aquatic microbial communities. Microbial Ecology, 28, 237-243.
- Thingstad, T.F., Nielsen, T.G., Hansen, A.S., & Levinsen, H. (2002) Control of bacterial production in cold waters. A theoretical analysis of mechanisms relating bacterial production and zooplankton biomass in Disko Bay, Western Greenland. Marine Ecology-Progress Series, 228, 15-24.
- Thomson, D.H. (1982) Marine benthos in the Eastern Canadian High Arctic: multivariate analysis of standing crop and community structure. Arctic, 35, 61-74.
- Tickell, C. (1997). Foreward: The value of diversity. In Marine Biodiversity: Patterns and Processes (eds. R.F.G. Ormond, John D. Gage, and Martin V. Angel). Cambridge University Press, Cambridge.
- Tilman, D. (1996) Biodiversity: Population versus ecosystem stability. Ecology, 77, 350-363.
- Van Es, & Meyer-Reil. Biomass and metabolic activity of heterotrophic marine bacteria. In: Advances in Microbial Ecology Plenum (ed. K. Marshall). New York.
- Vaque, D., Calderon-Paz, J.I., Guixa-Boixereu, N., & Pedros-Alio, C. (2002) Spatial distribution of microbial biomass and activity (bacterivory and bacterial production) in the northern Weddell Sea during the austral summer (January 1994). Aquatic Microbial Ecology, 29, 107-121.
- Voytek, M.A. & Ward, B.B. (1995) Detection of ammonium-oxidizing bacteria of the

beta-subclass of the class Proteobacteria in aquatic samples with PCR.

Applied and Environmental Microbiology, 61, 1444-1450.

Walsh, J.J., McRoy, C.P., Coachman, L.K., Goering, J.J., Nihoul, J.J., Whitledge, T.E., Blackburn, T.H., Parker, P.L., Wirick, C.D., Shuert, P.G., Grebmeier, J.M., Springer, A.M., Tripp, R.D., Hansell, D.A., Djenidi, S., Deleersnijder, E., Henriksen, K., Lund, B.A., Andersen, P., Mullerkarger, F.E., & Dean, K. (1989) Carbon and nitrogen cycling within the Bering and Chukchi Seas – source regions for organic matter effecting AOU demands of the Arctic Ocean. Progress in Oceanography, 22, 277-359.

Wassmann, P., Bauerfeind, E., Fortier, M., Fukuchi, M., Hargrave, B., Noji, T., Nothig, E.M., Olli, K., Peinert, R., Sasaki, H., & Shevchenko, V. P. (2003) Particulate organic carbon flux to the Arctic Ocean sea floor. In: *The Arctic Ocean Organic Carbon Cycle: Present and Past* (Eds. R. Stein and R. W. Macdonald) Springer, NY (in review).

Weinbauer, M.G., Fuks D., & Peduzzi, P. (1993) Distribution of viruses and dissolved DNA along a coastal trophic gradient in the northern Adriatic Sea. Applied and Environmental Microbiology, 59, 4074-4082.

Weinbauer, M.G., Wilhelm, S.W., Suttle, C.A., & Garza, D.R. (1997) Photoreactivation compensates for UV damage and restores infectivity to natural marine virus communities. Applied and Environmental Microbiology, 63, 2200-2205.

Weinbauer, M.G., Wilhelm, S.W., Suttle, C.A., Pledger, R.J., & Mitchell, D.L. (1999) Sunlight-induced DNA damage and resistance in natural viral communities. Aquatic Microbial Ecology, 17, 111-120.

- Weingartner, T. J., K. Coyle, B. Finney, R. Hopcroft, T. Whitley, R. Brodeur, M. Dagg, E. Farley, D. Haidvogel, L. Halderson, A. Hermann, S. Hinkley, J. Napp, P. Staben, T. Kline, C. Lee, E. Lessard, T. Royer, & Strom, S. The Northeast Pacific GLOBEC Program: Coastal Gulf of Alaska. Oceanography, Special Issue, 15, 2, 48-63.
- Weingartner, T.J., K. Aagaard, K. Shimada, R. Woodgate, D. Cavalieri, & Danielson, S. (2001) Circulation on the Central Chukchi Sea Shelf. In Western Arctic Shelf-Basin Interaction, Albuquerque, N.M., USA. SBI Project Office, 1015 Research Dr. Suite 100, Bldg. A., Knoxville, TN, 37932.
- Wells, L.E. & Deming, J.W. (2003) Abundance of Bacteria, the Cytophaga-Flavobacterium cluster and Archaea in cold oligotrophic waters and nepheloid layers of the Northwest Passage, Canadian Archipelago. Aquatic Microbial Ecology, 31, 19-31.
- Welschmeyer, N.A. (1994) Fluorometric analysis of chlorophyll-*a* in the presence of chlorophyll-*b* and pheopigments. Limnology and Oceanography, 39, 1985-1992.
- Werner, I. & Gradinger, R. (2002) Under-ice amphipods in the Greenland Sea and Fram Strait (Arctic): environmental controls and seasonal patterns below the pack ice. Marine Biology, 140, 317-326.
- Whitman, W.B., Coleman, D.C., & Wiebe, W.J. (1998) Prokaryotes: The unseen majority. Proceedings of the National Academy of Sciences of the United States of America, 95, 6578-6583.
- Wilhelm, S.W., Jeffrey, W.H., Suttle, C.A., & Mitchell, D.L. (2002) Estimation of biologically damaging UV levels in marine surface waters with DNA and viral

- dosimeters. Photochemistry and Photobiology, 76, 268-273.
- Wilhelm, S.W. & Suttle, C.A. (1999) Viruses and nutrient cycles in the sea – viruses play critical roles in the structure and function of aquatic food webs. Bioscience, 49, 781-788.
- Wilhelm, S.W., Weinbauer, M.G., Suttle, C.A., & Jeffrey, W.H. (1998) The role of sunlight in the removal and repair of viruses in the sea. Limnology and Oceanography, 43, 586-592.
- Wilhelm, S.W., Weinbauer, M.G., Suttle, C.A., Pledger, R.J., & Mitchell, D.L. (1998) Measurements of DNA damage and photoreactivation imply that most viruses in marine surface waters are infective. Aquatic Microbial Ecology, 14, 215-222.
- Wommack, K.E. & Colwell, R.R. (2000) Virioplankton: Viruses in aquatic ecosystems. Microbiology and Molecular Biology Reviews, 64, 69-114.
- Yager, P.L. & Deming, J.W. (1999) Pelagic microbial activity in an arctic polynya: Testing for temperature and substrate interactions using a kinetic approach. Limnology and Oceanography, 44, 1882-1893.
- Zenkevitch, L. (1963) Biology of the Seas of the U.S.S.R. Interscience Publishers, New York, New York.
- Zobell, CE. (1942) Bacteria of the marine world. Scientific Monthly, 55, 320-330.

APPENDICES

Appendix A. Stations occupied during the Laurier 2000 cruise. Station number (#), station name, date occupied (MM/DD/YY), coordinates (°N and °W), and depth (meters) are shown.

Station number	Station name	Date	Latitude (°N)	Longitude (°W)	Depth (m)
3	BD-1	07/08/00	54.533	-131.428	65
4	BD-2	07/09/00	55.623	-135.013	210
5	BD-3	07/10/00	57.775	-140.358	3229
13	KY-1	07/11/00	59.928	-144.000	53
23	SW-1	07/12/00	59.895	-148.691	78
32	KD-1	07/13/00	57.532	-152.023	64
34	BD-4	07/14/00	55.786	-155.344	58
35	BD-5	07/15/00	54.647	-159.445	76
36	BCS-1	07/16/00	54.321	-165.631	70
37	BCS-4	07/17/00	59.317	-170.933	72
38	SLIP-1	07/18/00	62.014	-175.057	80
39	SLIP-2	07/18/00	62.052	-175.208	80
40	SLIP-3	07/18/00	62.394	-174.587	71
41	SLIP-5	07/19/00	62.566	-173.553	65
42	SLIP-4	07/19/00	63.028	-173.458	70
43	BCS-6	07/19/00	63.850	-172.399	56
44	UTBS-5	07/19/00	64.667	-169.883	47
45	UTBS-2	07/19/00	64.683	-169.099	45
46	UTBS-4	07/19/00	64.959	-169.884	45
47	UTBS-1	07/20/00	64.992	-169.137	48
48	BRS-1	07/20/00	65.654	-168.218	39
49	BRS-2	07/20/00	65.667	-168.397	52
50	BRS-3	07/20/00	65.682	-168.566	51
51	BRS-4	07/20/00	65.700	-168.717	50
52	BRS-5	07/20/00	65.716	-168.899	47
53	UTN-1	07/21/00	66.708	-168.399	30
54	UTN-2	07/21/00	67.051	-168.732	46
55	UTN-3	07/21/00	67.333	-168.992	50
56	UTN-4	07/21/00	67.501	-168.912	50
57	UTN-5	07/22/00	67.671	-168.957	50
58	UTN-6	07/22/00	67.738	-168.432	50
59	UTN-7	07/22/00	67.998	-168.932	57
60	BD-6	07/22/00	69.198	-166.150	31
61	BD-7	07/24/00	71.159	-158.403	47
62	BD-8	07/25/00	71.298	-156.997	48
63	BD-9	07/27/00	70.908	-159.496	38
64	BD-10	07/28/00	71.095	-154.893	14
65	BD-11	07/29/00	70.818	-151.547	14

Appendix A. Continued.

Station number	Station name	Date	Latitude (°N)	Longitude (°W)	Depth (m)
66	BD-12	07/31/00	70.195	-143.029	24
67	H-5	08/01/00	69.913	-138.522	230
68	H-4	08/01/00	69.837	-138.606	188
69	H-3	08/01/00	69.759	-138.688	171
70	H-2	08/01/00	69.679	-138.771	74
71	H-1	08/01/00	69.612	-138.841	33
72	BD-13	08/08/00	70.651	-127.758	78
73	BD-14	08/09/00	71.847	-125.372	67
74	BD-15	08/10/00	70.067	-124.117	49
75	BD-16	08/12/00	68.185	-113.950	106
76	BD-17	08/14/00	67.838	-115.140	30
77	BD-18	08/16/00	68.228	-113.787	160
78	BD-19	08/17/00	68.440	-110.825	87
79	BD-20	08/17/00	69.039	-105.002	18
80	BD-21	08/19/00	68.387	-97.357	22
81	BD-21B	08/19/00	68.387	-97.357	22
82	BD-22	08/21/00	68.427	-96.651	20
83	BD-23	08/21/00	68.616	-95.885	17
84	BD-24	08/23/00	68.868	-95.061	70
85	BD-25	08/23/00	69.717	-96.080	36
86	BD-26	08/24/00	69.401	-94.105	44
87	BD-27	08/26/00	69.523	-93.546	14
89	BD-28	08/26/00	69.179	-94.877	97
91	BD-29	08/27/00	68.641	-98.951	54
92	BD-30	08/28/00	68.271	-100.026	52
93	BD-31	08/29/00	68.547	-101.747	88
95	BD-32	08/30/00	69.117	-100.735	46
101	TP-1	09/01/00	68.650	-108.283	29
103	EI-11	09/02/00	67.849	-111.278	84
105	EI-9	09/02/00	67.888	-111.359	392
107	EI-7	09/02/00	68.054	-111.298	311
110	EI-5	09/02/00	68.270	-111.214	181
112	EI-3	09/02/00	68.396	-111.055	153
114	EI-1	09/02/00	68.462	-110.966	54
115	DU-1	09/02/00	68.790	-113.840	26
116	DU-2	09/03/00	68.792	-113.846	40
117	DU-3	09/03/00	68.761	-114.061	49
118	DU-4	09/03/00	68.730	-144.171	38
119	DU-5	09/03/00	68.712	-114.419	29
120	DU-5B	09/03/00	68.712	-114.419	29

Appendix A. Continued.

Station number	Station name	Date	Latitude (°N)	Longitude (°W)	Depth (m)
121	CP-5	09/03/00	69.583	-118.402	520
122	CP-4	09/04/00	69.517	-118.502	437
123	CP-3	09/04/00	69.437	-118.600	315
124	CP-2	09/04/00	69.351	-118.717	158
125	CP-1	09/04/00	69.284	-118.827	33
127	AG-5	09/04/00	69.284	-118.827	600
128	AG-5B	09/06/00	70.547	-122.925	666
129	AG-1	09/06/00	69.871	-122.941	51
130	AG-2	09/06/00	69.972	-122.945	206
131	AG-3	09/07/00	70.040	-122.941	294
132	AG-4	09/07/00	70.181	-122.942	396
133	AG-5	09/07/00	70.555	-122.899	70
134	AG-T	09/08/00	70.799	-125.003	319
135	LW-1	09/08/00	72.399	-129.513	443
136	LW-2	09/08/00	72.407	-129.680	590
137	LW-3	09/09/00	72.555	-130.293	600
138	CK-5	09/11/00	71.942	-127.750	419
139	CK-5B	09/11/00	71.942	-127.750	419
140	CK-4	09/11/00	71.942	-127.000	350
141	CK-3	09/11/00	71.942	-126.650	190
142	CK-2	09/11/00	71.942	-126.266	47
143	CK-1	09/11/00	71.942	-125.998	25
144	AGT-2	09/12/00	71.568	-130.584	269
145	AGT-2B	09/12/00	71.568	-130.584	43
146	AGT-3	09/13/00	71.298	-126.495	460
147	WB-1	09/13/00	70.560	-126.433	320
148	WB-2	09/13/00	70.477	-126.933	274
149	WB-3	09/13/00	70.430	-127.208	189
150	WB-3B	09/13/00	70.430	-127.208	193
151	WB-4	09/13/00	70.408	-127.308	53
152	WB-5	09/13/00	70.400	-127.374	34
153	WB-6	09/13/00	70.400	-127.411	24
154	AGT-4	09/14/00	70.250	-121.667	439
155	DT-1	09/14/00	69.651	-120.818	30
156	DT-2	09/14/00	69.683	-120.701	226
157	DT-3	09/14/00	69.717	-120.666	239
158	DT-4	09/14/00	69.800	-120.500	260
159	DT-5	09/15/00	69.983	-120.083	489
160	BD-33	09/16/00	68.390	-112.868	165
161	BD-34	09/16/00	68.958	-106.674	101

Appendix A. Continued.

Station number	Station name	Date	Latitude (°N)	Longitude (°W)	Depth (m)
162	BD-35	09/20/00	68.479	-99.854	38
163	BD-36	09/20/00	68.211	-100.089	45
164	BD-37	09/21/00	68.275	-100.033	35
165	BD-38	09/21/00	68.239	-99.984	57

Appendix B. A listing of water Column CTD measurements (courtesy of E. Carmack, Institute of Ocean Sciences) for the Laurier 2000 cruise.

Station number	Station name	Bottom temp. (°C)	Surface temp. (°C)	Bottom salinity (ppt)	Surface salinity (ppt)	Bottom sigma-t ((kg m ⁻³) -1000)
3	BD-1	6.951	12.204	32.874	29.379	25.692
4	BD-2	7.791	12.739	32.568	32.161	25.252
5	BD-3	3.739	13.479	34.213	32.194	27.437
13	KY-1	6.862	13.217	32.149	24.937	25.132
23	SW-1	6.048	10.952	31.906	30.081	25.115
32	KD-1	7.283	8.046	32.102	31.982	24.996
34	BD-4	6.681	8.282	32.478	32.257	25.436
35	BD-5	9.352	9.371	31.718	31.763	25.285
36	BCS-1	5.849	6.591	32.597	32.264	25.711
37	BCS-4	2.082	9.103	32.353	32.303	26.216
38	SLIP-1	-1.562	8.141	32.116	31.089	26.513
39	SLIP-2	-1.630	8.072	32.009	31.184	26.409
40	SLIP-3	-1.466	8.045	31.851	31.463	26.281
41	SLIP-5	-1.319	8.365	31.926	31.600	26.329
42	SLIP-4	-1.647	7.858	32.302	31.875	26.677
43	BCS-6	-0.985	7.748	32.595	30.500	26.842
44	UTBS-5	-0.410	3.307	32.527	31.030	26.714
45	UTBS-2	-0.406	3.253	32.304	31.516	26.533
46	UTBS-4	-0.152	3.643	32.489	31.597	26.648
47	UTBS-1	-0.325	1.041	32.330	32.199	26.541
48	BRS-1	8.286	10.086	30.536	30.050	23.515
49	BRS-2	3.664	10.028	31.634	30.043	25.361
50	BRS-3	3.252	7.597	31.973	31.803	25.708
51	BSR-4	1.775	7.370	32.032	31.554	25.999
52	BRS-5	-0.383	6.227	32.278	32.206	26.505
53	UTN-1	N/A	N/A	N/A	N/A	N/A
54	UTN-2	2.991	3.328	31.944	31.902	25.731
55	UTN-3	0.616	1.578	32.334	32.081	26.417
56	UTN-4	0.653	2.031	32.439	32.153	26.499
57	UTN-5	0.718	1.818	32.541	32.133	26.574
58	UTN-6	0.486	2.133	32.515	32.448	26.585
59	UTN-7	0.748	3.592	32.637	32.014	26.634
60	BD-6	5.237	5.552	31.411	30.705	24.808
61	BD-7	1.895	1.964	31.012	29.298	25.141
62	BD-8	2.263	5.082	29.296	29.299	24.411
63	BD-9	3.515	5.082	30.432	29.299	23.213
64	BD-10	-1.570	1.791	31.362	13.544	25.883
65	BD-11	-1.655	0.973	31.018	5.015	25.605

Appendix B. Continued.

Station number	Station name	Bottom temp. (°C)	Surface temp. (°C)	Bottom salinity (ppt)	Surface salinity (ppt)	Bottom sigma-t ((kg m⁻³) -1000)
66	BD-12	-1.642	-0.385	32.047	23.802	26.462
67	H-5	-0.725	3.357	34.146	6.000	28.102
68	H-4	-1.411	4.142	33.465	7.355	26.650
69	H-3	-1.498	5.347	33.431	9.064	27.596
70	H-2	-1.554	6.312	32.833	10.837	27.105
71	H-1	-1.503	7.401	26.693	11.835	27.053
72	BD-13	-1.298	3.601	32.167	25.585	26.523
73	BD-14	-1.438	1.148	32.629	24.756	26.922
74	BD-15	-1.303	5.596	32.253	20.542	26.595
75	BD-16	0.538	6.303	28.839	24.135	23.559
76	BD-17	-0.029	8.297	27.831	18.991	22.791
77	BD-18	0.796	4.596	28.890	25.199	23.576
78	BD-19	-0.710	0.373	28.738	28.082	23.617
79	BD-20	N/A	N/A	N/A	N/A	N/A
80	BD-21	4.553	N/A	22.679	N/A	N/A
81	BD-21B	4.553	4.567	22.679	22.532	17.953
82	BD-22	0.058	4.550	22.457	22.679	17.731
83	BD-23	0.483	0.050	22.211	22.457	17.702
84	BD-24	0.106	0.480	23.956	22.211	19.460
85	BD-25	-0.777	0.100	31.026	23.956	25.039
86	BD-6	0.286	-0.770	22.183	31.026	18.081
87	BD-27	4.824	0.280	17.883	22.183	13.996
89	BD-28	-1.126	5.120	24.738	17.855	20.343
91	BD-29	-1.044	3.162	27.692	25.875	22.785
92	BD-30	2.671	3.893	26.557	25.139	21.398
93	BD-31	-1.452	2.451	29.263	26.529	24.129
95	BD-32	-0.611	1.450	29.516	26.537	24.249
101	TP-1	1.453	5.264	27.406	24.947	22.261
103	EI-11	-0.891	6.196	28.664	23.891	22.582
105	EI-9	-1.212	6.125	29.038	23.939	23.916
107	EI-7	0.602	5.463	27.645	24.958	28.500
110	EI-5	1.430	4.966	27.509	25.522	23.627
112	EI-3	4.528	5.700	25.656	24.902	23.608
114	EI-1	-0.910	5.529	28.550	25.155	23.482
115	DU-1	2.652	4.810	27.394	25.477	22.082
116	DU-2	N/A	N/A	N/A	N/A	N/A
117	DU-3	-1.306	4.256	32.297	25.769	26.632
118	DU-4	N/A	N/A	N/A	N/A	N/A
119	DU-5	1.484	4.209	28.296	25.830	22.985
120	DU-5B	4.100	N/A	25.899	N/A	N/A

Appendix B. Continued.

Station number	Station name	Bottom temp. (°C)	Surface temp. (°C)	Bottom salinity (ppt)	Surface salinity (ppt)	Bottom sigma-t ((kg m⁻³) -1000)
121	CP-5	0.220	3.843	34.746	26.016	28.459
122	CP-4	N/A	N/A	N/A	N/A	N/A
123	CP-3	0.144	4.162	34.713	26.006	28.443
124	CP-2	N/A	N/A	N/A	N/A	N/A
125	CP-1	-0.275	4.276	31.385	24.547	25.754
127	AG-5	-0.551	N/A	31.995	N/A	N/A
128	AG-5B	-0.519	3.120	31.949	26.962	28.432
129	AG-1	-1.361	2.933	32.243	25.679	26.594
130	AG-2	N/A	N/A	N/A	N/A	N/A
131	AG-3	-0.017	4.479	34.587	23.985	19.033
132	AG-4	N/A	N/A	N/A	N/A	N/A
133	AG5	1.720	N/A	29.475	N/A	N/A
134	AG-T	-0.943	2.633	31.655	27.282	28.430
135	LW-1	-0.706	N/A	31.667	N/A	N/A
136	LW-2	N/A	N/A	N/A	N/A	N/A
137	LW-3	-1.230	N/A	31.519	N/A	N/A
138	CK-5	0.309	1.818	34.854	26.561	28.535
139	CK-5B	0.969	N/A	29.550	N/A	N/A
140	CK-4	N/A	N/A	N/A	N/A	N/A
141	CK-3	-1.319	2.277	33.369	26.456	27.524
142	CK-2	N/A	N/A	N/A	N/A	N/A
143	CK-1	1.263	2.128	28.762	26.036	23.397
144	AGT-2	0.216	-0.654	34.602	24.860	28.341
145	AGT-2B	-0.794	N/A	28.188	N/A	N/A
146	AGT-3	0.291	2.830	34.979	23.457	28.640
147	WB-1	-1.481	3.640	32.457	22.019	28.528
148	WB-2	N/A	N/A	N/A	N/A	N/A
149	WB-3	-1.459	N/A	32.574	N/A	N/A
150	WB-3B	-1.447	2.353	32.991	23.751	27.225
151	WB-4	N/A	N/A	N/A	N/A	N/A
152	WB-5	-1.153	1.585	32.520	22.399	26.800
153	WB-6	-1.017	1.760	32.378	22.086	26.666
154	AGT-4	0.228	3.385	34.797	24.896	28.500
155	DT-1	-0.927	3.391	32.130	25.935	26.450
156	DT-2	N/A	N/A	N/A	N/A	N/A
157	DT-3	-0.221	3.361	34.431	26.147	28.262
158	DT-4	N/A	N/A	N/A	N/A	N/A
159	DT-5	0.226	3.302	34.775	25.429	28.482
160	BD-33	0.326	4.454	28.939	25.458	23.663
161	BD-34	-0.975	0.457	28.908	27.992	23.786

Appendix B. Continued.

Station number	Station name	Bottom temp. (°C)	Surface temp. (°C)	Bottom salinity (ppt)	Surface salinity (ppt)	Bottom sigma-t ((kg m⁻³) -1000)
162	BD-35	N/A	N/A	N/A	N/A	N/A
163	BD-36	N/A	N/A	N/A	N/A	N/A
164	BD-37	N/A	N/A	N/A	N/A	N/A
165	BD-38	N/A	N/A	N/A	N/A	N/A

Appendix C. This is a listing of water column chlorophyll *a* for the Laurier 2000 cruise. Station number, station name, bottom water chlorophyll *a* concentration, surface water chlorophyll *a* concentration, and integrated total water column chlorophyll *a* concentration are shown.

Station number	Station name	Bottom chl <i>a</i> (mg L ⁻¹)	Surface chl <i>a</i> (mg L ⁻¹)	Integrated chl <i>a</i> to euphotic depth (mg m ⁻²)	Integrated chl <i>a</i> total water column (mg m ⁻²)
3	BD-1	0.198	2.756	46.92	56.09
4	BD-2	0.266	0.576	16.37	30.55
5	BD-3	0.012	0.252	9.68	93.05
13	KY-1	0.197	1.632	35.33	45.74
23	SW-1	0.222	4.040	91.34	127.12
32	KD-1	0.624	3.084	63.49	95.47
34	BD-4	0.460	4.360	75.96	102.17
35	BD-5	0.124	0.988	60.49	131.56
36	BCS-1	0.832	3.236	78.16	152.55
37	BCS-4	0.350	0.308	18.66	51.28
38	SLIP-1	0.290	0.344	14.36	37.70
39	SLIP-2	0.377	0.412	15.40	37.85
40	SLIP-3	0.380	0.332	13.33	40.76
41	SLIP-5	0.448	0.302	7.10	20.98
42	SLIP-4	0.379	0.127	6.13	21.03
43	BCS-6	2.220	0.444	20.22	75.62
44	UTBS-5	1.432	0.788	28.16	54.55
45	UTBS-2	2.136	1.904	29.86	64.85
46	UTBS-4	2.392	1.576	59.21	113.31
47	UTBS-1	1.384	1.040	32.08	61.12
48	BRS-1	1.312	1.124	37.35	52.79
49	BRS-2	0.668	0.860	16.40	30.97
50	BRS-3	0.648	0.236	9.73	24.17
51	BRS-4	3.964	0.336	24.63	103.27
52	BRS-5	7.080	0.484	111.37	285.35
53	UTN-1	N/A	N/A	N/A	N/A
54	UTN-2	0.872	0.608	16.60	31.27
55	UTN-3	16.160	16.880	431.00	745.40
56	UTN-4	14.920	14.040	273.90	528.50
57	UTN-5	9.960	19.800	545.30	784.78
58	UTN-6	9.600	27.200	507.30	719.34
59	UTN-7	21.920	0.612	122.67	620.27
60	BD-6	0.362	0.164	9.47	10.97
61	BD-7	0.844	0.428	16.05	30.75
62	BD-8	0.536	0.556	14.09	25.69

Appendix C. Continued.

Station number	Station name	Bottom chl <i>a</i> (mg L ⁻¹)	Surface chl <i>a</i> (mg L ⁻¹)	Integrated chl <i>a</i> to euphotic depth (mg m ⁻²)	Integrated chl <i>a</i> total water column (mg m ⁻²)
63	BD-9	0.424	0.820	19.87	24.55
64	BD-10	4.560	0.812	37.47	37.47
65	BD-11	2.960	2.336	45.18	45.18
66	BD-12	0.111	3.048	17.78	17.78
67	H-5	0.055	3.424	20.76	40.97
8	H-4	0.031	1.996	16.56	29.02
69	H-3	0.024	5.480	34.20	40.52
70	H-2	0.122	5.240	47.78	52.23
71	H-1	0.085	6.320	50.50	50.50
72	BD-13	3.156	0.254	8.68	140.57
73	BD-14	0.134	0.097	4.22	17.41
74	BD-15	1.020	0.282	10.61	25.32
75	BD-16	0.100	0.436	32.79	118.33
76	BD-17	0.948	0.704	21.75	24.07
77	BD-18	0.126	0.019	11.12	318.42
78	BD-19	0.129	0.162	21.25	84.55
79	BD-20	0.267	0.224	4.57	4.57
80	BD-21	0.005	0.086	1.40	1.40
81	BD-21B	0.012	0.003	0.26	0.26
82	BD-22	0.000	0.000	0.00	0.00
83	BD-23	0.003	0.001	0.05	0.05
84	BD-24	0.009	0.025	0.53	1.42
85	BD-25	0.153	0.007	1.11	1.71
86	BD-26	0.288	0.031	4.08	8.79
87	BD-27	0.251	0.182	1.93	1.93
89	BD-28	0.000	0.000	0.04	0.09
91	BD-29	0.195	0.001	0.31	3.05
92	BD-30	0.628	0.132	5.43	5.43
93	BD-31	0.242	0.357	14.63	40.68
95	BD-32	1.736	0.367	19.02	19.02
101	TP-1	0.121	0.125	1.62	1.62
103	EI-11	0.003	0.000	0.05	0.75
105	EI-9	0.006	0.016	1.00	33.82
107	EI-7	0.009	0.072	2.17	17.47
110	EI-5	0.023	0.133	3.03	42.55
112	EI-3	0.031	0.075	1.85	21.17
114	EI-1	2.624	0.017	2.56	42.15
115	DU-1	0.318	0.078	3.78	3.78

Appendix C. Continued.

Station number	Station name	Bottom chl <i>a</i> (mg L ⁻¹)	Surface chl <i>a</i> (mg L ⁻¹)	Integrated chl <i>a</i> to euphotic depth (mg m ⁻²)	Integrated chl <i>a</i> entire water column (mg m ⁻²)
116	DU-2	N/A	N/A	N/A	N/A
117	DU-3	0.134	0.512	12.76	20.30
118	DU-4	N/A	N/A	N/A	N/A
119	DU-5	0.440	0.492	10.63	10.63
120	DU-5B	N/A	N/A	N/A	N/A
121	CP-5	0.010	0.027	0.60	20.01
122	CP-4	N/A	N/A	N/A	N/A
123	CP-3	0.030	0.122	2.98	37.85
124	CP-2	N/A	N/A	N/A	N/A
125	CP-1	0.044	0.169	3.00	3.94
127	AG-5	N/A	N/A	1.05	66.74
128	AG-5B	0.169	0.063	N/A	N/A
129	AG-1	0.000	0.011	0.23	0.23
130	AG-2	N/A	N/A	N/A	N/A
131	AG-3	0.006	0.000	0.10	4.70
132	AG-4	N/A	N/A	N/A	N/A
133	AG-5	N/A	N/A	N/A	N/A
134	AG-T	0.001	0.104	1.75	5.84
135	LW-1	N/A	N/A	N/A	N/A
136	LW-2	N/A	N/A	N/A	N/A
137	LW-3	N/A	N/A	N/A	N/A
138	CK-5	0.004	0.037	0.89	21.57
139	CK-5B	N/A	N/A	N/A	N/A
140	CK-4	N/A	N/A	N/A	N/A
141	CK-3	0.025	0.047	2.29	22.36
142	CK-2	N/A	N/A	N/A	N/A
143	CK-1	0.266	0.173	4.05	4.05
144	AGT-2	0.010	0.188	2.79	26.66
145	AGT-2B	N/A	N/A	N/A	N/A
146	AGT-3	0.017	0.412	7.41	43.31
147	WB-1	0.020	0.412	6.72	226.60
148	WB-2	N/A	N/A	N/A	N/A
149	WB-3	N/A	N/A	6.00	11.31
150	WB-3B	0.074	0.456	N/A	N/A
151	WB-4	N/A	N/A	N/A	N/A
152	WB-5	0.212	0.552	6.42	8.60
153	WB-6	0.216	0.524	6.45	6.66
154	AGT-4	0.013	0.260	4.31	35.84

Appendix C. Continued.

Station number	Station name	Bottom chl <i>a</i> (mg L⁻¹)	Surface chl <i>a</i> (mg L⁻¹)	Integrated chl <i>a</i> to euphotic depth (mg m⁻²)	Integrated chl <i>a</i> entire water column (mg m⁻²)
155	DT-1	0.157	0.171	7.01	8.48
156	DT-2	N/A	N/A	N/A	N/A
157	DT-3	0.030	0.163	3.88	18.64
158	DT-4	N/A	N/A	N/A	N/A
159	DT-5	0.015	0.215	3.99	34.02
160	BD-33	0.082	0.330	7.93	66.22
161	BD-34	0.544	1.152	38.30	99.33
162	BD-35	N/A	N/A	N/A	N/A
163	BD-36	N/A	N/A	N/A	N/A
164	BD-37	N/A	N/A	N/A	N/A
165	BD-38	N/A	N/A	N/A	N/A

Appendix D. This is a listing of macroinfaunal measurements taken during the Laurier 2000 cruise. Station number, station name, faunal abundance, faunal wet weight biomass, faunal organic carbon biomass, community Shannon-Weaver species diversity index, and community Shannon-Weaver species evenness index are listed below.

Station number	Station name	Faunal abundance (no. of ind. m ⁻²)	Wet weight biomass (g m ⁻²)	Organic carbon biomass (gC m ⁻²)	S-W diversity (H')	S-W evenness (J)
3	BD-1	3397.50	353.05	10.47	2.47	0.61
13	KY-1	7722.50	227.31	7.33	0.90	0.30
34	BD-4	1045.00	197.51	2.82	2.61	0.69
37	BCS-4	1210.00	64.39	3.06	2.94	0.86
38	SLI-P1	1342.50	737.53	22.64	2.63	0.75
39	SLIP-2	5102.50	2239.09	61.13	2.75	0.79
40	SLIP-3	1357.50	922.47	25.08	2.62	0.73
41	SLIP-5	2795.00	312.29	11.39	1.66	0.48
42	SLIP-4	1342.50	430.10	17.59	2.44	0.72
44	UTBS-5	2037.50	599.91	22.23	3.00	0.82
45	UTBS-2	9820.00	301.78	14.61	2.17	0.56
46	UTBS-4	7445.00	461.87	21.75	2.04	0.53
47	UTBS-1	12277.50	522.90	24.20	2.37	0.64
53	UTN-1	2795.00	675.36	10.56	2.67	0.73
54	UTN-2	2745.00	318.29	13.11	2.53	0.72
55	UTN-3	4485.00	1437.83	57.83	2.86	0.77
56	UTN-4	4100.00	497.16	22.13	2.40	0.68
57	UTN-5	4087.50	277.76	14.55	2.24	0.62
58	UTN-6	1927.50	704.83	27.89	2.58	0.71
59	UTN-7	4612.80	983.03	42.27	1.40	0.41
60	BD-6	882.50	73.87	3.13	2.68	0.74
61	BD-7	4987.80	180.47	6.20	N/A	N/A
62	BD-8	10470.00	276.69	15.79	1.94	0.49
65	BD-11	707.50	12.00	0.63	0.64	0.24
71	H-1	755.00	12.47	0.68	2.27	0.66
72	BD-13	4182.50	202.57	7.74	1.96	0.51
75	BD-16	177.50	3.53	0.16	2.15	0.76
76	BD-17	1580.00	143.66	5.25	2.10	0.61
77	BD-18	615.00	49.32	1.22	2.21	0.69
78	BD-19	705.00	10.51	0.45	1.41	0.50
79	BD-20	4420.00	266.53	9.36	2.49	0.69
83	BD-23	2332.50	188.78	4.46	1.94	0.60
84	BD-24	567.50	20.46	0.61	2.52	0.81
85	BD-25	815.00	167.63	5.18	2.99	0.82
86	BD-26	660.00	132.08	1.54	1.87	0.65
87	BD-27	910.00	50.29	1.54	2.16	0.67
91	BD-29	377.50	40.58	1.39	2.38	0.71

Appendix D. Continued.

Station number	Station name	Faunal abundance (no. of ind. m⁻²)	Wet weight biomass (g m⁻²)	Organic carbon biomass (gC m⁻²)	S-W diversity (H')	S-W evenness (J)
92	BD-31	567.50	17.80	0.89	2.33	0.74
95	BD-32	2092.50	430.50	13.09	2.75	0.72
101	TP-1	2160.00	271.04	6.68	2.74	0.75
103	EI-11	190.00	3.59	0.21	1.72	0.64
114	EI-1	945.00	14.26	0.66	1.88	0.58
141	CK-3	260.00	41.17	1.22	2.55	0.81
152	WB-5	6770.00	363.76	21.76	1.79	0.49
160	BD-33	195.00	12.31	0.35	1.81	0.67
165	BD-38	1097.50	36.53	1.28	1.59	0.48

Appendix E. This is a listing of dominant station macroinfaunal animals from the Laurier 2000 cruise.

Station number	Station name	Dominant 3 taxa by abundance (no. ind. m ⁻²)	Dominant taxa % of total abundance (%)	Dominant 3 taxa by wet weight (g m ⁻²)	Dominant taxa % of total wet weight (%)	Dominant 3 taxa by carbon weight (gC m ⁻²)	Dominant taxa % of total carbon weight (%)
3	BD-1	Thyasiridae	44.90	Veneridae	72.80	Veneridae	68.70
		Foraminifera	10.20	Pelecypoda	11.00	Pelecypoda	10.40
		Magelonidae	4.90	Foraminifera	5.10	Lumbrineridae	4.70
13	KY-1	Foraminifera	79.30	<i>N. radiata</i>	40.90	<i>Yoldia sp.</i>	36.70
		Lumbrineridae	8.50	<i>M. calcarea</i>	26.40	<i>M. calcarea</i>	28.70
		<i>N. radiata</i>	3.60	<i>Yoldia sp.</i>	25.10	<i>N. radiata</i>	24.10
34	BD-4	Foraminifera	28.70	<i>E. parma</i>	69.80	<i>E. parma</i>	39.10
		Ophiuridae	22.70	Ophiuridae	17.00	Ampharetidae	17.70
		Ostracod	7.20	Ampharetidae	3.70	Ophiuridae	16.70
37	BCS-4	Leuconidae	13.60	<i>M. calcarea</i>	26.10	Nephtyidae	24.20
		<i>Yoldia sp.</i>	9.30	Nephtyidae	16.00	<i>M. calcarea</i>	19.20
		Phoxocephalidae	8.30	<i>N. radiata</i>	15.90	Maldanidae	13.10
38	SLIP-1	<i>N. belloti</i>	21.60	<i>N. radiata</i>	58.70	<i>N. radiata</i>	36.40
		<i>N. radiata</i>	20.70	<i>N. belloti</i>	25.10	<i>N. belloti</i>	31.90
		Capitellidae	11.00	<i>M. calcarea</i>	4.70	Rhynchocoela	9.90
39	SLIP-2	<i>N. radiata</i>	23.00	<i>N. radiata</i>	65.90	<i>N. radiata</i>	45.90
		Maldanidae	14.70	<i>N. belloti</i>	12.50	<i>N. belloti</i>	17.80
		<i>N. belloti</i>	8.60	Maldanidae	5.60	Maldanidae	14.40
40	SLIP-3	<i>N. radiata</i>	29.70	<i>N. radiata</i>	50.30	<i>N. radiata</i>	42.10
		Capitellidae	13.40	<i>M. calcarea</i>	10.00	Sipunculidae	15.60
		Orbiniidae	9.90	Sipunculidae	9.40	<i>M. calcarea</i>	12.90
41	SLIP-5	<i>N. radiata</i>	39.00	<i>N. belloti</i>	32.30	<i>N. belloti</i>	34.60
		<i>N. belloti</i>	38.50	<i>M. calcarea</i>	26.10	<i>M. calcarea</i>	25.10
		<i>M. calcarea</i>	5.00	<i>N. radiata</i>	24.00	<i>N. radiata</i>	12.50

Appendix E. Continued.

Station number	Station name	Dominant 3 taxa by abundance (no. ind. m ⁻²)	Dominant taxa % of total abundance (%)	Dominant 3 taxa by wet weight (g m ⁻²)	Dominant taxa % of total wet weight (%)	Dominant 3 taxa by carbon weight (gC m ⁻²)	Dominant taxa % of total carbon weight (%)
42	SLIP-4	Orbiniidae	20.90	<i>N. belloti</i>	29.70	<i>N. belloti</i>	28.30
		Pectinariidae	20.10	Pectinariidae	21.00	Pectinariidae	23.10
		<i>N. belloti</i>	15.50	<i>N. radiata</i>	17.50	Rhynchocoela	19.10
44	UTBS-5	Tellinidae	11.90	<i>M. calcarea</i>	92.20	<i>M. calcarea</i>	87.10
		<i>N. belloti</i>	10.80	Nephtyidae	3.80	Nephtyidae	7.40
		<i>Yoldia sp.</i>	8.70	<i>N. belloti</i>	1.30	Maldanidae	1.40
45	UTBS-2	<i>Ampelisca sp.</i>	38.60	<i>Ampelisca sp.</i>	32.40	<i>Ampelisca sp.</i>	45.60
		Isaeidae	17.70	Astartidae	23.70	<i>M. calcarea</i>	10.70
		Phoxocephalidae	8.50	<i>M. calcarea</i>	14.80	Astartidae	7.40
46	UTBS-4	<i>Ampelisca sp.</i>	50.00	<i>M. calcarea</i>	40.90	<i>Ampelisca sp.</i>	32.00
		<i>Byblis sp.</i>	12.80	<i>Ampelisca sp.</i>	22.20	<i>M. calcarea</i>	30.40
		Phoxocephalidae	7.50	<i>N. belloti</i>	13.70	<i>N. belloti</i>	11.30
47	UTBS-1	<i>Ampelisca sp.</i>	29.10	<i>M. calcarea</i>	39.00	<i>M. calcarea</i>	29.50
		<i>Byblis sp.</i>	18.50	<i>Ampelisca sp.</i>	18.10	<i>Ampelisca sp.</i>	26.60
		Lysianassidae	10.40	Astartidae	12.00	<i>Byblis sp.</i>	9.50
53	UTN-1	Tellinidae	22.80	<i>E. parma</i>	76.40	<i>E. parma</i>	39.10
		Phoxocephalidae	17.60	Styelidae	8.90	Priapulidae	14.60
		Orbiniidae	9.70	Priapulidae	5.10	Anthozoa	12.90
54	UTN-2	Phoxocephalidae	33.60	<i>M. calcarea</i>	79.90	<i>M. calcarea</i>	67.80
		Capitellidae	9.00	Nephtyidae	10.00	Nephtyidae	17.40
		Tellinidae	8.10	Anthozoa	4.20	Anthozoa	6.30
55	UTN-3	Phoxocephalidae	22.10	<i>M. calcarea</i>	52.60	<i>M. calcarea</i>	45.80
		Sigalionidae	7.90	<i>Yoldia sp.</i>	31.90	<i>Yoldia sp.</i>	37.30
		Capitellidae	7.40	<i>N. belloti</i>	5.80	<i>N. belloti</i>	5.60
56	UTN-4	Haustoriidae	26.90	<i>M. calcarea</i>	65.00	<i>M. calcarea</i>	51.10
		Phoxocephalidae	18.70	<i>Yoldia sp.</i>	9.20	<i>Yoldia sp.</i>	9.70
		<i>Byblis sp.</i>	12.70	Maldanidae	5.90	Maldanidae	9.30

Appendix E. Continued.

Station number	Station name	Dominant 3 taxa by abundance (no. ind. m ⁻²)	Dominant taxa % of total abundance (%)	Dominant 3 taxa by wet weight (g m ⁻²)	Dominant taxa % of total wet weight (%)	Dominant 3 taxa by carbon weight (gC m ⁻²)	Dominant taxa % of total carbon weight (%)
57	UTN-5	Haustoriidae	42.70	<i>M. calcarea</i>	28.50	<i>M. calcarea</i>	19.10
		<i>N. belloti</i>	9.00	<i>N. belloti</i>	17.90	Anthozoa	15.30
		Capitellidae	8.40	Anthozoa	13.10	Haustoriidae	14.70
58	UTN-6	<i>N. belloti</i>	20.00	<i>M. calcarea</i>	55.00	<i>M. calcarea</i>	48.60
		Sigalionidae	16.70	<i>N. belloti</i>	33.20	<i>N. belloti</i>	32.70
		Haustoriidae	11.80	Anthozoa	5.10	Anthozoa	7.90
59	UTN-7	Haustoriidae	61.90	<i>N. belloti</i>	57.80	<i>N. belloti</i>	52.40
		<i>N. belloti</i>	19.10	<i>M. calcarea</i>	25.30	<i>M. calcarea</i>	20.60
		Sigalionidae	5.80	Haustoriidae	4.80	Haustoriidae	10.30
60	BD-6	Orbiniidae	26.10	Sternaspidae	26.40	Sternaspidae	25.50
		Sternaspidae	15.30	Gastropoda	14.50	Gastropoda	21.10
		Isaeidae	12.20	Anthozoa	11.30	Anthozoa	16.20
61	BD-7	Isaeidae	78.30	<i>Clinocardium sp.</i>	39.20	<i>Clinocardium sp.</i>	31.90
		Foraminifera	3.40	Cardiidae	24.20	Cardiidae	19.70
		<i>Byblis sp.</i>	3.30	Echinoidea	9.70	Isaeidae	14.30
62	BD-8	Foraminifera	39.30	<i>Byblis sp.</i>	46.50	<i>Byblis sp.</i>	55.50
		<i>Byblis sp.</i>	24.90	Anthozoa	18.00	Anthozoa	19.20
		Isaeidae	14.70	Astartidae	13.00	Nephtyidae	7.50
65	BD-11	Foraminifera	87.60	Idotheidae	41.20	Idotheidae	57.80
		<i>P. arctica</i>	3.90	<i>M. moesta</i>	17.30	Sternaspidae	12.00
		Idotheidae	2.10	Sternaspidae	15.50	<i>M. moesta</i>	11.50
71	H-1	Isaeidae	44.00	<i>A. nephtheidae</i>	21.70	Nephtyidae	22.40
		Sigalionidae	14.90	Nephtyidae	16.90	<i>A. nephtheidae</i>	16.00
		<i>Byblis sp.</i>	7.00	Isaeidae	12.30	Isaeidae	15.40
72	BD-13	Foraminifera	51.80	<i>S. groenlandicus</i>	30.10	<i>Ampelisca sp.</i>	34.30
		Lampropidae	11.80	<i>Ampelisca sp.</i>	19.30	<i>S. groenlandicus</i>	22.10
		<i>Ampelisca sp.</i>	9.20	Astartidae	15.20	Nephtyidae	8.90

Appendix E. Continued.

Station number	Station name	Dominant 3 taxa by abundance (no. ind. m ⁻²)	Dominant taxa % of total abundance (%)	Dominant 3 taxa by wet weight (g m ⁻²)	Dominant taxa % of total wet weight (%)	Dominant 3 taxa by carbon weight (gC m ⁻²)	Dominant taxa % of total carbon weight (%)
75	BD-16	<i>Yoldia sp.</i>	42.30	<i>Yoldia sp.</i>	36.20	<i>Yoldia sp.</i>	37.90
		Cardiidae	9.90	Priapulidae	23.10	Priapulidae	23.20
		Capitellidae	9.90	Cardiidae	21.10	Cardiidae	13.20
76	BD-17	Thyasiridae	31.60	Astartidae	41.80	Maldanidae	47.70
		Maldanidae	31.00	Maldanidae	24.90	Astartidae	17.20
		Synaptidae	8.20	Myidae	15.50	Myidae	11.90
77	BD-18	<i>P. arctica</i>	27.20	Foraminifera	55.80	Oweniidae	32.00
		Thyasiridae	23.60	Foraminifera	15.10	Foraminifera	22.50
		Oweniidae	14.20	Oweniidae	11.50	Lumbrinereidae	21.50
78	BD-19	<i>P. arctica</i>	62.40	Foraminifera	40.40	Nephtyidae	33.00
		Echiuridae	17.40	Nephtyidae	19.50	Maldanidae	29.30
		Lumbrinereidae	3.90	Maldanidae	17.90	Oweniidae	10.90
79	BD-20	Ostracoda	29.70	<i>P. arctica</i>	28.40	Maldanidae	25.20
		Thyasiridae	13.90	Astartidae	14.90	<i>P. arctica</i>	15.30
		<i>P. arctica</i>	10.70	Maldanidae	12.60	Pectinariidae	13.10
83	BD-23	Astartidae	46.00	Astartidae	36.50	Astartidae	23.10
		Lampropidae	13.70	<i>P. arctica</i>	23.50	<i>P. arctica</i>	18.90
		<i>P. arctica</i>	12.30	Ectoprocta	16.80	Rhynchocoela	11.70
84	BD-24	Astartidae	21.60	Astartidae	71.40	Astartidae	36.00
		Leuconidae	15.40	<i>Byblis sp.</i>	3.90	<i>Byblis sp.</i>	8.80
		<i>Byblis sp.</i>	11.90	Maldanidae	3.70	Maldanidae	8.60
85	BD-25	Foraminifera	18.40	<i>Yoldia sp.</i>	25.80	<i>Yoldia sp.</i>	39.20
		Lumbrinereidae	14.10	Foraminifera	19.10	Mytilidae	12.10
		Thyasiridae	6.40	Mytilidae	13.30	Foraminifera	6.20
		Maldanidae	6.40				

Appendix E. Continued.

Station number	Station name	Dominant 3 taxa by abundance (no. ind. m ⁻²)	Dominant taxa % of total abundance (%)	Dominant 3 taxa by wet weight (g m ⁻²)	Dominant taxa % of total wet weight (%)	Dominant 3 taxa by carbon weight (gC m ⁻²)	Dominant taxa % of total carbon weight (%)
86	BD-26	Foraminifera Cirratulidae Astartidae <i>P. arctica</i>	47.30 15.50 6.40 6.40	Porifera Astartidae Nephtyidae	95.90 0.80 0.70	Porifera Rhynchocoela Nephtyidae	82.00 4.40 4.30
87	BD-27	Haustoriidae Orbiniidae Lysianassidae	42.90 11.30 9.90	Astartidae Haustoriidae Priapulidae	64.20 6.40 5.60	Astartidae Haustoriidae Orbiniidae	31.50 19.40 9.40
91	BD-29	<i>Ampelisca sp.</i> Maldanidae Lyonsiidae	41.70 8.60 6.60	Mytilidae Lyonsiidae Hiatellidae	22.10 21.20 18.30	Mytilidae Lyonsiidae Hiatellidae	18.00 17.30 15.00
92	BD-30	Lampropidae Astartidae Ostracoda	22.50 14.30 8.10	Astartidae Hiatellidae Holothuroidea	47.00 12.40 12.10	Astartidae Hiatellidae Cardiidae	31.60 15.50 11.70
93	BD-31	<i>Yoldia sp.</i> Thyasiridae <i>N. radiata</i>	27.30 22.90 11.50	Maldanidae Thyasiridae <i>N. radiata</i>	26.30 18.60 18.10	Maldanidae Oweniidae <i>Ampelisca sp.</i>	37.00 11.60 10.50
95	BD-32	Sabellidae Ostracoda Ophiuridae	26.60 13.60 8.60	Sabellidae Astartidae Balanoidae	20.30 19.90 16.80	Sabellidae Astartidae Echinodermata	50.10 9.80 8.90
101	TP-1	Foraminifera Thyasiridae <i>Yoldia sp.</i>	29.30 8.90 8.70	Astartidae Mytilidae <i>M. calcarea</i>	61.90 18.50 6.50	Astartidae Mytilidae <i>M. calcarea</i>	37.70 21.00 9.30
103	EI-11	Capitellidae Foraminifera <i>N. radiata</i>	53.90 15.80 5.30	Magelonidae Capitellidae Ectoprocta	35.80 24.40 12.40	Magelonidae Capitellidae Cylichnidae	42.30 28.70 9.80

Appendix E. Continued.

Station number	Station name	Dominant 3 taxa by abundance (no. ind. m ⁻²)	Dominant taxa % of total abundance (%)	Dominant 3 taxa by wet weight (g m ⁻²)	Dominant taxa % of total wet weight (%)	Dominant 3 taxa by carbon weight (gC m ⁻²)	Dominant taxa % of total carbon weight (%)
114	EI-1	<i>P. arctica</i>	52.40	Maldanidae	20.20	Maldanidae	30.50
		Thyasiridae	13.20	Oweniidae	15.20	Oweniidae	22.60
		<i>N. belloti</i>	5.60	Thyasiridae	13.50	<i>Ampelisca sp.</i>	11.20
141	CK-3	Oweniidae	24.00	Asteroidea	39.50	Oweniidae	39.80
		Foraminifera	15.40	Foraminifera	25.20	Asteroidea	24.00
		<i>P. arctica</i>	13.50	Oweniidae	17.10	Foraminifera	8.50
152	WB-5	<i>Ampelisca sp.</i>	54.50	<i>Ampelisca sp.</i>	58.30	<i>Ampelisca sp.</i>	66.20
		Isaeidae	11.50	Cardiidae	11.00	Idotheidae	9.90
		Foraminifera	7.60	Idotheidae	8.00	Cardiidae	5.20
160	BD-33	Echiuridae	37.20	Astartidae	34.80	Polychaeta	49.80
		<i>P. arctica</i>	30.80	Foraminifera	22.80	Astartidae	18.20
		Isaeidae	6.40	Polychaeta	19.60	Foraminifera	8.00
165	BD-38	<i>P. arctica</i>	65.40	Mytilidae	29.30	Lumbrinereidae	25.90
		Thyasiridae	7.50	<i>P. arctica</i>	21.30	Mytilidae	23.50
		Maldanidae	4.30	Astartidae	18.10	<i>P. arctica</i>	11.60

Appendix F. Listed below are surface sediment measurements for the Laurier 2000 cruise (all processed in the Marine Ecology and Biogeochemistry Lab, University of Tennessee, Knoxville (Grebmeier and Cooper, unpubl. data).

Station number	Station name	Sed chl <i>a</i> (mg m ⁻²)	TON (%)	TOC (%)	C/N (wt./wt.)	Modal phi grain size (Ø)
3	BD1	N/A	0.05	0.30	6.06	4
4	BD2	N/A	N/A	N/A	N/A	N/A
5	BD3	N/A	N/A	N/A	N/A	N/A
13	KY1	0.94	0.05	0.55	11.38	5
23	SW1	N/A	N/A	N/A	N/A	N/A
32	KD1	N/A	N/A	N/A	N/A	N/A
34	BD4	4.44	0.07	0.54	8.33	3
35	BD5	N/A	N/A	N/A	N/A	N/A
36	BCS1	3.05	N/A	N/A	N/A	N/A
37	BCS4	15.19	0.11	0.71	6.23	5
38	SLIP1	22.05	0.16	1.06	6.50	5
39	SLIP2	13.80	0.15	0.94	6.20	5
40	SLIP3	18.86	0.17	1.00	6.01	5
41	SLIP5	20.29	0.13	0.85	6.71	5
42	SLIP4	22.53	0.20	1.24	6.08	5
43	BCS6	N/A	N/A	N/A	N/A	N/A
44	UT-BS5	13.28	0.06	0.40	6.78	4
45	UT-BS2	26.27	0.06	0.34	5.66	3
46	UT-BS4	19.81	0.05	0.31	5.91	4
47	UT-BS1	27.95	0.03	0.23	6.66	3
48	BRS1	N/A	N/A	N/A	N/A	N/A
49	BRS2	N/A	N/A	N/A	N/A	N/A
50	BRS3	N/A	N/A	N/A	N/A	N/A
51	BSR4	N/A	N/A	N/A	N/A	N/A
52	BRS5	N/A	N/A	N/A	N/A	N/A
53	UTN1	22.27	0.08	0.50	6.37	5
54	UTN2	21.79	0.08	0.54	7.01	5
55	UTN3	28.54	0.11	0.69	6.20	4
56	UTN4	17.40	0.14	0.88	6.18	5
57	UTN5	22.40	0.17	1.07	6.17	5
58	UTN6	17.53	0.20	1.25	6.18	5
59	UTN7	14.19	0.31	1.58	5.06	5
60	BD6	38.67	0.05	0.53	9.62	3
61	BD7	12.63	0.03	0.35	10.39	3
62	BD8	10.88	0.09	0.59	6.80	0
63	BD9	20.68	0.08	1.08	13.92	N/A
64	BD10	N/A	N/A	N/A	N/A	N/A
65	BD11	6.86	0.20	1.86	9.30	5

Appendix F. Continued.

Station number	Station name	Sed chl <i>a</i> (mg m⁻²)	TON (%)	TOC (%)	C/N (wt./wt.)	Modal phi grain size (Ø)
66	BD12	8.44	N/A	N/A	N/A	5
67	H5	N/A	N/A	N/A	N/A	N/A
68	H4	N/A	N/A	N/A	N/A	N/A
69	H3	N/A	N/A	N/A	N/A	N/A
70	H2	N/A	N/A	N/A	N/A	N/A
71	H1	4.09	0.09	0.63	7.31	5
72	BD13	5.54	0.08	0.62	8.21	5
73	BD14	12.01	0.12	0.88	7.40	5
74	BD15	15.16	0.15	1.08	7.10	5
75	BD16	6.38	0.13	0.63	5.01	5
76	BD17	20.71	0.05	0.32	6.01	5
77	BD18	4.05	0.15	0.77	5.05	5
78	BD-19	7.26	0.09	0.47	5.24	5
79	BD-20	26.66	0.11	0.58	5.46	5
80	BD-21	43.77	0.04	0.19	4.69	2
81	BD-21B	N/A	N/A	N/A	N/A	N/A
82	BD-22	0.09	0.10	0.46	4.76	5
83	BD-23	0.01	N/A	N/A	N/A	5
84	BD-24	0.14	0.07	0.34	4.71	5
85	BD-25	1.48	0.10	0.47	4.59	5
86	BD-26	0.42	0.09	0.50	5.76	5
87	BD-27	20.32	0.14	0.83	5.79	5
89	BD-28	7.54	0.14	0.78	5.62	5
91	BD-29	0.19	0.11	0.60	5.65	5
92	BD-30	8.29	0.08	0.53	6.34	5
93	BD-31	15.39	0.06	0.32	5.42	5
95	BD-32	17.18	0.06	0.25	4.39	0
101	TP-1	10.68	N/A	N/A	N/A	4
103	EI-11	1.84	0.10	0.52	5.11	5
105	EI-9	0.08	0.09	0.44	4.89	5
107	EI-7	0.53	0.09	0.47	5.30	5
110	EI-5	0.75	0.10	0.50	5.20	5
112	EI-3	0.48	0.10	0.50	4.96	5
114	EI-1	0.21	0.07	0.35	4.64	5
115	DU-1	N/A	N/A	N/A	N/A	N/A
116	DU-2	N/A	N/A	N/A	N/A	N/A
117	DU-3	N/A	N/A	N/A	N/A	N/A
118	DU-4	N/A	N/A	N/A	N/A	N/A
119	DU-5	N/A	N/A	N/A	N/A	N/A
120	DU-5B	N/A	N/A	N/A	N/A	N/A

Appendix F. Continued.

Station number	Station name	Sed chl <i>a</i> (mg m⁻²)	TON (%)	TOC (%)	C/N (wt./wt.)	Modal phi grain size (Ø)
121	CP-5	N/A	0.15	0.95	6.16	5
122	CP-4	N/A	N/A	N/A	N/A	N/A
123	CP-3	N/A	0.18	0.93	5.06	5
124	CP-2	N/A	N/A	N/A	N/A	N/A
125	CP-1	1.85	N/A	N/A	N/A	5
127	AG-5	N/A	N/A	N/A	N/A	N/A
128	AG-5B	N/A	N/A	N/A	N/A	N/A
129	AG-1	3.84	1.07	0.66	0.62	0
130	AG-2	N/A	N/A	N/A	N/A	N/A
131	AG-3	N/A	0.16	1.15	7.06	3
132	AG-4	N/A	N/A	N/A	N/A	N/A
133	AG-5	N/A	N/A	N/A	N/A	N/A
134	AG-T	N/A	N/A	N/A	N/A	5
135	LW-1	N/A	N/A	N/A	N/A	N/A
136	LW-2	N/A	N/A	N/A	N/A	N/A
137	LW-3	N/A	N/A	N/A	N/A	N/A
138	CK-5	N/A	N/A	N/A	N/A	N/A
139	CK-5B	N/A	N/A	N/A	N/A	N/A
140	CK-4	N/A	N/A	N/A	N/A	N/A
141	CK-3	0.90	N/A	0.76	1.66	5
142	CK-2	N/A	N/A	N/A	N/A	5
143	CK-1	N/A	N/A	N/A	N/A	3
144	AGT-2	N/A	N/A	N/A	N/A	N/A
145	AGT-2B	N/A	N/A	N/A	N/A	N/A
146	AGT-3	N/A	N/A	N/A	N/A	N/A
147	WB-1	N/A	N/A	N/A	N/A	N/A
148	WB-2	N/A	N/A	N/A	N/A	5
149	WB-3	N/A	N/A	N/A	N/A	N/A
150	WB-3B	N/A	N/A	N/A	N/A	N/A
151	WB-4	N/A	N/A	N/A	N/A	N/A
152	WB-5	14.84	N/A	1.27	9.06	5
153	WB-6	N/A	N/A	N/A	N/A	N/A
154	AGT-4	N/A	N/A	N/A	N/A	N/A
155	DT-1	14.32	N/A	N/A	N/A	0
156	DT-2	N/A	N/A	N/A	N/A	N/A
157	DT-3	N/A	N/A	N/A	N/A	N/A
158	DT-4	N/A	N/A	N/A	N/A	N/A
159	DT-5	N/A	N/A	N/A	N/A	N/A
160	BD-33	5.81	N/A	0.67	5.04	5
161	BD-34	8.15	N/A	0.77	5.74	5

Appendix F. Continued.

Station number	Station name	Sed chl <i>a</i> (mg m⁻²)	TON (%)	TOC (%)	C/N (wt./wt.)	Modal phi grain size (Ø)
162	BD-35	25.03	N/A	0.60	5.58	5
163	BD-36	12.79	N/A	0.38	5.69	5
164	BD-37	17.82	N/A	0.21	4.67	5
165	BD-38	12.05	N/A	0.58	5.59	5

Appendix G. Listed below is the benthic Spearman's rho correlation matrix for Laurier 2000 Bering and Chukchi Sea stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. Cells in **yellow indicate significant positive correlation**, cells in **magenta indicate significant negative correlation**. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Station depth (m)	Bot. water salinity (ppt)	Bot. water temp. (°C)	Bot. water chl <i>a</i> (mg L ⁻¹)	Int chl <i>a</i> (WC) (mg m ⁻²)	Int. chl <i>a</i> (euph.) (mg m ⁻²)	Sed. chl <i>a</i> (mg m ⁻²)	Macroinfaunal abund. (no. indiv m ⁻²)	Macroinfaunal biomass (g m ⁻²)	Macroinfaunal biomass (gC m ⁻²)	Modal grain size (Ø)	Sed. TOC (%)	Sed. C/N (wt./wt.)	S-W diversity (H')	S-W evenness (J)
Station depth (m)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water salinity (ppt)	0.268 0.185 26	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water temp. (°C)	0.425 0.030 26	-0.241 0.236 26	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water chl <i>a</i> (mg L ⁻¹)	-0.229 0.261 26	0.562 0.003 26	-0.002 0.991 26	*	*	*	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (WC) (mg m ⁻²)	-0.016 0.936 26	0.742 0.0001 26	-0.041 0.841 26	0.830 0.0001 26	*	*	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (euph.) (mg m ⁻²)	-0.269 0.185 26	0.619 0.001 26	0.182 0.375 26	0.826 0.0001 26	0.935 0.0001 26	*	*	*	*	*	*	*	*	*	*
Sed. chl <i>a</i> (mg m ⁻²)	0.401 0.079 20	-0.175 0.473 19	-0.254 0.293 19	-0.196 0.420 19	-0.107 0.663 19	-0.223 0.359 19	*	*	*	*	*	*	*	*	*
Macroinfaunal abund. (no. indiv m ⁻²)	-0.316 0.174 20	0.127 0.604 19	-0.118 0.632 19	0.541 0.017 19	0.357 0.133 19	0.393 0.096 19	-0.409 0.074 20	*	*	*	*	*	*	*	*
Macroinfaunal biomass (g m ⁻²)	0.361 0.118 20	0.254 0.293 19	-0.400 0.090 19	0.254 0.293 19	0.360 0.130 19	0.211 0.387 19	-0.048 0.840 20	0.149 0.531 20	*	*	*	*	*	*	*
Macroinfaunal biomass (gC m ⁻²)	0.316 0.175 20	0.228 0.348 19	-0.535 0.018 19	0.405 0.085 19	0.426 0.069 19	0.284 0.238 19	0.137 0.565 20	0.351 0.129 20	0.826 0.0001 20	*	*	*	*	*	*
Modal grain size (Ø)	0.599 0.007 19	0.191 0.448 18	-0.207 0.409 18	-0.133 0.600 18	0.058 0.819 18	-0.050 0.845 18	0.258 0.287 19	-0.400 0.090 19	0.289 0.230 19	0.139 0.570 19	*	*	*	*	*
Sed. TOC (%)	0.535 0.015 20	0.135 0.581 19	-0.091 0.710 19	0.065 0.792 19	0.074 0.764 19	0.021 0.932 19	0.491 0.033 19	-0.429 0.067 19	0.339 0.156 19	0.356 0.135 19	0.777 0.0001 19	*	*	*	*
Sed. C/N (wt./wt.)	-0.317 0.174 20	-0.584 0.009 19	0.396 0.093 19	-0.489 0.034 19	-0.601 0.007 19	-0.342 0.152 19	-0.148 0.544 19.000	-0.253 0.296 19	-0.310 0.197 19	-0.439 0.060 19	-0.270 0.265 19	-0.264 0.261 20	*	*	*
S-W diversity (H')	0.050 0.844 18	-0.047 0.859 17	-0.260 0.314 17	-0.294 0.252 17	-0.039 0.881 17	-0.113 0.667 17	0.135 0.593 18	-0.459 0.056 18	0.459 0.055 18	0.294 0.236 18	0.075 0.768 18	0.055 0.829 18	0.270 0.279 18	*	*
S-W evenness (J)	0.155 0.539 18	-0.080 0.761 17	-0.342 0.179 17	-0.370 0.143 17	-0.105 0.687 17	-0.195 0.453 17	0.182 0.470 18	-0.473 0.048 18	0.470 0.049 18	0.317 0.200 18	0.116 0.646 18	0.087 0.732 18	0.255 0.306 18	0.983 0.0001 18	*

Appendix H. Listed below is the benthic Spearman's rho correlation matrix for Laurier 2000 Canadian Archipelago stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Cells in **yellow indicate significant positive correlation**, cells in **magenta indicate significant negative correlation**. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Station depth (m)	Bot. water salinity (ppt)	Bot. water temp. (°C)	Bot. water chl <i>a</i> (mg L ⁻¹)	Int. chl <i>a</i> (WC) (mg m ⁻²)	Int. chl <i>a</i> (euph.) (mg m ⁻²)	Sed. chl <i>a</i> (mg m ⁻²)	Macrofaunal abund. (no. indiv m ⁻²)	Macrofaunal biomass (g m ⁻²)	Macrofaunal biomass (gC m ⁻²)	Modal grain size (Ø)	Sed. TOC (%)	Sed. C/N (wt./wt.)	S-W diversity (H')	S-W evenness (J)
Station depth (m)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water salinity (ppt)	0.572 0.0001 52	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water temp. (°C)	-0.229 0.102 52	-0.518 0.0001 52	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water chl <i>a</i> (mg L ⁻¹)	-0.343 0.015 50	0.103 0.505 44	-0.078 0.613 44	*	*	*	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (WC) (mg m ⁻²)	0.610 0.0001 50	0.439 0.002 49	-0.192 0.185 49	0.313 0.038 44	*	*	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (euph.) (mg m ⁻²)	0.036 0.805 49	0.287 0.048 48	-0.149 0.312 48	0.667 0.0001 43	0.687 0.0001 49	*									
Sed. chl <i>a</i> (mg m ⁻²)	-0.244 0.158 35	0.266 0.156 30	-0.065 0.734 30	0.334 0.066 31	0.150 0.421 31	0.541 0.002 31	*	*	*	*	*	*	*	*	*
Macrofaunal abund. (no. indiv m ⁻²)	-0.455 0.009 32	0.188 0.347 27	-0.147 0.465 27	0.360 0.065 27	-0.070 0.725 28	0.009 0.965 28	0.019 0.922 29	*	*	*	*	*	*	*	*
Macrofaunal biomass (g m ⁻²)	-0.528 0.002 32	0.042 0.834 27	0.072 0.722 27	0.357 0.067 27	-0.200 0.307 28	-0.047 0.814 28	0.106 0.585 29	0.790 0.0001 32	*	*	*	*	*	*	*
Macrofaunal biomass (gC m ⁻²)	-0.599 0.0001 32	0.058 0.775 27	0.067 0.738 27	0.301 0.127 27	-0.278 0.152 28	-0.089 0.654 28	0.188 0.328 29	0.768 0.0001 32	0.947 0.0001 32	*	*	*	*	*	*
Modal grain size (Ø)	0.212 0.178 42	-0.160 0.350 36	-0.026 0.882 36	0.027 0.873 36	0.286 0.086 37	0.103 0.542 37	-0.216 0.212 35	-0.015 0.937 31	-0.203 0.273 31	-0.247 0.181 31	*	*	*	*	*
Sed. TOC (%)	0.280 0.098 36	0.477 0.007 31	-0.093 0.617 31	0.042 0.825 30	0.067 0.716 32	-0.031 0.868 32	0.111 0.553 31	-0.024 0.904 28	-0.076 0.702 28	-0.132 0.504 28	0.097 0.575 36	*	*	*	*
Sed. C/N (wt./wt.)	-0.011 0.949 36	0.226 0.222 31	-0.179 0.335 31	0.374 0.042 30	0.127 0.489 32	0.237 0.191 32	0.267 0.146 31	0.213 0.276 28	0.225 0.250 28	0.193 0.325 28	0.303 0.073 36	0.567 0.000 36	*	*	*
S-W diversity (H')	-0.199 0.388 21	-0.060 0.808 19	0.249 0.304 19	0.159 0.502 20	-0.271 0.248 20	-0.111 0.640 20	-0.088 0.703 21	0.157 0.498 21	0.496 0.022 21	0.434 0.049 21	-0.403 0.070 21	-0.249 0.303 19	-0.251 0.3 19	*	*
S-W evenness (J)	0.122 0.598 21	-0.092 0.708 19	0.321 0.180 19	-0.233 0.322 20	-0.242 0.303 20	-0.097 0.684 20	-0.146 0.52y 21	-0.319 0.159 21	0.057 0.806 21	-0.029 0.902 21	-0.291 0.201 21	-0.235 0.334 19	-0.478 0.038 19	0.841 0.0001 21	*

Appendix I. Listed below is the benthic Spearman's rho correlation matrix for the Laurier 2000 stations combined overall. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. Cells in **yellow indicate significant positive correlation**, cells in **magenta indicate significant negative correlation**. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Station depth (m)	Bot. water salinity (ppt)	Bot. water temp. (°C)	Bot. water chl <i>a</i> (mg L ⁻¹)	Int. chl <i>a</i> (TWC) (mg m ⁻²)	Int. chl <i>a</i> (euph.) (mg m ⁻²)	Sed. chl <i>a</i> (mg m ⁻²)	Macroinfaunal abund. (no. indiv m ⁻²)	Macroinfaunal biomass (g m ⁻²)	Macroinfaunal biomass (gC m ⁻²)	Modal grain size (Ø)	Sed. TOC (%)	Sed. C/N (wt./wt.)	Macroinfaunal diversity (H')	Macroinfaunal evenness (J)
Station depth (m)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water salinity (ppt)	0.473 0.0001 100	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water temp. (°C)	-0.039 0.699 100	-0.174 0.078 103	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water chl <i>a</i> (mg L ⁻¹)	-0.593 0.0001 91	0.209 0.046 92	0.098 0.353 92	*	*	*	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (TWC) (mg m ⁻²)	0.099 0.350 91	0.378 0.0001 96	0.095 0.357 96	0.484 0.0001 89	*	*	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (euph.) (mg m ⁻²)	-0.149 0.149 96	0.270 0.008 95	0.127 0.218 95	0.658 0.0001 88	0.766 0.0001 96	*	*	*	*	*	*	*	*	*	*
Sed. chl <i>a</i> (mg m ⁻²)	-0.163 0.206 62	0.397 0.002 56	-0.057 0.675 56	0.485 0.0001 57	0.290 0.028 57	0.472 0.0001 57	*	*	*	*	*	*	*	*	*
Macroinfaunal abund. (no. indiv m ⁻²)	-0.233 0.076 59	0.412 0.002 53	0.163 0.245 53	0.500 0.0001 53	0.224 0.104 54	0.356 0.008 54	0.137 0.319 55	*	*	*	*	*	*	*	*
Macroinfaunal Biomass (g m ⁻²)	-0.081 0.544 59	0.502 0.0001 53	0.129 0.357 53	0.547 0.0001 53	0.264 0.053 54	0.386 0.004 54	0.306 0.023 55	0.768 0.0001 59	*	*	*	*	*	*	*
Macroinfaunal biomass (gC m ⁻²)	-0.133 0.315 59	0.488 0.0001 53	0.105 0.453 53	0.553 0.0001 53	0.238 0.083 54	0.370 0.006 54	0.390 0.003 55	0.802 0.0001 59	0.967 0.0001 59	*	*	*	*	*	*
Modal grain size (Ø)	0.247 0.038 71	-0.178 0.163 63	-0.275 0.029 63	-0.242 0.058 62	0.056 0.660 64	-0.118 0.351 64	-0.133 0.308 56	-0.262 0.049 57	-0.210 0.117 57	-0.227 0.090 57	*	*	*	*	*
Sed. TOC (%)	0.214 0.092 63	0.391 0.003 57	-0.226 0.091 57	0.170 0.211 56	0.120 0.369 58	0.087 0.516 58	0.371 0.005 56	-0.063 0.651 54	0.071 0.611 54	0.088 0.529 54	0.352 0.005 62	*	*	*	*
Sed. C/N (wt./wt.)	-0.218 0.086 63	0.408 0.002 57	0.016 0.907 57	0.376 0.004 56	0.172 0.198 58	0.414 0.001 58	0.220 0.103 56	0.355 0.009 53	0.268 0.053 53	0.273 0.048 53	-0.119 0.358 62	0.386 0.002 62	*	*	*
Macroinfaunal diversity (H')	-0.022 0.883 46	0.159 0.307 43	0.020 0.899 43	0.027 0.860 44	-0.103 0.507 44	-0.013 0.933 44	0.117 0.445 45	0.019 0.902 46	0.482 0.001 46	0.404 0.005 46	-0.230 0.124 46	-0.095 0.540 44	-0.007 0.964 43	*	*
Macroinfaunal evenness (J)	0.194 0.195 46	-0.049 0.754 43	-0.098 0.534 43	-0.264 0.083 44	-0.187 0.223 44	-0.209 0.173 44	-0.010 0.949 45	-0.342 0.020 46	0.173 0.251 46	0.091 0.548 46	0.018 0.904 46	-0.035 0.821 44	-0.224 0.150 43	0.869 0.0001 46	*

Appendix J. Bacterial and viral measurements taken during the Laurier 2000 (processed at the Aquatic Microbial Ecology Lab, University of Tennessee, Knoxville by A. Balsom).

Station number	Station name	Bottom water bacteria (BLP L ⁻¹)	Bottom water virus (VLP L ⁻¹)	Surface water bacteria (BLP L ⁻¹)	Surface water virus (VLP L ⁻¹)	Integrated water column bacteria (BLP m ⁻²)	Integrated water column virus (VLP m ⁻²)
3	BD-1	4.38x10 ⁸	1.28x10 ¹¹	1.44x10 ⁸	1.21x10 ¹⁰	4.77x10 ⁹	5.13x10 ¹⁴
4	BD-2	N/A	N/A	N/A	N/A	N/A	N/A
5	BD-3	N/A	N/A	N/A	N/A	N/A	N/A
13	KY-1	1.11x10 ⁸	1.29x10 ⁹	N/A	N/A	8.25x10 ⁹	3.33x10 ¹⁴
23	SW-1	N/A	N/A	N/A	N/A	N/A	N/A
32	KD-1	3.91x10 ⁸	5.44x10 ¹⁰	N/A	N/A	2.18x10 ¹⁰	4.11x10 ¹⁵
34	BD-4	2.68x10 ⁸	2.81x10 ¹⁰	2.76x10 ⁸	1.88x10 ⁹	2.29x10 ¹⁰	2.34x10 ¹⁵
35	BD-5	1.35x10 ⁸	2.13x10 ¹⁰	5.10x10 ⁸	1.29x10 ¹¹	1.28x10 ¹⁰	1.03x10 ¹⁵
36	BCS-1	2.05x10 ⁸	3.79x10 ¹⁰	N/A	N/A	1.18x10 ¹⁰	1.37x10 ¹⁵
37	BCS-4	4.04x10 ⁸	3.16x10 ¹⁰	N/A	N/A	9.62x10 ⁹	7.38x10 ¹⁴
38	SLIP-1	2.60x10 ⁸	2.23x10 ¹⁰	7.58x10 ⁸	7.45x10 ¹⁰	9.80x10 ⁹	6.04x10 ¹⁴
39	SLIP-2	3.62x10 ⁸	5.65x10 ¹⁰	8.73x10 ⁸	1.51x10 ¹¹	1.39x10 ¹⁰	1.56x10 ¹⁵
40	SLIP-3	3.84x10 ⁸	1.01x10 ¹¹	7.08x10 ⁸	5.54x10 ¹⁰	8.58x10 ⁹	1.83x10 ¹⁵
41	SLIP-5	4.55x10 ⁸	8.14x10 ¹⁰	2.35x10 ⁸	3.00x10 ¹⁰	7.95x10 ⁹	2.08x10 ¹⁵
42	SLIP-4	3.81x10 ⁸	2.87x10 ¹⁰	3.69x10 ⁸	1.60x10 ¹⁰	3.03x10 ⁹	6.62x10 ¹⁴
43	BCS-6	N/A	N/A	N/A	N/A	N/A	N/A
44	UTBS-5	4.79x10 ⁸	2.57x10 ¹⁰	4.16x10 ⁸	2.50x10 ¹⁰	1.16x10 ¹⁰	1.91x10 ¹⁵
45	UTBS-2	6.93x10 ⁸	1.15x10 ¹¹	2.65x10 ⁸	5.36x10 ¹⁰	1.26x10 ¹⁰	1.54x10 ¹⁵
46	UTBS-4	4.07x10 ⁸	5.95x10 ¹⁰	2.78x10 ⁸	8.94x10 ¹⁰	9.92x10 ⁹	1.05x10 ¹⁵
47	UTBS-1	4.45x10 ⁸	5.70x10 ¹⁰	1.17x10 ⁸	4.86x10 ¹⁰	1.01x10 ¹⁰	1.43x10 ¹⁵
48	BRS-1	N/A	N/A	N/A	N/A	N/A	N/A
49	BRS-2	N/A	N/A	N/A	N/A	N/A	N/A
50	BRS-3	N/A	N/A	N/A	N/A	N/A	N/A
51	BRS-4	N/A	N/A	N/A	N/A	N/A	N/A
52	BRS-5	N/A	N/A	N/A	N/A	N/A	N/A
53	UTN-1	N/A	N/A	N/A	N/A	N/A	N/A
54	UTN-2	3.72x10 ⁸	6.65x10 ¹⁰	N/A	N/A	7.87x10 ⁹	1.86x10 ¹⁵
55	UTN-3	1.64x10 ⁸	2.42x10 ¹⁰	3.08x10 ⁸	3.84x10 ¹⁰	6.70x10 ⁹	1.73x10 ¹⁵
56	UTN-4	4.02x10 ⁸	5.68x10 ¹⁰	2.40x10 ⁸	5.07x10 ¹⁰	1.18x10 ¹⁰	1.35x10 ¹⁵
57	UTN-5	3.91x10 ⁸	6.83x10 ¹⁰	3.12x10 ⁸	3.81x10 ¹⁰	1.15x10 ¹⁰	2.27x10 ¹⁵
58	UTN-6	5.99x10 ⁸	5.09x10 ¹⁰	4.60x10 ⁸	4.92x10 ¹⁰	1.48x10 ¹⁰	2.78x10 ¹⁵
59	UTN-7	5.67x10 ⁸	1.71x10 ¹⁰	N/A	N/A	1.18x10 ¹⁰	1.45x10 ¹⁵
60	BD-6	3.48x10 ⁸	6.41x10 ¹⁰	N/A	N/A	1.81x10 ¹⁰	1.42x10 ¹⁵
61	BD-7	1.32x10 ⁸	1.37x10 ¹⁰	N/A	N/A	5.57x10 ⁹	7.31x10 ¹⁴
62	BD-8	3.47x10 ⁸	8.08x10 ⁹	N/A	N/A	4.19x10 ⁹	3.67x10 ¹⁴
63	BD-9	N/A	N/A	N/A	N/A	N/A	N/A
64	BD-10	N/A	N/A	N/A	N/A	N/A	N/A

Appendix J. Continued.

Station number	Station name	Bottom water bacteria (BLP L ⁻¹)	Bottom water virus (VLP L ⁻¹)	Surface water bacteria (BLP L ⁻¹)	Surface water virus (VLP L ⁻¹)	Integrated water column bacteria (BLP m ⁻²)	Integrated water column virus (VLP m ⁻²)
65	BD-11	1.72x10 ⁸	9.94x10 ⁹	N/A	N/A	N/A	N/A
66	BD-12	N/A	N/A	N/A	N/A	N/A	N/A
67	H-5	N/A	N/A	N/A	N/A	N/A	N/A
68	H-4	N/A	N/A	N/A	N/A	N/A	N/A
69	H-3	N/A	N/A	N/A	N/A	N/A	N/A
70	H-2	N/A	N/A	N/A	N/A	N/A	N/A
71	H-1	7.86x10 ⁷	5.37x10 ⁹	2.73x10 ⁸	5.81x10 ¹⁰	N/A	N/A
72	BD-13	2.97x10 ⁸	1.10x10 ¹⁰	3.21x10 ⁸	1.44x10 ¹¹	3.80x10 ⁹	1.40x10 ¹⁴
73	BD-14	1.11x10 ⁸	9.10x10 ⁹	4.05x10 ⁸	6.85x10 ¹⁰	4.58x10 ⁹	2.49x10 ¹⁴
74	BD-15	1.12x10 ⁸	4.87x10 ⁹	5.86x10 ⁸	4.17x10 ¹⁰	3.18x10 ⁹	2.60x10 ¹⁴
75	BD-16	2.04x10 ⁸	1.59x10 ¹⁰	5.79x10 ⁸	1.16x10 ¹¹	7.37x10 ⁹	4.39x10 ¹⁴
76	BD-17	1.09x10 ⁸	9.51x10 ⁹	8.62x10 ⁸	9.19x10 ¹⁰	3.94x10 ⁹	2.10x10 ¹⁴
77	BD-18	9.50x10 ⁷	8.15x10 ⁹	5.31x10 ⁸	2.71x10 ¹⁰	4.89x10 ⁹	4.27x10 ¹⁴
78	BD-19	1.75x10 ⁸	1.63x10 ¹⁰	2.12x10 ⁸	6.33x10 ¹⁰	6.67x10 ⁹	4.51x10 ¹⁴
79	BD-20	N/A	N/A	N/A	N/A	N/A	N/A
80	BD-21	2.86x10 ⁸	1.48x10 ¹⁰	1.07x10 ⁸	1.44x10 ¹⁰	N/A	N/A
81	BD-21B	N/A	N/A	N/A	N/A	N/A	N/A
82	BD-22	1.68x10 ⁸	1.99x10 ¹⁰	N/A	N/A	N/A	N/A
83	BD-23	2.02x10 ⁸	1.52x10 ¹⁰	1.46x10 ⁹	7.12x10 ⁹	N/A	N/A
84	BD-24	1.77x10 ⁸	1.51x10 ¹⁰	N/A	N/A	5.58x10 ⁹	3.78x10 ¹⁴
85	BD-25	3.87x10 ⁸	2.46x10 ¹⁰	N/A	N/A	5.55x10 ⁹	5.09x10 ¹⁴
86	BD-26	1.17x10 ⁸	1.38x10 ¹⁰	N/A	N/A	5.22x10 ⁹	3.60x10 ¹⁴
87	BD-27	3.50x10 ⁸	1.53x10 ¹⁰	N/A	N/A	N/A	N/A
89	BD-28	N/A	N/A	N/A	N/A	N/A	N/A
91	BD-29	1.91x10 ⁸	8.72x10 ⁹	N/A	N/A	3.8x10 ⁹	2.95x10 ¹⁴
92	BD-30	1.69x10 ⁸	2.42x10 ¹⁰	4.63x10 ⁸	9.69x10 ⁹	N/A	N/A
93	BD-31	1.02x10 ⁸	6.32x10 ⁹	1.47x10 ⁸	4.65x10 ⁹	3.71x10 ⁹	4.13x10 ¹⁴
95	BD-32	8.91x10 ⁷	6.32x10 ⁹	2.72x10 ⁸	1.51x10 ¹⁰	2.66x10 ⁹	3.37x10 ¹⁴
101	TP-1	1.53x10 ⁸	1.54x10 ¹⁰	1.12x10 ⁸	6.13x10 ⁹	5.13x10 ⁹	3.38x10 ¹⁴
103	EI-11	9.00x10 ⁷	7.46x10 ⁹	1.52x10 ⁸	6.65x10 ⁹	4.10x10 ⁹	2.22x10 ¹⁴
105	EI-9	N/A	N/A	N/A	N/A	N/A	N/A
107	EI-7	N/A	N/A	N/A	N/A	N/A	N/A
110	EI-5	N/A	N/A	N/A	N/A	N/A	N/A
112	EI-3	N/A	N/A	N/A	N/A	N/A	N/A
114	EI-1	N/A	N/A	N/A	N/A	N/A	N/A
115	DU-1	N/A	N/A	N/A	N/A	N/A	N/A
116	DU-2	N/A	N/A	N/A	N/A	N/A	N/A

Appendix J. Continued.

Station number	Station name	Bottom water bacteria (BLP L ⁻¹)	Bottom water virus (VLP L ⁻¹)	Surface water bacteria (BLP L ⁻¹)	Surface water virus (VLP L ⁻¹)	Integrated water column bacteria (BLP m ⁻²)	Integrated water column virus (VLP m ⁻²)
117	DU-3	N/A	N/A	N/A	N/A	N/A	N/A
118	DU-4	N/A	N/A	N/A	N/A	N/A	N/A
119	DU-5	N/A	N/A	N/A	N/A	N/A	N/A
120	DU-5B	N/A	N/A	N/A	N/A	N/A	N/A
121	CP-5	N/A	N/A	N/A	N/A	N/A	N/A
122	CP-4	N/A	N/A	N/A	N/A	N/A	N/A
123	CP-3	N/A	N/A	N/A	N/A	N/A	N/A
124	CP-2	N/A	N/A	N/A	N/A	N/A	N/A
125	CP-1	1.29x10 ⁸	1.30x10 ¹⁰	5.43x10 ⁸	8.09x10 ⁹	2.83x10 ⁹	3.88x10 ¹⁴
127	AG-5	N/A	N/A	N/A	N/A	N/A	N/A
128	AG-5B	N/A	N/A	N/A	N/A	N/A	N/A
129	AG-1	N/A	N/A	N/A	N/A	N/A	N/A
130	AG-2	N/A	N/A	N/A	N/A	N/A	N/A
131	AG-3	N/A	N/A	N/A	N/A	N/A	N/A
132	AG-4	N/A	N/A	N/A	N/A	N/A	N/A
133	AG-5	N/A	N/A	N/A	N/A	N/A	N/A
134	AG-T	N/A	N/A	N/A	N/A	N/A	N/A
135	LW-1	N/A	N/A	N/A	N/A	N/A	N/A
136	LW-2	N/A	N/A	N/A	N/A	N/A	N/A
137	LW-3	N/A	N/A	N/A	N/A	N/A	N/A
138	CK-5	N/A	N/A	N/A	N/A	N/A	N/A
139	CK-5B	N/A	N/A	N/A	N/A	N/A	N/A
140	CK-4	N/A	N/A	N/A	N/A	N/A	N/A
141	CK-3	1.22x10 ⁸	1.21x10 ¹⁰	1.68x10 ⁸	1.30x10 ¹⁰	4.38x10 ⁹	3/14x10 ¹⁴
142	CK-2	N/A	N/A	N/A	N/A	N/A	N/A
143	CK-1	N/A	N/A	N/A	N/A	N/A	N/A
144	AGT-2	N/A	N/A	N/A	N/A	N/A	N/A
145	AGT-2B	N/A	N/A	N/A	N/A	N/A	N/A
146	AGT-3	N/A	N/A	N/A	N/A	N/A	N/A
147	WB-1	N/A	N/A	N/A	N/A	N/A	N/A
148	WB-2	N/A	N/A	N/A	N/A	N/A	N/A
149	WB-3	N/A	N/A	N/A	N/A	N/A	N/A
150	WB-3B	N/A	N/A	N/A	N/A	N/A	N/A
151	WB-4	N/A	N/A	N/A	N/A	N/A	N/A
152	WB-5	1.68x10 ⁸	1.64x10 ¹⁰	1.32x10 ⁸	1.10x10 ¹⁰	1.89x10 ⁹	2.17x10 ¹⁴
153	WB-6	N/A	N/A	N/A	N/A	N/A	N/A

Appendix J. Continued.

Station number	Station name	Bottom water bacteria (BLP L ⁻¹)	Bottom water virus (VLP L ⁻¹)	Surface water bacteria (BLP L ⁻¹)	Surface water virus (VLP L ⁻¹)	Integrated water column bacteria (BLP m ⁻²)	Integrated water column virus (VLP m ⁻²)
154	AGT-4	N/A	N/A	N/A	N/A	N/A	N/A
155	DT-1	N/A	N/A	N/A	N/A	N/A	N/A
156	DT-2	N/A	N/A	N/A	N/A	N/A	N/A
157	DT-3	N/A	N/A	N/A	N/A	N/A	N/A
158	DT-4	N/A	N/A	N/A	N/A	N/A	N/A
159	DT-5	N/A	N/A	N/A	N/A	N/A	N/A
160	BD-33	1.11x10 ⁸	2.40x10 ¹⁰	N/A	N/A	5.41x10 ⁹	3.99x10 ¹⁴
161	BD-34	7.62x10 ⁷	1.24x10 ¹⁰	2.21x10 ⁸	1.42x10 ¹⁰	3.31x10 ⁹	3.44x10 ¹⁴
162	BD-35	N/A	N/A	N/A	N/A	N/A	N/A
163	BD-36	N/A	N/A	N/A	N/A	N/A	N/A
164	BD-37	N/A	N/A	N/A	N/A	N/A	N/A
165	BD-38	N/A	N/A	N/A	N/A	N/A	N/A

Appendix K. Listed below is the microbial discrete depth water column Spearman's rho correlation matrix for Laurier 2000 Gulf of Alaska stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Temp (°C)	Salinity (ppt)	Chl <i>a</i> (mg L ⁻¹)	Bacterial abundance (BLP L ⁻¹)	Viral abundance (VLP L ⁻¹)
Depth (m)	*	*	*	*	*	*
Temp (°C)	-0.789 0.0001 52	*	*	*	*	*
Salinity (ppt)	0.464 0.001 52	-0.379 0.006 52	*	*	*	*
Chl <i>a</i> (mg L ⁻¹)	-0.434 0.001 52	0.264 0.058 52	-0.522 0.0001 52	*	*	*
Bacterial abundance (BLP L ⁻¹)	-0.401 0.028 30	0.188 0.319 30	-0.026 0.891 30	0.722 0.0001 30	*	*
Viral abundance (VLP L ⁻¹)	-0.365 0.047 30	0.179 0.345 30	-0.017 0.928 30	0.552 0.002 30	0.798 0.0001 30	*

Appendix L. Listed below is the microbial discrete depth water column Pearson's product-moment correlation matrix for Laurier 2000 Bering and Chukchi Sea stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the r value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Temp (°C)	Salinity (ppt)	Chl <i>a</i> (mg L ⁻¹)	Bacterial abundance (BLP L ⁻¹)	Viral abundance (VLP L ⁻¹)
Depth (m)	*	*	*	*	*	*
Temp (°C)	-0.571 0.0001 154	*	*	*	*	*
Salinity (ppt)	0.345 0.0001 154	-0.530 0.0001 154	*	*	*	*
Chl <i>a</i> (mg L ⁻¹)	-0.018 0.823 154	-0.305 0.0001 154	0.395 0.0001 154	*	*	*
Bacterial abundance (BLP L ⁻¹)	-0.043 0.655 112	-0.229 0.015 112	0.239 0.011 112	0.191 0.043 112	*	*
Viral abundance (VLP L ⁻¹)	-0.064 0.494 118	-0.179 0.053 118	0.102 0.273 118	0.249 0.006 118	0.228 0.015 112	*

Appendix M. Listed below is the microbial discrete depth water column Spearman's rho non-parametric correlation matrix for Laurier 2000 Beaufort Sea stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Temp (°C)	Salinity (ppt)	Chl <i>a</i> (mg L ⁻¹)	Bacterial abundance (BLP L ⁻¹)	Viral abundance (VLP L ⁻¹)
Depth (m)	*	*	*	*	*	*
Temp (°C)	-0.374 0.001 77	*	*	*	*	*
Salinity (ppt)	0.797 0.0001 77	-0.560 0.0001 77	*	*	*	*
Chl <i>a</i> (mg L ⁻¹)	-0.534 0.0001 77	0.228 0.046 77	-0.445 0.0001 77	*	*	*
Bacterial abundance (BLP L ⁻¹)	-0.419 0.033 26	0.506 0.008 26	-0.352 0.077 26	0.271 0.181 26	*	*
Viral abundance (VLP L ⁻¹)	-0.058 0.778 26	0.653 0.0001 26	-0.090 0.662 26	-0.450 0.021 26	0.403 0.041 26	*

Appendix N. Listed below is the microbial discrete depth water column Pearson's product-moment correlation matrix for Laurier 2000 Canadian Archipelago stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations and bolded cells in magenta indicate significant negative correlations. Top number in cell is the r value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Temp (°C)	Salinity (ppt)	Chl <i>a</i> (mg L ⁻¹)	Bacterial abundance (BLP L ⁻¹)	Viral abundance (VLP L ⁻¹)
Depth (m)	*	*	*	*	*	*
Temp (°C)	-0.272 0.0001 271	*	*	*	*	*
Salinity (ppt)	0.432 0.0001 271	-0.600 0.0001 271	*	*	*	*
Chl <i>a</i> (mg L ⁻¹)	-0.045 0.466 261	-0.692 0.0001 271	0.087 0.163 261	*	*	*
Bacterial abundance (BLP L ⁻¹)	-0.184 0.041 123	0.217 0.0160 123	-0.387 0.0001 123	0.116 0.202 122	*	*
Viral abundance (VLP L ⁻¹)	-0.055 0.535 129	0.006 0.945 129	-0.198 0.024 129	0.064 0.471 128	0.283 0.001 124	*

Appendix O. Listed below is the microbial discrete depth water column Pearson's product-moment correlation matrix for Laurier 2000 stations combined overall. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Temp (°C)	Salinity (ppt)	Chl <i>a</i> (mg L ⁻¹)	Bacterial abundance (BLP L ⁻¹)	Viral abundance (VLP L ⁻¹)
Depth (m)	*	*	*	*	*	*
Temp (°C)	-0.215 0.0001 554	*	*	*	*	*
Salinity (ppt)	0.293 0.0001 554	-0.139 0.0010 554	*	*	*	*
Chl <i>a</i> (mg L ⁻¹)	-0.066 0.126 544	-0.050 0.241 544	0.153 0.0001 544	*	*	*
Bacterial abundance (BLP L ⁻¹)	-0.124 0.033 293	0.164 0.005 293	0.206 0.0001 293	0.292 0.0001 292	*	*
Viral abundance (VLP L ⁻¹)	-0.053 0.357 305	0.150 0.009 305	0.431 0.0001 305	0.354 0.0001 304	0.610 0.0001 292	*

Appendix P. Listed below is the microbial Spearman's rho benthic correlation matrix for Laurier 2000 Bering/Chukchi Sea stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. **Bolded cells in yellow indicate significant positive correlations**, and **bolded cells in magenta indicate significant negative correlations**. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Depth	Bot. water sal	Bot. water temp.	Bot. water chl <i>a</i>	Bot. water virus	Bot. water bact.	Int chl <i>a</i> (WC)	Int chl <i>a</i> (euph.)	Sed chl <i>a</i>	Sed bact	Sed virus	Modal	TOC	C/N
	(m)	(ppt)	(°C)	(mg L ⁻¹)	(VLP L ⁻¹)	(BLP L ⁻¹)	(mg m ⁻²)	(mg m ⁻²)	(mg m ⁻²)	(BLP g ⁻¹)	(VLP g ⁻¹)	(Ø)	(%)	(wt./wt.)
Depth	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water sal	0.268 0.185 26	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water temp.	-0.425 0.030 26	-0.241 0.236 26	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water chl <i>a</i>	-0.229 0.261 26	0.562 0.003 26	-0.002 0.991 26	*	*	*	*	*	*	*	*	*	*	*
Bot. water virus	-0.271 0.262 19	-0.232 0.340 19	-0.077 0.753 19	-0.111 0.652 19	*	*	*	*	*	*	*	*	*	*
Bot. water bact.	-0.202 0.407 19	0.414 0.078 19	-0.218 0.371 19	0.386 0.103 19	0.323 0.178 19	*	*	*	*	*	*	*	*	*
Int chl <i>a</i> (WC)	-0.016 0.936 26	0.742 0.0001 26	-0.041 0.841 26	0.830 0.0001 26	-0.075 0.759 19	0.291 0.226 19	*	*	*	*	*	*	*	*
Int chl <i>a</i> (euph.)	-0.269 0.185 26	0.619 0.001 26	0.182 0.375 26	0.826 0.0001 26	-0.100 0.684 19	0.251 0.300 19	0.935 0.0001 26	*	*	*	*	*	*	*
Sed chl <i>a</i>	0.401 0.079 20	-0.175 0.473 19	-0.254 0.293 19	-0.196 0.420 19	0.004 0.989 19	-0.086 0.726 19	-0.107 0.663 19	-0.223 0.359 19	*	*	*	*	*	*
Sed bact.	-0.349 0.131 20	0.098 0.682 20	-0.126 0.596 20	0.128 0.591 20	0.044 0.858 19	0.225 0.355 19	0.026 0.915 20	0.090 0.705 20	0.204 0.403 19	*	*	*	*	*
Sed virus	0.032 0.894 20	0.002 0.995 20	-0.432 0.057 20	-0.173 0.466 20	0.119 0.627 19	-0.030 0.904 19	-0.125 0.600 20	-0.214 0.366 20	0.296 0.218 19	0.659 0.002 20	*	*	*	*
Modal (Ø)	0.599 0.007 19	0.191 0.448 18	-0.207 0.409 18	-0.133 0.600 18	0.000 1.000 18	0.041 0.870 18	0.058 0.819 18	-0.050 0.845 18	0.258 0.287 19	0.000 1.000 18	0.257 0.303 18	*	*	*
TOC (%)	0.535 0.015 20	0.135 0.581 19	-0.091 0.710 19	0.065 0.792 19	-0.209 0.404 18	0.013 0.958 18	0.074 0.764 19	0.021 0.932 19	0.491 0.033 19	0.151 0.538 19	0.221 0.363 19	0.777 0.0001 19	*	*
C/N (wt./wt.)	-0.317 0.174 20	-0.584 0.009 19	0.396 0.093 19	-0.489 0.034 19	-0.178 0.481 18	-0.449 0.061 18	-0.601 0.007 19	-0.342 0.152 19	-0.148 0.544 19	-0.076 0.759 19	-0.211 0.387 19	-0.270 0.265 19	-0.264 0.261 20	*

Appendix Q. Listed below is the microbial Spearman's rho benthic correlation matrix for Laurier 2000 Canadian Archipelago stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Bot. water sal (ppt)	Bot. water temp. (°C)	Bot. water chl <i>a</i> (mg L ⁻¹)	Bot. water virus (VLP L ⁻¹)	Bot. water bact. (BLP L ⁻¹)	Int. chl <i>a</i> (WC) (mg m ⁻²)	Int. chl <i>a</i> (euph.) (mg m ⁻²)	Sed chl <i>a</i> (mg m ⁻²)	Sed bact. (BLP g ⁻¹)	Sed virus (VLP g ⁻¹)	Modal (Ø)	TOC (%)	C/N (wt./wt.)
Depth (m)	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water sal (ppt)	0.572 0.0001 52	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water temp. (°C)	-0.229 0.102 52	-0.518 0.0001 52	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water chl <i>a</i> (mg L ⁻¹)	-0.343 0.015 50	0.103 0.505 44	-0.078 0.613 44	*	*	*	*	*	*	*	*	*	*	*
Bot. water virus (VLP L ⁻¹)	-0.131 0.541 24	-0.099 0.645 24	0.091 0.671 24	-0.263 0.214 24	*	*	*	*	*	*	*	*	*	*
Bot. water bact. (BLP L ⁻¹)	-0.284 0.178 24	-0.231 0.277 24	0.110 0.607 24	-0.257 0.226 24	0.547 0.006 24	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (WC) (mg m ⁻²)	0.610 0.0001 50	0.439 0.002 49	-0.192 0.185 49	0.313 0.038 44	-0.192 0.368 24	-0.370 0.075 24	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (euph.) (mg m ⁻²)	0.036 0.805 49	0.287 0.048 48	-0.149 0.312 48	0.667 0.0001 43	0.000 1.000 7	-0.321 0.482 7	0.687 0.0001 49	*	*	*	*	*	*	*
Sed chl <i>a</i> (mg m ⁻²)	-0.244 0.158 35	0.266 0.156 30	-0.065 0.734 30	0.334 0.066 31	-0.158 0.471 23	-0.060 0.785 23	0.150 0.421 31	0.541 0.002 31	*	*	*	*	*	*
Sed bact. (BLP g ⁻¹)	-0.208 0.287 28	-0.370 0.058 27	0.536 0.004 27	-0.135 0.502 27	0.344 0.099 24	0.046 0.831 24	-0.063 0.748 28	0.345 0.328 10	0.170 0.407 26	*	*	*	*	*
Sed virus (VLP g ⁻¹)	-0.076 0.706 27	-0.281 0.165 26	0.198 0.332 26	0.049 0.811 26	0.408 0.053 23	0.194 0.376 23	-0.013 0.949 27	0.008 0.983 9	0.149 0.476 25	0.690 0.0001 27	*	*	*	*
Modal (Ø)	0.212 0.178 42	-0.160 0.350 36	-0.026 0.882 36	0.028 0.873 36	0.044 0.839 24	0.014 0.950 24	0.286 0.086 37	0.103 0.542 37	-0.316 0.212 35	-0.099 0.615 28	0.107 0.595 27	*	*	*
TOC (%)	0.280 0.098 36	0.477 0.007 31	-0.093 0.617 31	0.042 0.825 30	-0.160 0.487 21	-0.067 0.773 21	0.067 0.716 32	-0.031 0.868 32	0.111 0.553 31	-0.280 0.175 25	0.137 0.525 24	0.097 0.575 36	*	*
C/N (wt./wt.)	-0.011 0.949 36	0.226 0.222 31	-0.179 0.335 31	0.374 0.042 30	-0.445 0.043 21	-0.252 0.271 21	0.127 0.489 32	0.237 0.191 32	0.267 0.146 31	-0.258 0.212 25	0.010 0.965 24	0.303 0.073 36	0.567 0.0001 36	*

Appendix R. Listed below is the microbial Spearman's rho benthic correlation matrix for Laurier 2000 stations combined overall. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Depth (m)	Bot. water sal (ppt)	Bot. water temp. (°C)	Bot. water chl <i>a</i> (mg L ⁻¹)	Bot. water virus (VLP L ⁻¹)	Bot. water bact. (BLP L ⁻¹)	Int. chl <i>a</i> (WC) (mg m ⁻²)	Int. chl <i>a</i> (euph.) (mg m ⁻²)	Sed chl <i>a</i> (mg m ⁻²)	Sed bact. (BLP g ⁻¹)	Sed virus (VLP g ⁻¹)	Modal (Ø)	TOC (%)	C/N (wt./wt.)
Depth (m)	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water sal (ppt)	0.457 0.0001 103	*	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water temp. (°C)	-0.147 0.139 103	-0.174 0.078 103	*	*	*	*	*	*	*	*	*	*	*	*
Bot. water chl <i>a</i> (mg L ⁻¹)	-0.399 0.0001 98	0.209 0.046 92	0.098 0.353 92	*	*	*	*	*	*	*	*	*	*	*
Bot. water virus (VLP L ⁻¹)	0.027 0.849 52	0.464 0.001 52	0.135 0.341 52	0.298 0.032 52	*	*	*	*	*	*	*	*	*	*
Bot. water bact. (BLP L ⁻¹)	-0.076 0.592 52	0.472 0.0001 52	0.119 0.402 52	0.405 0.003 52	0.788 0.0001 52	*	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (WC) (mg m ⁻²)	0.297 0.003 97	0.378 0.0001 96	0.095 0.357 96	0.484 0.0001 89	0.321 0.020 52	0.259 0.063 52	*	*	*	*	*	*	*	*
Int. chl <i>a</i> (euph.) (mg m ⁻²)	-0.149 0.149 96	0.270 0.008 95	0.127 0.218 95	0.658 0.0001 88	0.211 0.223 35	0.308 0.072 35	0.766 0.0001 96.000	*	*	*	*	*	*	*
Sed chl <i>a</i> (mg m ⁻²)	-0.163 0.206 62	0.397 0.002 56	-0.057 0.675 56	0.485 0.0001 57	0.449 0.001 48	0.465 0.001 48	0.290 0.028 57	0.472 0.0001 57	*	*	*	*	*	*
Sed bact. (BLP g ⁻¹)	-0.164 0.229 56	-0.134 0.331 55	0.167 0.222 55	-0.007 0.960 55	0.253 0.080 49	0.222 0.125 49	-0.014 0.918 56	-0.011 0.949 38	0.338 0.015 51	*	*	*	*	*
Sed virus (VLP g ⁻¹)	-0.009 0.949 55	0.058 0.680 54	-0.089 0.522 54	0.163 0.239 54	0.507 0.0001 48	0.434 0.002 48	0.090 0.512 55	0.046 0.789 37	0.463 0.001 50	0.784 0.0001 55	*	*	*	*
Modal (Ø)	0.247 0.038 71	-0.178 0.163 63	-0.275 0.029 63	-0.242 0.058 62	-0.199 0.170 49	-0.220 0.128 49	0.056 0.660 64	-0.118 0.351 64	-0.133 0.308 61	-0.078 0.580 53	0.083 0.559 52	*	*	*
TOC (%)	0.214 0.092 63	0.391 0.003 57	-0.226 0.091 57	0.170 0.211 56	-0.016 0.916 46	0.051 0.736 46	0.120 0.369 58	0.087 0.516 58	0.371 0.005 56	-0.029 0.841 50	0.187 0.198 49	0.352 0.005 62	*	*
C/N (wt./wt.)	-0.218 0.086 63	0.408 0.002 57	0.016 0.907 57	0.376 0.004 56	-0.047 0.761 45	0.007 0.965 45	0.172 0.198 58	0.414 0.001 58	0.220 0.103 56	-0.240 0.093 50	-0.162 0.265 49	-0.119 0.358 62	0.386 0.002 62	*

Appendix S. Listed below is the microbial-macrofaunal relationship Spearman's rho benthic correlation matrix for Laurier 2000 Bering and Chukchi Sea stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Bottom water viral abund. (VLP L ⁻¹)	Bottom water bact. abund. (BLP L ⁻¹)	Sed. bact. abund. (BLP g ⁻¹)	Sed. viral abund. (VLP g ⁻¹)	Macrofaunal abundance (no. indiv. m ⁻²)	Macrofaunal biomass (gC m ⁻²)	Macrofaunal diversity (H')	Macrofaunal evenness (J)
Bottom water viral abund. (VLP L ⁻¹)	*	*	*	*	*	*	*	*
Bottom water bact. abund. (BLP L ⁻¹)	0.323 178.000 19	*	*	*	*	*	*	*
Sed. bact. abund. (BLP g ⁻¹)	0.044 0.858 19	0.225 0.355 19	*	*	*	*	*	*
Sed. viral abund. (VLP g ⁻¹)	0.119 0.627 19	-0.030 0.904 19	0.659 0.002 20	*	*	*	*	*
Macrofaunal abundance (no. indiv. m ⁻²)	0.104 0.670 19	0.258 0.286 19	0.061 0.803 19	-0.197 0.418 19	*	*	*	*
Macrofaunal biomass (gC m ⁻²)	-0.191 0.433 19	0.177 0.468 19	0.153 0.533 19	0.144 0.557 19	0.351 0.129 20	*	*	*
Macrofaunal diversity (H')	-0.105 0.687 17	-0.306 0.232 17	0.076 0.772 17	0.363 0.152 17	-0.459 0.056 18	0.294 0.236 18	*	*
Macrofaunal evenness (J)	-0.114 0.663 17	-0.347 0.172 17	0.112 0.670 17	0.439 0.078 17	-0.473 0.048 18	0.317 0.200 18	0.983 0.0001 18	*

Appendix T. Listed below is the microbial-macroinfaunal relationship Spearman's rho benthic correlation matrix for Laurier 2000 Canadian Archipelago stations. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline** and **bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Bottom water viral abund. (VLP L ⁻¹)	Bottom water bact. abund. (BLP L ⁻¹)	Sed. bact. abund. (BLP g ⁻¹)	Sed. viral abund. (VLP g ⁻¹)	Macroinfaunal abundance (no. indiv. m ⁻²)	Macroinfaunal biomass (gC m ⁻²)	Macroinfaunal diversity (H')	Macroinfaunal evenness (J)
Bottom water viral abund. (VLP L ⁻¹)	*	*	*	*	*	*	*	*
Bottom water bact. abund. (BLP L ⁻¹)	0.547 0.006 24	*	*	*	*	*	*	*
Sed. bact. abund. (BLP g ⁻¹)	0.344 0.099 24	0.046 0.831 24	*	*	*	*	*	*
Sed. viral abund. (VLP g ⁻¹)	0.408 0.053 23	0.194 0.376 23	0.690 0.0001 27	*	*	*	*	*
Macroinfaunal abundance (no. indiv. m ⁻²)	-0.156 0.478 23	0.008 0.971 23	-0.152 0.448 27	-0.095 0.644 26	*	*	*	*
Macroinfaunal biomass (gC m ⁻²)	-0.176 0.422 23	0.042 0.847 23	-0.013 0.947 27	0.013 0.951 26	0.768 0.0001 32	*	*	*
Macroinfaunal diversity (H')	-0.223 0.390 17	-0.093 0.722 17	0.379 0.099 20	0.137 0.576 19	0.157 0.498 21	0.434 0.049 21	*	*
Macroinfaunal evenness (J)	-0.085 0.747 17	-0.054 0.837 17	0.426 0.061 20	0.076 0.756 19	-0.319 0.159 21	-0.029 0.902 21	0.841 0.0001 21	*

Appendix U. Listed below is the microbial-macroinfaunal relationship Spearman's rho benthic correlation matrix for Laurier 2000 stations combined overall. Please see List of Abbreviations and Definitions page for parameters. **Bold box outline and bold text** emphasize significant correlations. Bolded cells in yellow indicate significant positive correlations, and bolded cells in magenta indicate significant negative correlations. Top number in cell is the rho value, center number is p-value, and the bottom number is the sample size n.

	Bottom water viral abund. (VLP L ⁻¹)	Bottom water bact. abund. (BLP L ⁻¹)	Sed. bact. abund. (BLP g ⁻¹)	Sed. viral abund. (VLP g ⁻¹)	Macroinfaunal abundance (no. indiv. m ⁻²)	Macroinfaunal biomass (gC m ⁻²)	Macroinfaunal diversity (H')	Macroinfaunal evenness (J)
Bottom water viral abund. (VLP L ⁻¹)	*	*	*	*	*	*	*	*
Bottom water bact. abund. (BLP L ⁻¹)	0.788 0.0001 52	*	*	*	*	*	*	*
Sed. bact. abund. (BLP g ⁻¹)	0.253 0.080 49	0.222 0.125 49	*	*	*	*	*	*
Sed. viral abund. (VLP g ⁻¹)	0.507 0.0001 48	0.434 0.002 48	0.784 0.0001 55	*	*	*	*	*
Macroinfaunal abundance (no. indiv. m ⁻²)	0.260 0.071 49	0.385 0.006 49	0.043 0.761 52	0.111 0.437 51	*	*	*	*
Macroinfaunal biomass (gC m ⁻²)	0.458 0.001 49	0.541 0.0001 49	0.203 0.149 52	0.393 0.004 51	0.802 0.0001 59	*	*	*
Macroinfaunal diversity (H')	0.258 0.103 41	0.107 0.505 41	0.294 0.055 43	0.349 0.024 42	0.019 0.902 46	0.404 0.005 46	*	*
Macroinfaunal evenness (J)	0.091 0.572 41	-0.075 0.643 41	0.294 0.056 43	0.327 0.034 42	-0.342 0.020 46	0.091 0.548 46	0.869 0.0001 46	*

VITA

Arianne Lynn Balsom was born in Madison, Wisconsin on December 20, 1976. She was raised in Madison where she attended school until transferring her sophomore year to Bearden High School in Knoxville, Tennessee from which she graduated. She attended the University of the South in Sewanee, Tennessee before transferring to the University of Tennessee, Knoxville, where she double-majored with a B.A. in Marine Biology through the Individualized Major program, and a B.S. in Ecology and Evolutionary Biology in 2000. She then continued on at the University of Tennessee under the guidance of Dr. Jackie Grebmeier to receive a M.S. in Ecology and Evolutionary Biology with a concentration in Biological Oceanography in 2003.