DECADAL CHANGES IN MACROBENTHOS ALONG A LATITUDINAL GRADIENT ON THE WEST ANTARCTIC PENINSULA CONTINENTAL SHELF

A THESIS SUBMITTED TO
THE GLOBAL ENVIRONMENTAL SCIENCE
UNDERGRADUATE DIVISION IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

BACHELOR OF SCIENCE
IN
GLOBAL ENVIRONMENTAL SCIENCE
May 2011

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I certify that I have read this thesis and that, in my opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

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ACKNOWLEDGMENTS

I would like to thank every member of Craig Smith's lab, especially Pavica Srsen, Fabio De Leo, and Iris Altamira, for their continuous and ongoing help with macrofaunal identification, Jane Schoonmaker, Leona Anthony, and everyone in the G.E.S. family for their genuine caring and assistance, Heather Norton for her positive encouragement, Craig Smith, for his patience and understanding throughout my entire opportunity of working with him, and Marisa, for her endless love and unconditional support.

ABSTRACT

As a result of rapid regional warming of the Antarctic Peninsula there has been an increase in melt-water (Clarke et al., 2007; Scambos et al., 2003), the loss of seven ice shelves (Vaughn and Doake, 1996), and a decrease in sea-ice concentration and duration along the Western Antarctic Peninsula continental shelf (WAPcs) and Bellinghausen Sea (Jacobs and Comiso, 1997; Smith and Stammerjohn, 2001). Our quantitative research of macrobenthic abundance (N/m^2), biomass (g/m^2), and mean body size (g/N) on the WAPcs reveal significant latitudinal gradients and decadal changes since 1985 (Mühlenhardt-Siegel, 1988). We hypothesize that these decadal changes are associated with decadal rates of decreased and increased overlying primary productivity in the northern and southern subregions of the WAPcs, respectively, which is in turn a function of overall decreased sea-ice cover (Montes-Hugo et al., 2009).

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LIST OF ABBREVIATIONS

AASW	Antarctic Surface Water
AFDW	Ash-free dry weight
cm	Centimeters
Chl a	Chlorophyll concentration, measured in (mg/m3)
FOODBANCS	Food for the Benthos on the Antarctic Continental Shelf research
m	meters
mg	milligrams
NSF	The National Science Foundation
nsWAPcs	Northern subregion of the WAP continental shelf (61° to 64.5°, S)
PAL-LTER	The Palmer Long Term Ecological Research Project
Preservation Sol.	4% Formaldehyde buffered with Sodium Tetraborate Decahydrate
POM	Particulate Organic Matter
ssWAPcs	Southern subregion of the WAP (63.8° to 67.8°, S)
WAPcs	Western Antarctic Peninsula continental shelf

CHAPTER 1: INTRODUCTION

An Introduction to Benthic Organisms

The polar regions of Antarctica are home to native and endemic fauna, both within the terrestrial and marine environments. Antarctic organisms are of interest to scientific researchers for multiple reasons, including their environmental isolation and evolution in harsh environmental conditions (Hempel, 1985), as well as their response to a rapidly changing climate (Clarke et al., 2007). This study focuses on the ecological composition of the numerous marine organisms that live in or on the seafloor, collectively referred to as the benthos. These benthic organisms, which are operationally subdivided by their size, inhabit seafloors of all the oceans, including our area of study: the continental shelf of the Western Antarctic Peninsula (WAPcs, 60°S to 75°S).

The megafauna (or megazoobenthos) are a collection of benthic organisms defined by sizes larger than 3cm or "large enough to be identified in bottom photographs," whereas macrofauna (the focus of this study) are defined as benthic organisms greater in size than 500μm (0.5mm) yet smaller than the megafauna (Gage and Tyler, 1992). Meiofauna, the smallest of the three size classes, are defined as organisms within the size range of 62μm – 500μm (Giere, 2009). Some taxonomic groups, such as copepoda and oligochaeta, are conventionally included in meiofauna, as are some groups excluded from it (Hulings and Gray, 1971). Broad taxonomic phyla of benthos have been used in this study and other scientific reports for categorizing patterns of macrofaunal community structure and biomass, including the mollusca and echinodermata, as well as classes such as the polychaeta and crustacea (Muhlenhardt-Siegel, 1988) based on their relative dominance within the macrofauna.

Benthic-Pelagic Coupling on the Antarctic Shelf

Suspension and deposit feeding benthic organisms, as well as sediment microbes, rely on the particulate organic matter or phytodetrital "rain" generated from overlying primary production. The relationship between the processes of the water column and the benthic, seen in the transfer of surface nutrients to the seafloor, is referred to as Benthic-Pelagic Coupling (Longhurst, 1983). The continental shelf of the WAP (WAPcs) is especially impacted by these seasonal fluxes of particulate organic matter (POM) to the seafloor. Reports from the Palmer Long-Term Ecological Research (PAL-LTER) study area indicate very strong seasonality. The highest and lowest POM fluxes ever measured among the world's oceans were recorded on the Antarctic shelf in the austral summer and austral wintertime, respectively (Karl, 1996). This seasonal flux, a consequence of variations in sunlight between the austral summer and winter seasons (Eicken, 1992) has ramifications for benthic ecosystem and structure (Clarke, 1985; Dayton, 1990; Arntz et al., 1994; Smith et al., 2006) which may include changes in benthic biomass, feeding behaviors, animal growth, developmental modes, reproductive strategies, bioturbation rates and carbon burial (Smith et al. 2006, 2008).

In addition to increased photoperiod (i.e. duration of light) associated with pulsing of organic matter from the euphotic zone of the Antarctic surface water (AASW), the amount of primary productivity of the WAP shelf is also a function of sea-ice extent and duration, as well as water stratification (Eicken, 1992; Smith et al., 2006). As a result, benthic community structure will be an ecological end member to test our understanding of Benthic-Pelagic coupling along the WAP shelf. Moreover, it's expected that changes in monthly and annual extent/duration of sea-ice, water stratification, and annual changes in primary productivity, as a function of latitude, will be reflected in measurements of benthic community structure and composition, including biomass and abundance per square meter.

A Benthic “Food bank” of Labile Organic Matter

Intense seasonal variation in primary productivity over the WAP continental shelf (WAPcs) and the consequent strong pulses of POM, coupled with the low-temperatures, are thought to be responsible for high standing concentrations of organic matter (Arntz et al., 1994) on the WAPcs. However, multiple studies have found that macrofauna of the WAP continental shelf consistently feed, grow, and reproduce throughout the year with little variability despite seasonal variation in POM flux (Glover et al., 2008; Smith et al., 2006, 2008; Galley et al., 2008; Sumida et al., 2008). Mincks et al. (2005) have postulated that the underlying reason is due to the presence of a persistent “food bank” of labile organic matter in sediments which accumulate at the seafloor and persist throughout the year. As a consequence, Smith et al. (2006) argue that benthic parameters such as inventories of labile organic matter and benthic biomass may act as “low-pass” filters, only responding to longer-term changes in water column production, which will allow researchers to examine how climate-driven changes act on a ecosystem not readily perturbed.

Climate Change and the Western Antarctic Peninsula

Especially important to our understanding of Antarctic benthic ecology is to figure out how rapid changes in the polar climate alter the regional benthic ecosystem.

Major changes in the high-latitude region include, as a result of rapid regional warming of the Antarctic Peninsula, the collapse of seven ice shelves in the past 50 years (Vaughan and Doake, 1996), an increase in melt-water associated with rapid retreat of ice shelves and marine glaciers (Clarke et al., 2007; Scambos et al., 2003) as well as a decrease in sea-ice concentration and duration over the last two decades in the WAPcs and Bellingshausen sea (Jacobs and Comiso, 1997; Smith and Stammerjohn, 2001; Parkinson, 2002; Liu et al., 2004). Indeed, the rate of atmospheric temperature increase on the WAP exceeds any other region of the Southern Hemisphere and is only paralleled by northwestern North America and the Siberian Plateau in the Northern Hemipshere, -- of the three regions, only the WAP is maritime (Trenberth et al., 2007). Such rapid changes in the atmosphere and AASW above the continental shelf of the WAP are expected to induce changes in benthic processes, such as faunal abundance, biomass, reproduction and recruitment, which are hypothesized to act as “low-pass” filters (Smith and DeMaster, 2008).

Recently, Montes-Hugo et al. (2009) looked at biological changes associated with regional climate change of the WAPcs, specifically changes in chlorophyll a (Chl a) concentration associated with phytoplankton communities, as a function of water-column mixing, which is in turn a function of ice-cover, cloudiness, and windiness. As seen in Figure 1, Montes-Hugo et al. (2009) found that with respect to 1978 – 1986, satellite-derived Chl a concentration has decreased by a factor of 2 in the northern subregion of the WAPcs (nsWAPcs, 61° to 64.5° S, 59° to 65.8° W) and increased by a factor of 1.5 in the southern subregion of the WAPcs (ssWAPcs, 63.8° to 67.8° S, 64.4° to 73.0° W).

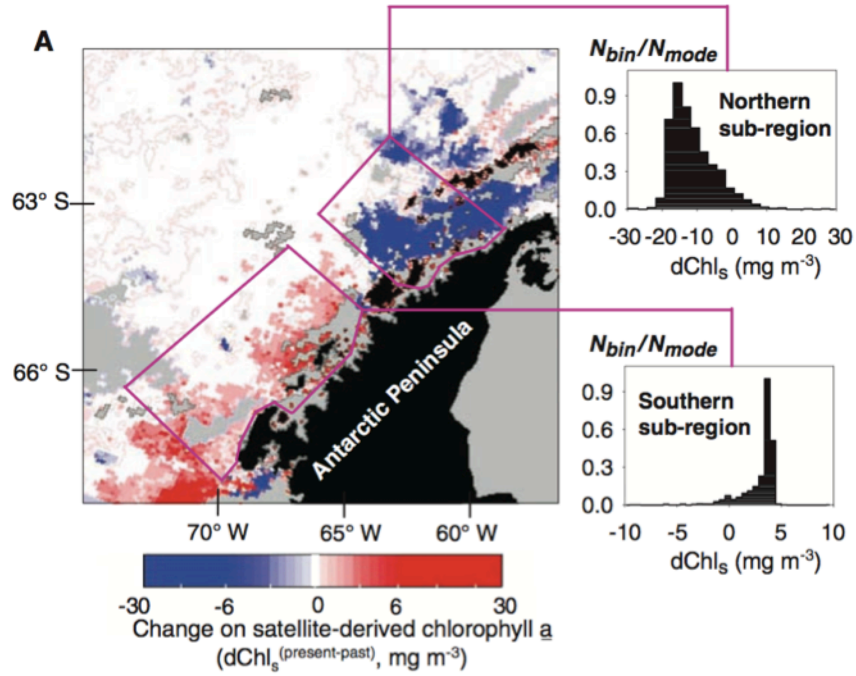


Figure 1: Changes in Chl a derived from satellite observation (dChl$_s$, mg m^{-3}) between 1978 – 1986 and 1997 – 2006 along the WAPcs, from Montes-Hugo et al. (2009).

Montes-Hugo (2009) attributed the decrease in the nsWAPcs primary productivity to increased cloudiness (decreased sunlight), persistently stronger winds, and decreased summer sea-ice extent; conditions driving phytoplankton cells into a deeper mixed layer with overall less light availability for photosynthesis. In comparison to the nsWAP, mean annual sea-ice cover is greater in the ssWAP (Figure 25) and Montes-Hugo argues that in this region any decrease in sea-ice cover over the surface mixed layer facilitates favorable conditions for phytoplankton growth.

As a result of the rapid climate change occurring on the order of decades at the WAPcs, an objective of our research is to better understand how the anthropogenic warming may affect benthic pelagic coupling and consequently the macrobenthic ecosystem. Through the comparison of our quantitative data of macrofauna to some of the earliest quantitative data available on the benthic ecosystem of the WAPcs, we hope to better understand how the benthos have adapted to decadal regional warming of the WAPcs and further predict how they will respond to a continuously changing climate.

Quantitative Reports on the Macrobenthos

The benthic ecosystem of the Antarctic continental shelf is characterized by especially high biomass levels (Knox, 1994) and high variability (Gutt, 1991). To add to this variability, much of the earlier published research on Antarctic benthos as a whole lack quantitative data (Arnaud, 1992) due to qualitative sampling methods of the macrobenthos (i.e., using Beam or Aggassiz trawls, Epibenthic sleds, Anchor Dredges, etc). Furthermore, macrobenthic samples of the WAPcs have been retrieved predominantly from shallow depths (<100m). Numerous studies have described the shallow inshore benthic community of the Antarctic continental shelf as dominated by sessile organisms such as sponges as well as anemones and cnidarians, but unfortunately do not provide comparable data for our sampling at ~600m depth (Dayton et al, 1970; Gerdes et al., 1992; Sáiz-Salinas et al, 1998).

Another major confounding factor is the lack of quantitative data in our specific region of sampling along the WAPcs. Quantitative sampling of Antarctic benthos has occurred at similar depths, yet Stammerjohn et al. (2008) have illustrated the strong differences in physical environmental conditions by location on the Antarctic continental shelf (e.g. increasing sea-ice concentration and duration in the Ross Sea, vs. rapid decline in the Bellinghausen Sea). Pipenburg et al. (2002) have also underscored strong differences by location in biological communities, e.g. high – Antarctic samples in the Weddell Sea on the eastern side of the Antarctic Peninsula are dominated by sponges, in comparison to the polychaeta dominated WAPcs. Inherently, early comparable studies for quantitative analysis of macrofaunal communities for insight into climate change are limited, especially since the Bellinghausen Sea west of the Antarctic Peninsula is one of the least explored (Saiz et al., 2008).

In contrast to other benthic research of her time, Mühlenhardt-Siegel (1988) provided an early example of quantitative macrobenthic research along a latidudinal transect of the WAP from 60°S - 68°S from November, 1984 to April, 1985, which this study was modeled after to provide a direct decadal comparison (Figure 26). Mühlenhardt-Siegel (1988) collected eighty-six quantitative grab samples from 42 stations within a depth range of 60 – 850m, sieved macrofaunal samples on a 0.5mm sieve, and taxonomically sorted them to the crustacea, mollusca, echinodermata, and polychaeta, measuring both abundance and wet-weight per taxonomic group. Statistical analyses were run on her raw data from the Antarctic Peninsula, and significant interactions between latitude, depth, and biomass are shown (Figure 27) and discussed in the Results and Discussion chapter.

<u>Objectives of this research</u>

The objective of this study is to quantify the macrofauna retrieved from box-corer samples which were collected in March 2008 from the first cruise of the FOODBANCS-2 (Food for the Benthos on the Antarctic Continental Shelf) research program, in order to compare our macrofaunal abundance and biomass data to both overlying sea-ice and primary productivity data as well as to similar data obtained along the same latitudinal gradient by earlier investigators in 1984 - 1985.

Specifically, this study is designed to answer three questions:

1) How do total or taxon biomass, abundance, and mean body size of macrofauna of the WAPcs vary as a function of latitude?

2) Is there any evidence of decadal variation in macrobenthic biomass and abundance along the WAPcs?

3) How do biomass and abundance of macrofauna vary as a function of primary productivity and mean annual sea-ice cover?

CHAPTER 2: METHODS

Field Methods

The samples were collected as part of the second study of the Food for the Benthos on the Antarctic Continental Shelf (FOODBANCS - 2) research program aboard the R/V Laurence Gould (Figure 28, Appendix) from five stations, AA, B, E, F, and G from 63.1°S to 68.1°S during March of 2008. All macrofaunal samples were obtained by a 0.250 m^2 box corer (Figure 29, Appendix), with a sub-core area of 0.25m x 0.25m or 0.0625 m^2. Samples were preserved in 4% formaldehyde (or 10% formalin) buffered with sodium tetraborate decahyrate. During the first cruise of FOODBANCS-2 in March 2008, a total of 11 samples (three from station AA, two from station B, three from station F, and three from station G) were used in this study. See Table 1 for each station, latitude and longitude, as well as depth, CRS reference number, depth partition associated with each sample, and sampling date.

Extraction

Samples were prepared for taxonomic sorting by the addition of Rose Bengal to the preservation solution in the sample container. The red stain of Rose Bengal adhered to the membrane of faunal species and allowed for easy identification and extraction of the macrofauna from the sediment. After a period of at least 2.5 hours (overnight in most cases) the stained samples were ready and prepared for extraction.

Table 1: Station, Latitude and Longitude, Depth (in meters), CRS Reference number, Depth Partition (in centimeters), and Sampling Date of each sample taken along the Western Antarctic Peninsula continental shelf (WAPcs).

Station	Latitude, Longitude	Depth (m)	CRS Number	Depth Partition into Sediment (cm)	Sampling Date
AA	63° 3'15.00"S 61°35'30.00"W	578	934	0 – 5	Mar. 2008
AA	63° 3'15.00"S 61°35'30.00"W	578	934	5 – 10	Mar. 2008
AA	63° 3'15.00"S 61°35'30.00"W	578	942	0 – 5	Mar. 2008
AA	63° 3'15.00"S 61°35'30.00"W	578	942	5 – 10	Mar. 2008
AA	63° 3'15.00"S 61°35'30.00"W	578	950	0 – 5	Mar. 2008
AA	63° 3'15.00"S 61°35'30.00"W	578	950	5 – 10	Mar. 2008
B	64°48'18.00"S 65°21'18.00"W	578	962	0 – 5	Mar. 2008
B	64°48'18.00"S 65°21'18.00"W	578	962	5 – 10	Mar. 2008
B	64°48'18.00"S 65°21'18.00"W	578	968	0 – 5	Mar. 2008
B	64°48'18.00"S 65°21'18.00"W	578	968	5 – 10	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	994	0 – 5	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	994	5 – 10	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	999	0 – 5	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	999	5 – 10	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	999	10 – End	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	1001	0 – 5	Mar. 2008
F	66°59'25.00"S 69°43'0.00"W	590	1001	5 – 10	Mar. 2008
G	68° 5'14.35"S 71° 0'56.62"W	582	1013	0 – 5	Mar. 2008
G	68° 5'14.35"S 71° 0'56.62"W	582	1013	5 – 10	Mar. 2008
G	68° 5'14.35"S 71° 0'56.62"W	582	1017	0 – 5	Mar. 2008
G	68° 5'14.35"S 71° 0'56.62"W	582	1017	5 – 10	Mar. 2008
G	68° 5'14.35"S 71° 0'56.62"W	582	1021	0 – 5	Mar. 2008
G	68° 5'14.35"S 71° 0'56.62"W	582	1021	5 – 10	Mar. 2008

Sieving the box-corer samples

Macrofaunal samples were separated from the sediment via 500µm and 300µm sieves, and the >500µm fraction and 500µm - 300µm fraction were separated and stored. The fraction smaller than 300µm was not the focus of this research project, since it contained by definition the meiofauna, and was subsequently stored. The >500µm fractions containing the stained macrofauna were then prepared for sorting with stereoscopic microscopes, and stored in preservation solution.

Sorting

The specific >500µm fraction was transferred to a petri dish filled with water (Figure 2). Because the fumes of the preservation solution are suspected to be carcinogenic, the sorter at the stereoscopic microscope transferred the sieved partition to water and sorted the sediment in water.

Sorting of an individual sample at a particular depth required 4 - 24 hours of total sorting time depending on the concentration of macrofaunal individuals and sediment composition. All handling of macrofaunal organisms was done via fine forceps.

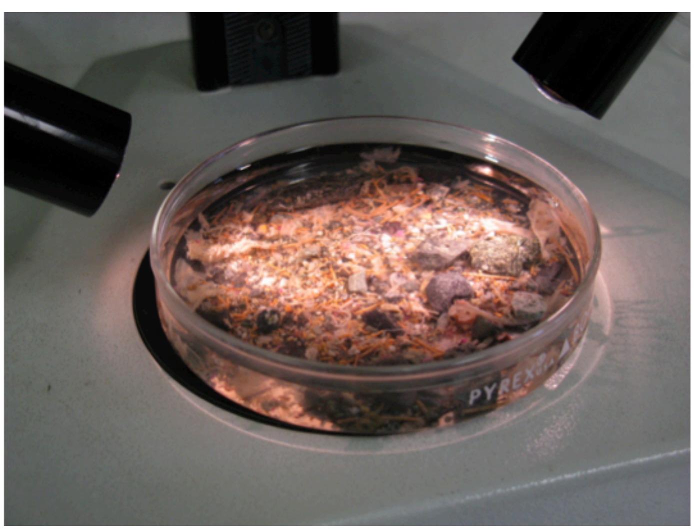


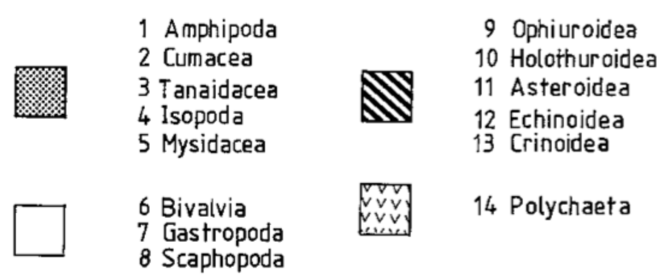
Figure 2: Sediment collection from a partition of a sample with macrofaunal organisms already partially extracted.

When a sample could not be completely sorted in one session, the sorted section of the sample was transferred to a permanent container filled with the preservation solution. The remaining unsorted sample would be transferred to a separate container in the same preservation solution until it could be sorted and transferred to the same permanent container as the previously sorted material. Any organisms found belonging to the meiofauna (e.g. copepoda, oligochaeta) were not separated further but placed together into a “miscellaneous” vial. All other macrofaunal taxa (e.g. tanaidacea, scaphopoda) were placed in their own taxon specific vial labeled accordingly with the CRS reference number. All macrofaunal organisms were sorted from the sediment according to major taxonomic classes similar to the classifications used by Mühlenhardt-Siegel (1988) when applicable (Table 2).

<u>Abundance</u>

Abundance counts of polychaeta and other macrofauna were taken by counting the macrofaunal head. If the head was not included in a fragment of a macrofaunal individual, that fragment was not counted in the abundance, but rather was labeled as a “fragment” of the particular taxon order (e.g. “polychaete frag) to still be included in the wet weight biomass measurements. Abundance counts were normalized by dividing the individuals per taxon per sediment partition, by the number of sub-cores per partition and the area of the sub-core ($0.0625m^2$) to yield N/m^2.

Table 2: Macrofaunal taxonomic classifications from Mühlenhardt-Siegel (1988). Crustacea (1 – 5), Mollusca (6 – 8), Echinodermata (9 – 13), and Annelida (14).



Normalized abundance data were then statistically tested as a function of latitude. Pearson's, as well as Spearman's rank (corrected for a non-parametric measure between two variables) correlation coefficients were included in the analysis for both total abundance (N/m^2) as a function of latitude (Row 1, Table 15), as well as taxon abundance per square meter as a function of latitude (Rows 4 – 7, Table 15). A Kruskal-Wallis test (i.e. a non-parametric one-way ANOVA) was included to test for significant variation between latitudes (Table 5), and the nsWAPcs and ssWAPcs (Table 6).

Biomass

Wet-weight biomass measurements were carried out after all taxa abundance counts had been verified. Individual macrofaunal taxa were prepared for weighing by emptying the vial of a taxon (e.g. polychaete) into a small petri dish. Two kimwipes were placed adjacent to the stereomicroscope and used to absorb water from the macrofaunal organisms and assure that no extra surface water was remaining on the exterior surface of them (e.g. between the chelipads of a tanaid, or the chaete of a polychaete). Adjacent to the kimwipes was a Denver Instrument APX-60 balance (accuracy +/- 0.2 mg, precision 0.1mg) with plasticized weighing paper on the stage (to assure little water absorption).

After macrofaunal individuals were dabbed on the kimwipes (which are very efficient at absorption), placed on plasticized weighing paper and weighed, the macrofauna and weighing paper were immediately placed in a water-filled petri dish to prevent further drying.

Similar to the normalization of abundance, wet-weight biomass measurements were also normalized to g/m^2.

Normalized biomass data were also tested as a function of latitude. Pearson's, as well as Spearman's rank correlation coefficients were included in the analysis for both total biomass (g/m^2) as a function of latitude (Row 2, Table 15), as well as taxon biomass (g/m^2) as a function of latitude (Rows 8 – 11, Table 15). Kruskal-Wallis tests were also included to test if biomass (g/m^2) varied significantly between latitudes (Table 9) and between the nsWAPcs and the ssWAPcs (Table 10).

Mean Macrofaunal Body Size

Because both individuals per square meter as well as grams per square meter could be measured per taxon per sample, the mean individual body size was calculated simply by taking the wet-weight biomass and dividing by abundance, i.e. g/m^2 / N/m^2 = g/N, or mass per individual.

Total and taxa g/N from each sample were correlated with latitude (Row 3, Table 15; Rows 12 - 15, Table 15). In addition, mean body size was tested for statistical variation along the WAPcs (Table 13) and between the nsWAPcs and ssWAPcs (Table 14). In addition, a visual representation of the average taxon body size with latitude was produced (Figures 23 & 24).

Graphing Programs

Abundance (N/m^2), biomass (g/m^2), and mean body size (g/N) were calculated in Microsoft Excel 2008. Graphing programs used included Microsoft Excel 2008 and Matlab R2008b. The standard error associated with each station was calculated from the standard deviation divided by the sample size for each station (i.e. 3, for station AA).

Matlab R2008b was used to produce the 3D scatter plot (Figure 27) of data from Mühlenhardt-Siegel (1988).

Statistical Analyses of FOODBANCS 2 Data

Data from FOODBANCS 2 were tested for statistical significance in Minitab v.16. Primary tests for statistical significance included non-parametric correlations (Spearman's ranked correlation coefficient) between latitude and: total N/m^2 per sample per station, total g/m^2 per sample per station, and total g/N per sample per station (Rows 1 – 3 in Table 15; original data in Tables 3, 7, and 11, respectively). Other tests included non-parametric correlations between latitude and: taxon abundance per square meter (Rows 4 – 7, Table 15), taxon biomass per square meter (Rows 8 – 11, Table 15), and taxon mean body size per square meter (Rows 12 – 15, Table 15). In addition to the Spearman's ranked correlation coefficient, the parametric Pearson's correlation coefficient was included for comparison. Both correlation coefficients include P-values corresponding to significance (<0.05).

Additional non-parametric tests included Kruskal-Wallis tests, which are similar to a one-way Analysis of Variance (ANOVA) with the exception that the Kruskal-Wallis test does not require that populations have normal distributions or any other specific distribution (Triola, 2007). Kruskal-Wallis tests of significant difference between: latitude vs. abundance (Table 5), biomass (Table 9), and mean body size (Table 13) per sample for each station, as well as tests between nsWAPcs and ssWAPcs abundance (Table 6) biomass (Table 9) and mean body size (Table 14) were included.

Statistical Analyses of Mühlenhardt-Siegel (1988)

Data from Mühlenhardt-Siegel (1988) were also tested for significance in Minitab v.16. Latitude, depth, and biomass data (Figure 3) from Mühlenhardt-Siegel (1988) at individual stations along the Antarctic Peninsula (Figure 4) were tested for significant regressions. For a comparison of the locations of stations used in FOODBANCS-2 and Mühlenhardt-Siegel (1988), see Figure 26.

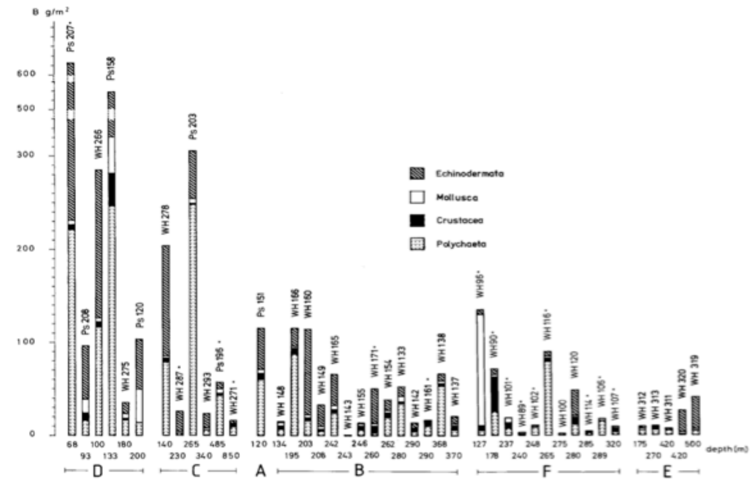


Figure 3: Total macrofaunal biomass (g/m^2) per sample per region from Mühlenhardt-Siegel (1988). X – axis values indicate sampling depth, y-axis indicates biomass (g/m^2). "D" region corresponds to the "northern Antarctic peninsula," "C" to "South Sheltand Islands," and "E," to the "southern Antarctic peninsula."

Additional Data from Mühlenhardt-Siegel (1988)

Additional data used from Mühlenhardt-Siegel (1988) include relative and mean abundance (N/m^2) (Figure 13) as well as relative and mean biomass (g/m^2) (Figure 22), for the northern and southern subregions of the WAPcs (nsWAPcs and ssWAPcs, respectively. A table of Mann-Whitney-U-tests testing for

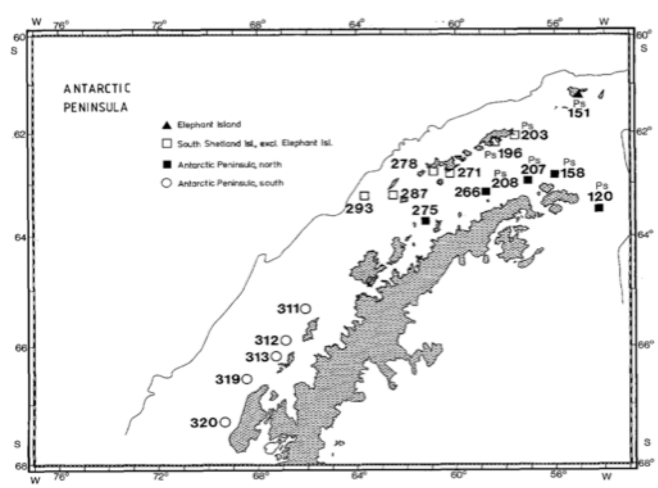


Figure 4: Stations where latitude, depth, and biomass were recorded from Mühlenhardt-Siegel* (1988) *along the Antarctic Peninsula.

statistical significance in biomass (g/m^2) and abundance (N/m^2) between regions of the Antarctic Peninsula was also included (Table 17).

Analysis of Sea-Ice Data

Lastly, additional sea-ice data were included (Figure 25) to determine if mean total and taxon abundances (N/m^2), biomass (g/m^2), and mean body size (g/N) statistically correlate (Spearmean's Rank) with annual sea-ice cover (in mo/yr) by using mean values of sea-ice cover (months/year, 4-data points) at each AA, B, F, and G station. The results may be found in the Appendix (Table 16).

Sources of Error

Most sources of error or variability in this project originate from the nature of the study. Variability in sampling depths between stations from Mühlenhardt-Siegel (1988) and the resulting variability in biomass measurements from those stations introduce a source of error for comparison purposes of the macrobenthos between 1985 and 2008. While a statistical test for decreasing biomass with latitude and depth was significant (P = 0.05) there was still documented variability between similar latitudes and depth (Figure 27). In addition, "wet-weight" biomass measurements are criticized as more prone to error compared to ash-free dry-weight (AFDW), however for comparison purposes to Mühlenhardt-Siegel (1988), as well as for preservation of specimens, wet-weight measurements were used.

Other sources of potential error in constructing decadal changes in this project include the limited sampling and general lack of quantitative knowledge on the macrofauna of the WAPcs and Bellinghausen Sea prior to this study (Arnaud et al., 1992; Pipenberg et al., 2002). Additional macrofaunal sampling beyond the 11 samples used in FOODBANCS 2 (Table 1) would strengthen statistical testing, however considering that over 10,000 macrofaunal organisms were extracted from these 11 samples, a limitation to this study is the considerable amount of time required for macrofaunal extraction from the sediment alone.

Other sources of error include the extraction of the macrofauna from the sediment. It's very likely that some individual macrofaunal organisms were overlooked and not extracted from the sediment. However, because every sample was rigorously examined for individual organisms, any remaining macrofauna will likely not alter any general trends. However, further examination is likely to refine the standard error associated with each taxon per station.

For records purposes, this study extracted numerous organisms associated with taxonomic and size-based definitions that exclude the macrofauna. Any organisms taxonomically belonging to meiofauna (Hulings and Gray, 1971) were not included in this study (e.g. copepoda, nematoda, foramnifera, oligochaeta etc.), and a single megabenthic organism, *Limopsis marionensis*, found in the CRS 968 0 – 5cm partition (Station B, Table 1) was not included due to it size (> 4cm) and incomparable status to the macrozoobenthos of Mühlenhardt-Siegel (1988). For reference purposes, the individual L. marionensis organism weighed 22.7755 grams (Figure 17).

CHAPTER 4: RESULTS & DISCUSSION

Overall, 10,260 macrofaunal organisms were extracted from a total of 11 samples belonging to four different stations (AA, B, F, and G) spanning 63.1°S to 68.1°S along the WAPcs. After briefly presenting the results of each respective macrobenthic parameter, decadal and latitudinal variation of macrofaunal abundance (N/m^2), biomass (g/m^2), and mean body size (g/N) along the WAPcs will be discussed in detail, respectively, in relation to overlying primary productivity and mean annual sea-ice cover.

Abundance (N/m^2) Results

Normalized abundance (N/m^2) for each particular taxa (Table 2) were compiled to broad taxonomic group (Table 3) and graphed (Figure 5). The mean total abundance (N/m^2) per station was also determined (Table 4) and graphed (Figure 4) as well as individual mean abundances per taxon for each station (Figures 6 – 9).

Table 3: Normalized abundance (N/m^2) for polychaeta, mollusca, crustacea, and echinodermata per station. Total abundance per square meter was calculated for each sample (CRS#) for each station (last column).

CRS# - Station	Polychaeta (N/m^2)	Mollusca (N/m^2)	Crustacea (N/m^2)	Echinodermata (N/m^2)	Totals per sample (N/m^2)
934-AA	5157.3	330.7	800.0	37.3	6325.3
942-AA	7413.3	442.7	602.7	21.3	8480.0
950-AA	5861.3	373.3	752.0	48.0	7034.7
962-B	6136.0	552.0	1200.0	8.0	7896.0
968-B	6128.0	264.0	720.0	0.0	7112.0
994-F	5088.0	264.0	560.0	24.0	5936.0
999-F	6712.0	256.0	624.0	8.0	7600.0
1001-F	4368.0	208.0	408.0	8.0	4992.0
1013-G	7216.0	352.0	104.0	40.0	7712.0
1017-G	4800.0	208.0	104.0	0.0	5112.0
1021-G	1332.0	120.0	20.0	8.0	1480.0

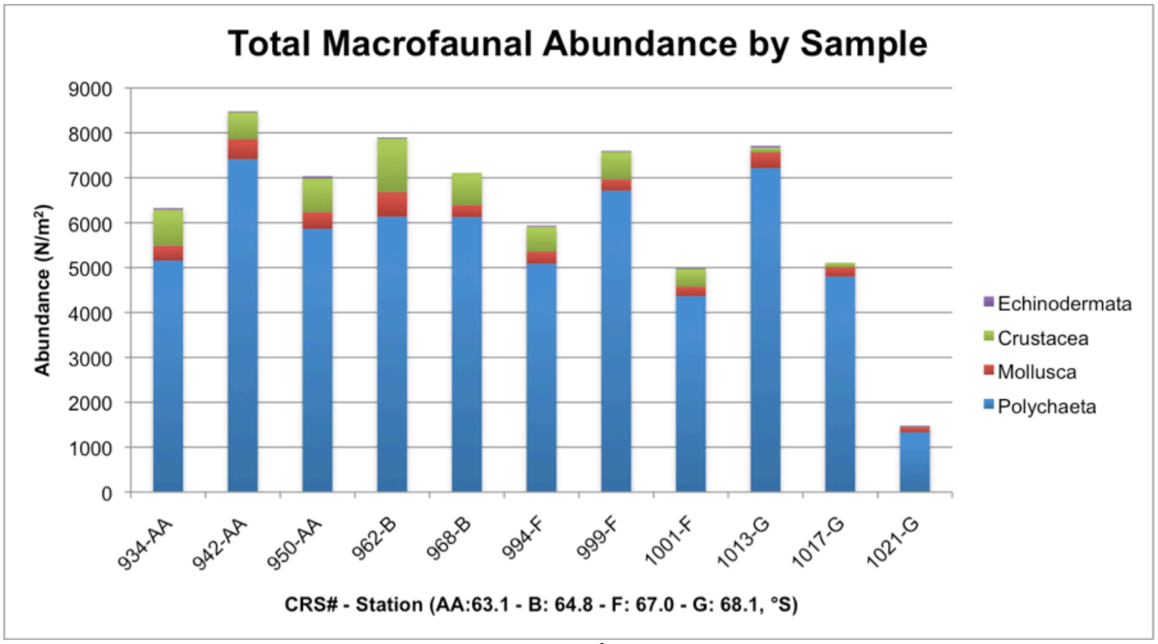


Figure 5: Total macrofaunal abundance counts (N/m^2) for polychaeta, mollusca, crustacea, and echinodermata per sample. Total (N/m^2) per sample is reflected in the height of the column.

Table 4: Abundance (N/m^2) at each individual of polychaeta, mollusca, crustacea, echinodermata, along with the standard error (S.E) associated with each taxa. The mean values of abundance (N/m^2) ranged from 4768 – 7504 N/m^2.

Station	Polychaeta (N/m^2)	Polychaeta S.E.	Mollusca (N/m^2)	Mollusca S.E.	Crustacea (N/m^2)	Crustacea S.E.	Echinodermata (N/m^2)	Echinodermata S.E.	Totals (N/m^2)
AA	6144.0	666.41	382.22	32.64	718.22	59.42	35.56	7.75	7280.00
B	6132.0	4.00	408.00	144.00	960.00	240.00	4.00	4.00	7504.00
F	5389.3	693.23	242.67	17.49	530.67	64.06	13.33	5.33	6176.00
G	4449.3	1707.59	226.67	67.62	76.00	28.00	16.00	12.22	4768.00
B-F-G Average	5222.5	231.02	278.00	16.10	467.50	49.58	12.00	49.58	5980.00

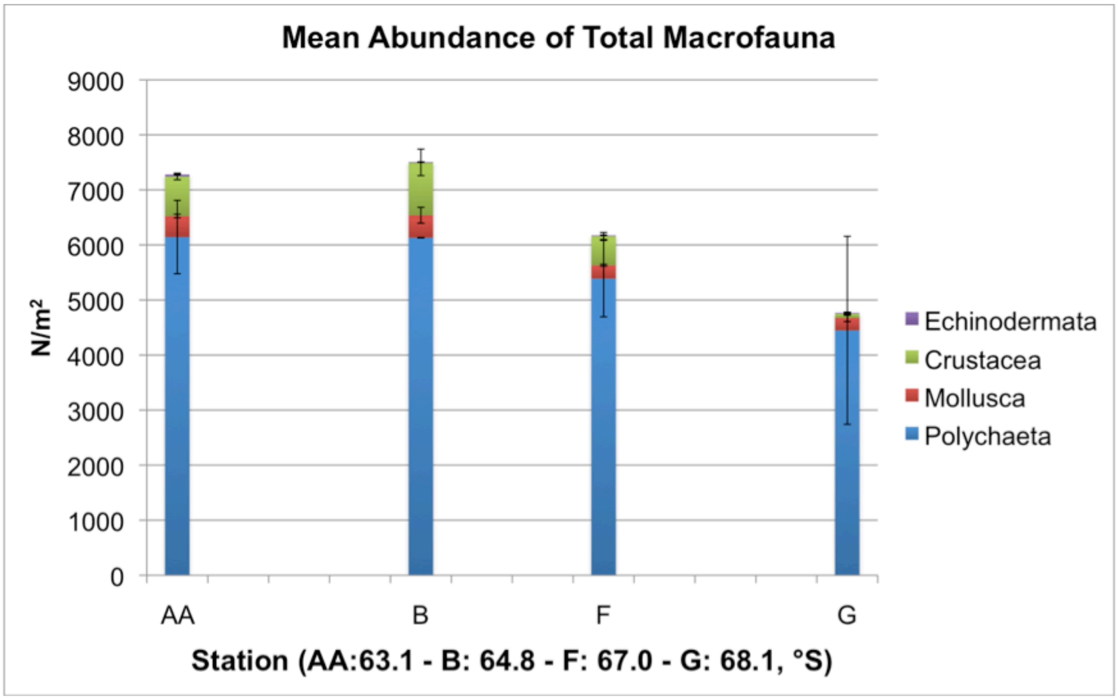


Figure 6: Mean abundance of total polychaeta, mollusca, crustacea, and echinodermata per square meter (N/m^2) at each individual station. Mean values ranged from 4768 – 7504/m^2. Error bars reflect the standard error for each taxa at each station.

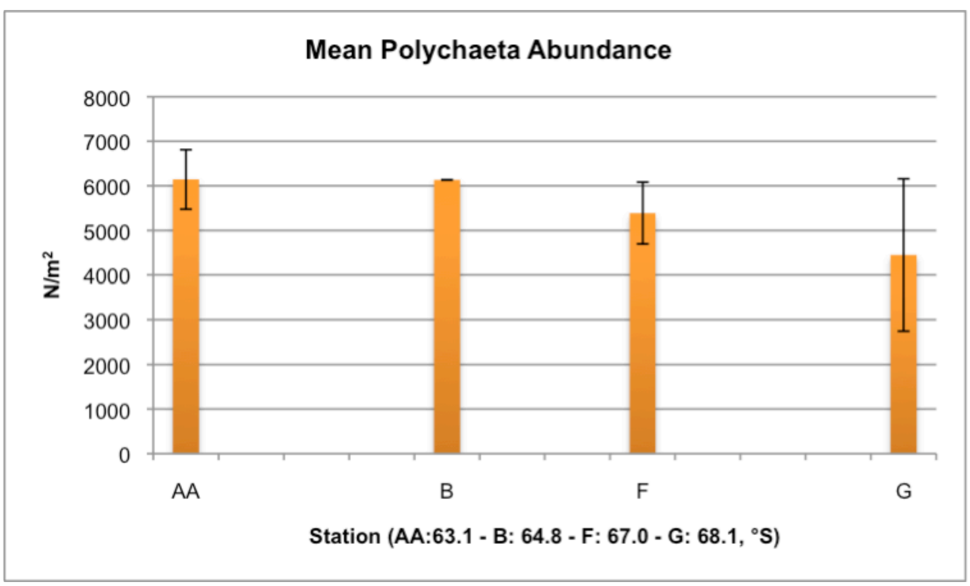


Figure 7: Mean polychaeta abundance per square meter (N/m^2) for stations AA, B, F, and G. Error bars reflect the standard error at each station.

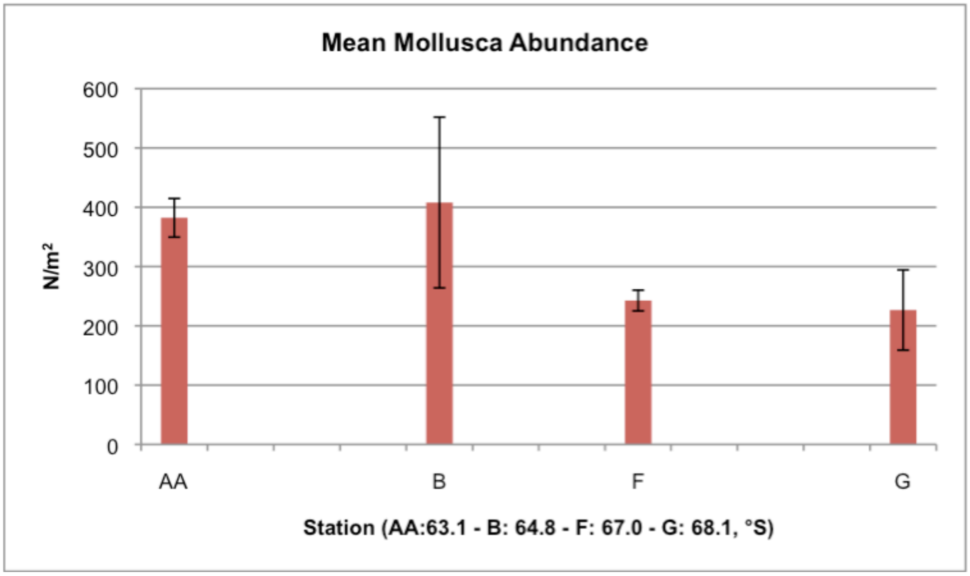


Figure 8: Mean mollusca abundance per square meter (N/m²) for stations AA, B, F, and G. Error bars reflect the standard error at each station.

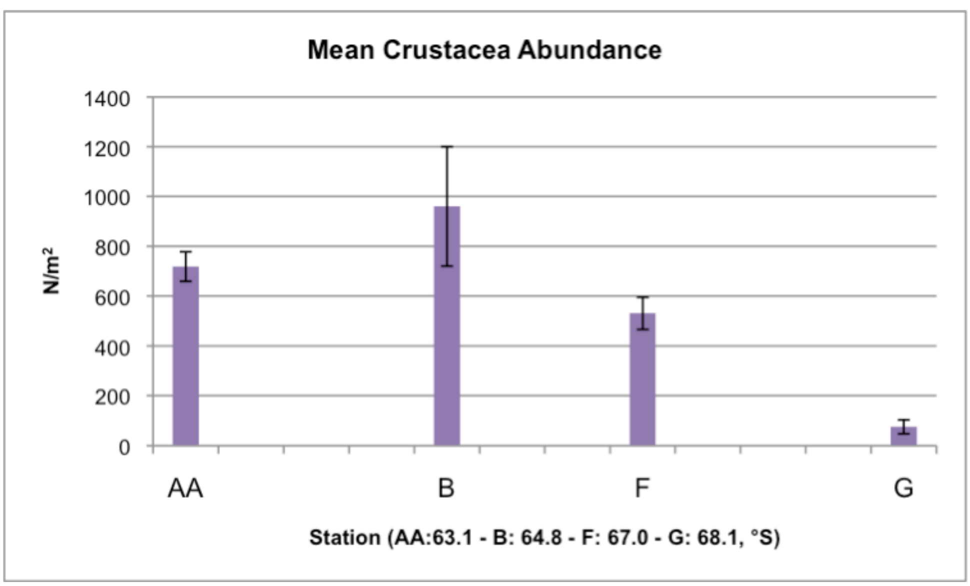


Figure 9: Mean crustacea abundance per square meter (N/m²) for stations AA, B, F, and G. Error bars reflect the standard error at each station.

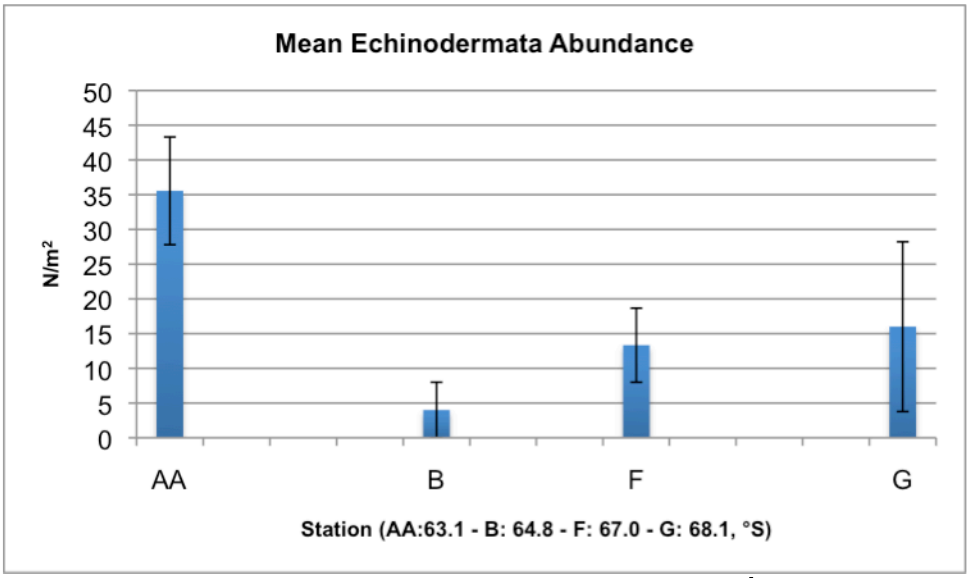


Figure 10: Mean echinodermata abundance per square meter (N/m²) for stations AA, B, F, and G. Error bars reflect the standard error at each station.

In addition, relative abundance (N/m²) per subregion of the WAPcs was also generated (Figure 11 & 12) for comparison against relative abundance (N/m²) per subregion compiled by Mühlenhardt-Siegel (1988) (Figure 13).

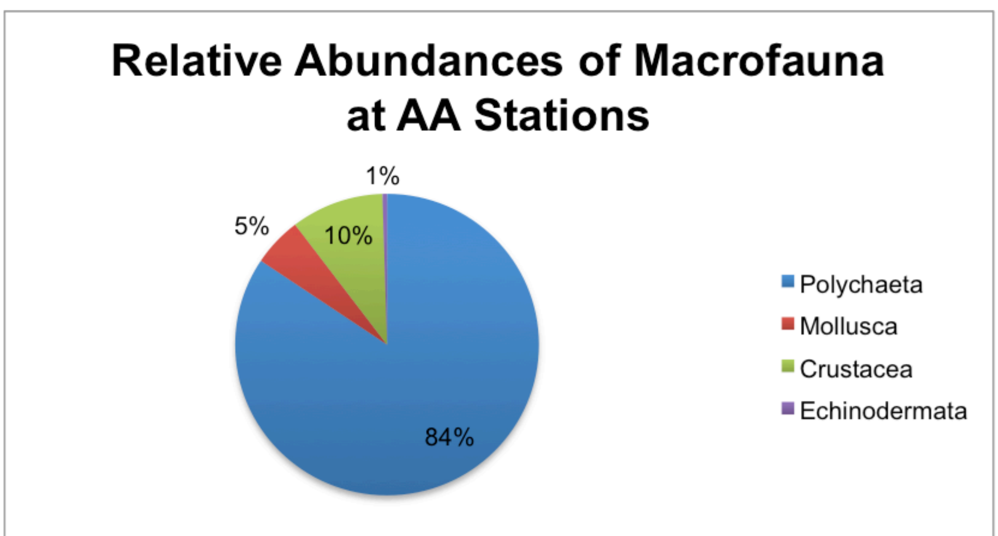


Figure 11: Relative abundances of macrofauna (N/m²) for AA Stations, reflecting the nsWAPcs. Polychaeta: 84%, Crustacea: 10%, Mollusca: 5%, Echinodermata: 1%. Total mean N/m²: 7280.

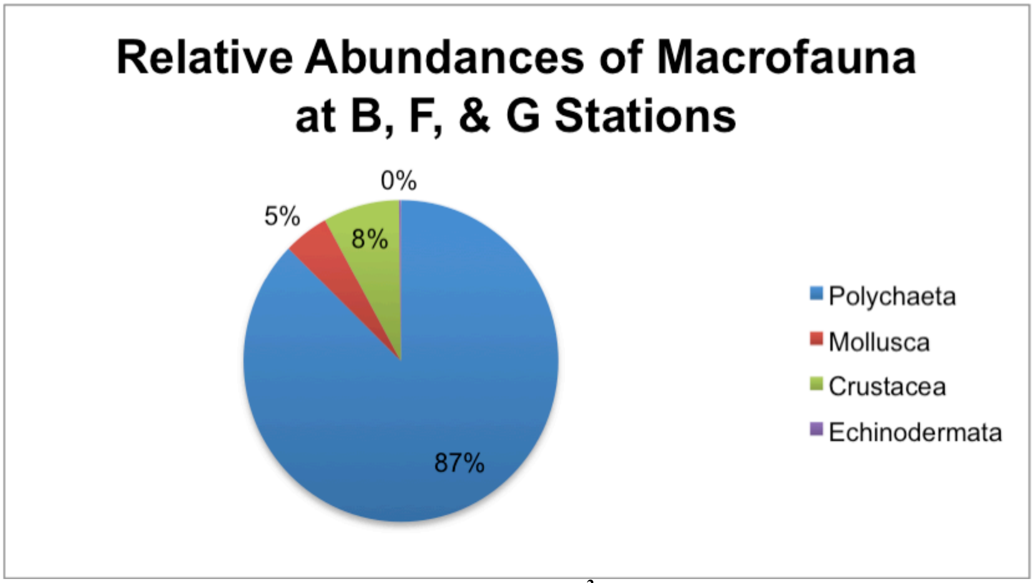


Figure 12: Relative abundances of macrofauna (N/m^2) for B, F, and G Stations, reflecting the ssWAPcs. Polychaeta: 87%, Crustacea: 8%, Mollusca: 5%, Echinodermata: <1%. Total mean N/m^2: 5980.

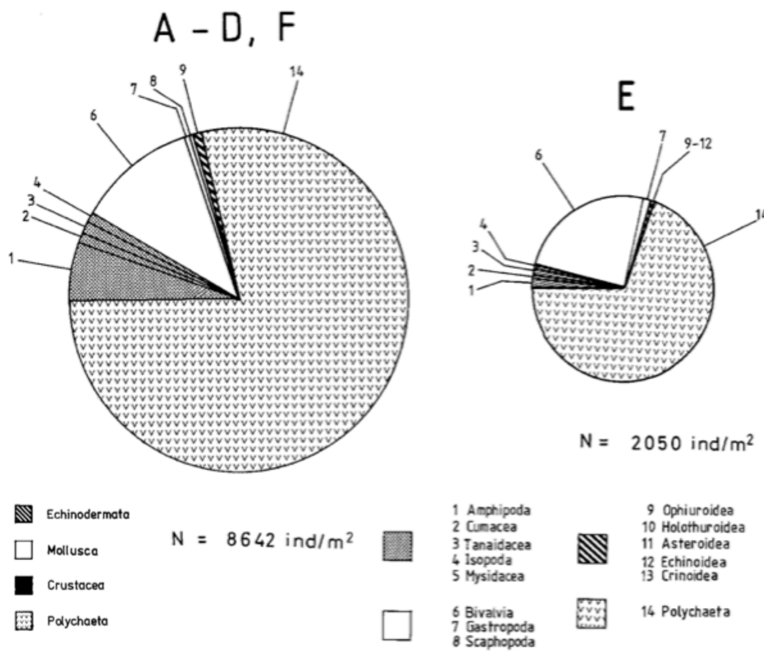


Figure 13: Relative macrofaunal abundance (N/m^2) per region. Regions "A-D, F" reflects the nsWAPcs with a mean N/m^2 of 8642. Region "E" reflects the ssWAPcs with a mean N/m^2 of 2050. Legend provides thatching type associated with broad taxonomic group. From Mühlenhardt-Siegel (1988).

Finally, latitudinal variation of total macrofaunal abundance (N/m^2) both along the WAPcs (Table 5) and between the nsWAPcs and the ssWAPcs (Table 6) were tested for statistical significance via Kruskal-Wallis tests, as described in the Methods: Statistical Analyses of FOODBANCS 2 Data. Results indicate no significant variation along the WAPcs, nor between the nsWAPcs and the ssWAPcs ($P > 0.05$).

Table 5: Kruskal-Wallis Test on total macrofaunal N/m^2 vs. latitude (63.1°S – station AA, 64.8°S – station B, 67.0°S – station F, and 68.1°S – station G). P-value of 0.488 indicates that macrofaunal abundance per square meter does significantly vary between latitudinal stations.

Kruskal-Wallis Test on N/m^2 vs. Latitude				
Latitude	N	Median	Average Rank	Z
63.1	12	522.7	25.9	1.08
64.8	8	636.0	24.4	0.47
67	12	336.0	22.2	-0.11
68.1	12	112.0	18.1	-1.38
Overall	44		22.5	
H = 2.43	DF = 3	P = 0.488		
H = 2.43	DF = 3	P = 0.487 (adjusted for ties)		

Table 6: Kruskal-Wallis Test on variation of total macrofaunal N/m^2 between the nsWAPcs (represented by macrofaunal N/m^2 of station AA) and the ssWAPcs (macrofaunal N/m^2 of stations B, F, and G with average latitude of 66.6°S). P-value of 0.280 indicates that there is no significant variation in total macrofaunal N/m^2 between the nsWAPcs and the ssWAPcs

Kruskal-Wallis Test on nsWAPcs N/m^2 vs. ssWAPcs N/m^2				
Latitude	N	Median	Average Rank	Z
63.1	12	522.7	25.9	1.08
66.6	32	264.0	21.2	-1.08
Overall	44		22.5	
H = 1.17	DF =1	P = 0.280		
H = 1.17	DF = 1	P = 0.280 (adjusted for ties)		

Discussion of Abundance

In response to our first question, “Does total or taxon abundance vary as a function of latitude?” our results from the Kruskal-Wallis test (Table 5) indicate no significant variation in total abundance (N/m^2) with latitude, nor between the nsWAP and the ssWAP (Table 6), indicated by the P-values of 0.487 and 0.280, respectively. In addition, using Spearman’s ranked correlation coefficient we found a r_s of -0.445 and a P-value of 0.170 (Row 1, Table 15) which was not statistically significant ($P < 0.05$).

It should be noted, however, that when analyzing taxon abundances (N/m^2) our study found significant negative correlations in decreasing trends of mollusca abundance (N/m^2) (Figure 8; P-value of 0.025 and r_s of -0.666, Row 5, Table 15) and in crustacea abundance (N/m^2) (Figure 9; P-value of 0.002 and r_s of -0.831, Row 6, Table 15) with increasing latitude. We did not find any significant correlations with polychaeta or echinodermata abundance (N/m^2) (Figure 7 & Figure 10; Rows 4 & 7, Table 15). Overall, our results indicate little variation of macrofaunal abundance (N/m^2) with latitude or between the nsWAPcs or the ssWAPcs.

In response to our second question “Is there any evidence of decadal variation in macrobenthic abundance along the WAPcs?” In 1984 – ’85, Mühlenhardt-Siegel (1988) found an average of 8642 N/m^2 in the nsWAPcs, an average of 2050 N/m^2 in the ssWAPcs, and a significant variation in macrofaunal abundance between these regions of the WAPcs (Figure 13; D vs. E, Abundance, Table 17). In comparison, our study found an average of 7280 N/m^2 in the nsWAPcs (Figure 11) vs. an average of 5980 N/m^2 in the ssWAPcs (Figure 12) and no significant variations in total abundance with or between latitudes (Tables 5 - 6; Row 1, Table 15).

Intriguingly, the abundance (N/m^2) found in our study at the ssWAPcs (stations B, F, and G) is over twice that found in the ssWAP in 1985 (Figure 12 vs. Figure 13). In addition, we found much greater relative abundances of polychaeta, and less so of mollusca, crustacea, and echinodermata at both nsWAP and ssWAP sampling sites (Figures 11 & 12) compared to Mühlenhardt-Siegel (1988) (Figure 13), suggesting a change in macrobenthic diversity in the ssWAPcs since 1985. Overall, Mühlenhardt-Siegel (1988) found a statistically significant greater abundance of macrofauna in the nsWAPcs compared to the ssWAPcs ("D vs. E," Abundance, Table 17) and a more taxonomically diverse assemblage of macrofauna in both regions. Samples from FOODBANCS-2 have comparatively less taxonomic diversity and abundance (N/m^2) in the nsWAPcs, and less taxonomic diversity and greater abundance (N/m^2) in the ssWAPcs, suggesting a decadal homogenization of the WAPcs since 1985.

In response to last question, "Do total and taxon abundance vary as a function of primary productivity and sea-ice cover," our results show an increase of abundance N/m^2 in the ssWAPcs and a decrease in the nsWAPcs since 1985, which is consistent with changes in decadal primary productivity rates on the WAPcs (Figure 1) from Montes-Hugo (2009). These results suggest a link that with increased primary production over-time there are increases in macrofaunal abundance (N/m^2). However, also important to note is that overall macrofaunal abundances (N/m^2) are still higher in the nsWAPcs compared to the ssWAPcs, suggesting that despite a strong decadal decrease in Chl a production in the nsWAPcs and increase in the ssWAP, overall production levels are still higher in the nsWAPcs compared to the ssWAPcs, most likely due to changes in mean annual sea-ice cover in the ssWAP compared to the nsWAPcs (Montes-Hugo, 2009).

Overall, this is evidence that macrofaunal abundance N/m^2 is a function of the overall amount as well as the rate of change in primary productivity of the WAPcs, which is further driven by changes in mean annual sea-ice cover (Eicken et al., 1992; Smith et al., 2006) in addition to other factors such as cloudiness and wind strength (Montes-Hugo et al., 2009)

Biomass (g/m^2) Results

Normalized biomass (g/m^2) for each particular taxa (Table 2) were compiled to broad taxonomic group (Table 7) and graphed (Figure 14). The mean total biomass (g/m^2) per station was also determined (Table 8) and graphed (Figure 15) as well as individual mean abundances per taxon for each station (Figures 16 – 19).

Table 7: Normalized biomass (g/m^2) for polychaeta, mollusca, crustacea, and echinodermata per station. Total biomass per square meter was calculated for each sample (CRS#) for each station (last column).

CRS# - Station	Polychaeta (g/m^2)	Mollusca (g/m^2)	Crustacea (g/m^2)	Echinodermata (g/m^2)	Totals per sample (g/m^2)
934-AA	13.64	0.74	2.51	10.67	27.55
942-AA	11.39	0.70	1.32	11.05	24.46
950-AA	10.09	3.55	5.66	9.71	29.02
962-B	9.51	1.17	0.18	0.21	11.07
968-B	8.00	0.30	0.12	0.01	8.42
994-F	15.32	0.40	0.24	0.48	16.44
999-F	12.60	0.12	1.20	0.08	14.01
1001-F	7.54	0.53	0.55	0.01	8.64
1013-G	10.88	0.15	0.01	0.15	11.19
1017-G	9.14	0.18	0.05	0.02	9.38
1021-G	2.09	0.10	0.12	0.02	2.33

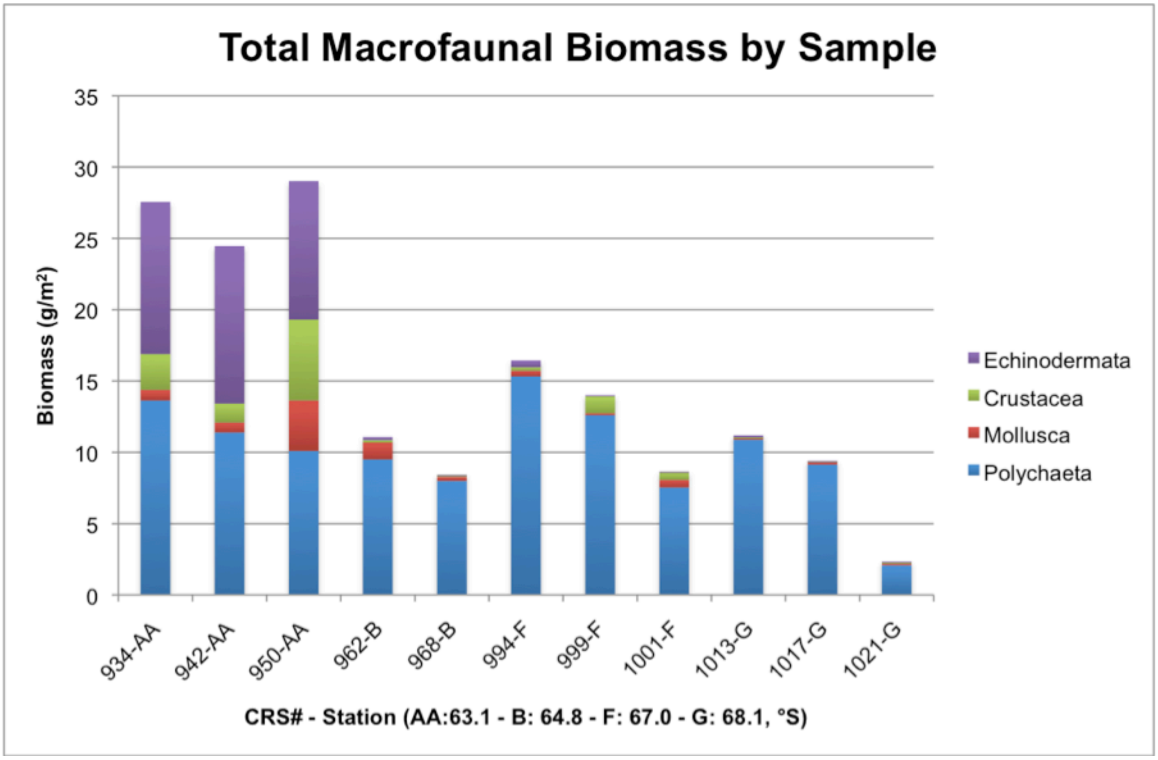


Figure 14: Total macrofaunal biomass (g/m^2) for polychaeta, mollusca, crustacea, and echinodermata per sample. Total (g/m^2) per sample is reflected in the height of the column.

Table 8: Biomass (g/m^2) at each individual of polychaeta, mollusca, crustacea, echinodermata, along with the standard error (S.E) associated with each taxa. The mean values of biomass (g/m^2) ranged from 7.64 – 27.01 g/m^2.

Station	Polychaeta (g/m^2)	Polychaeta S.E.	Mollusca (g/m^2)	Mollusca S.E.	Crustacea (g/m^2)	Crustacea S.E.	Echinodermata (g/m^2)	Echinodermata S.E.	Totals (g/m^2)
AA	11.71	1.03	1.66	0.94	3.16	1.29	10.48	0.40	27.01
B	8.75	0.76	0.73	0.44	0.15	0.03	0.11	0.10	9.74
F	11.82	2.28	0.35	0.12	0.66	0.28	0.19	0.15	13.03
G	7.37	2.69	0.14	0.02	0.06	0.03	0.06	0.04	7.64
B-F-G Average	9.39	0.49	0.37	0.04	0.31	0.05	0.12	0.02	10.19

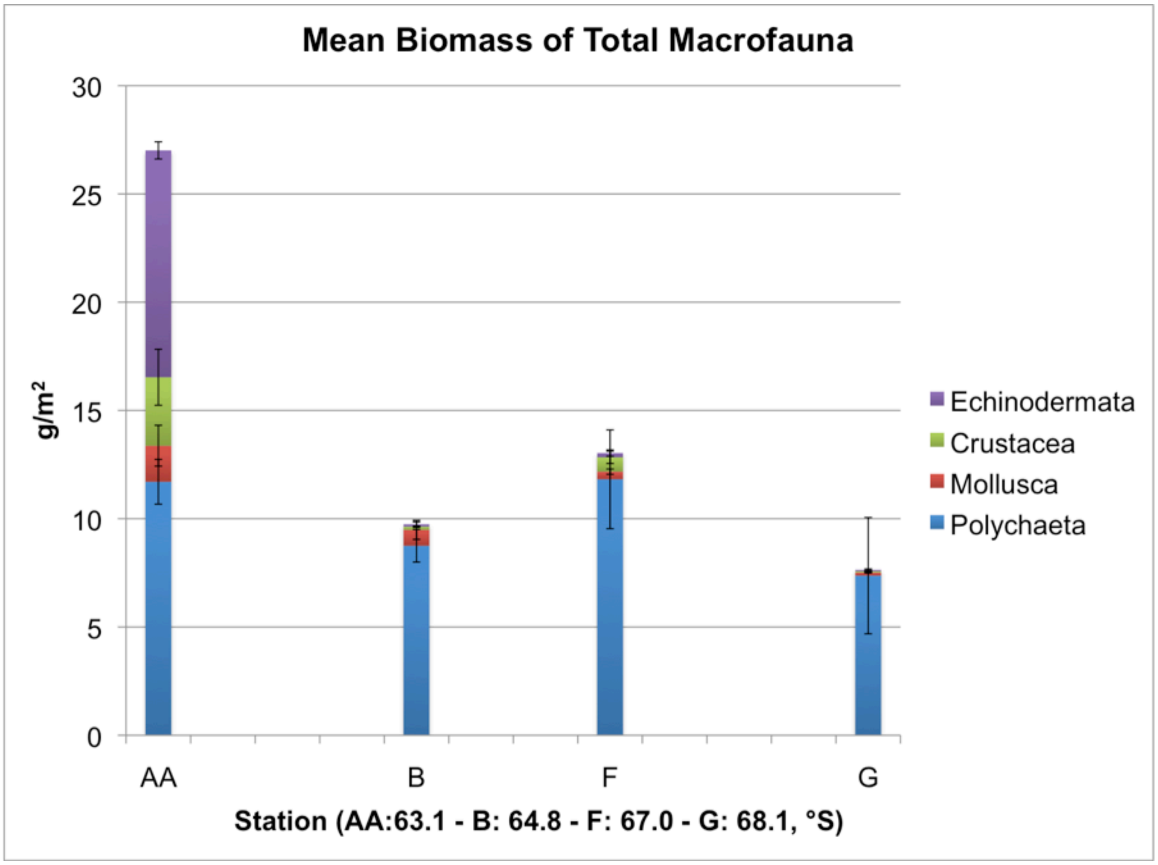


Figure 15: Mean biomass of total polychaeta, mollusca, crustacea, and echinodermata per square meter at each individual station. Total mean values ranged from 7.64 – 27.01 g/m². Error bars reflect the standard error for each taxa at each station.

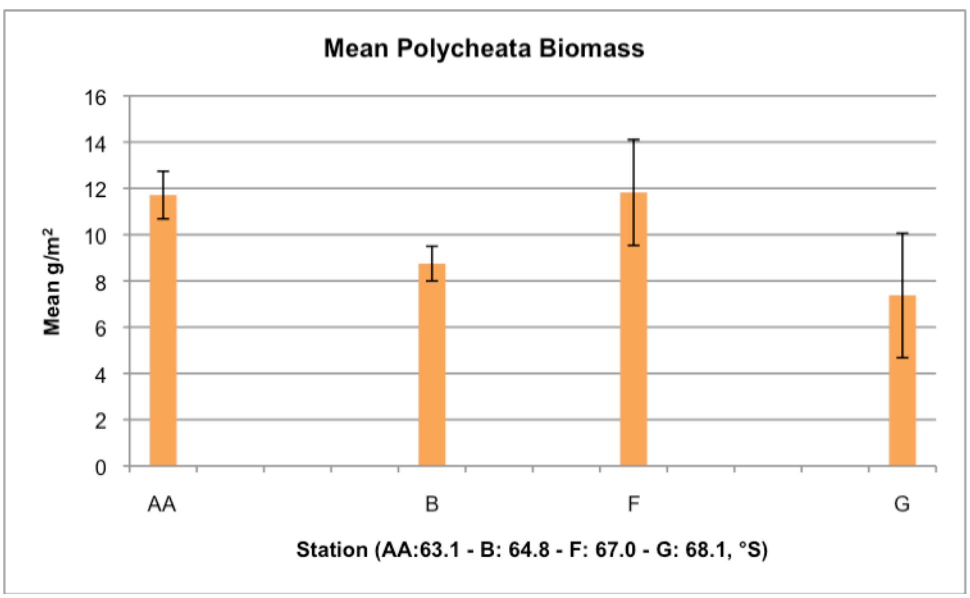


Figure 16: Mean polychaeta biomass per square meter (g/m²) for stations, AA, B, F, and G. Error bars reflect the standard error at each station.

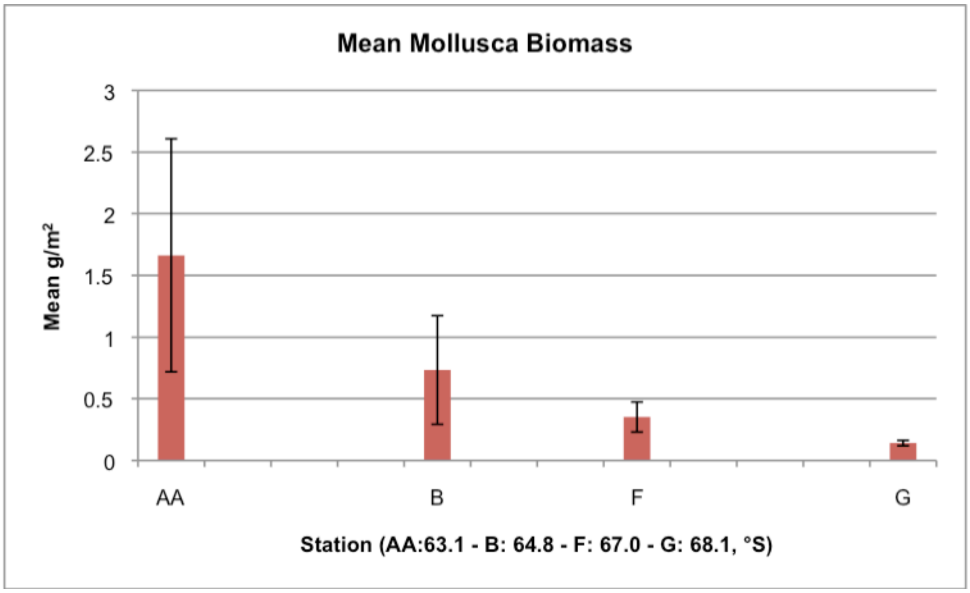


Figure 17: Mean mollusca biomass per square meter (g/m^2) for stations, AA, B, F, and G. Error bars reflect the standard error at each station.

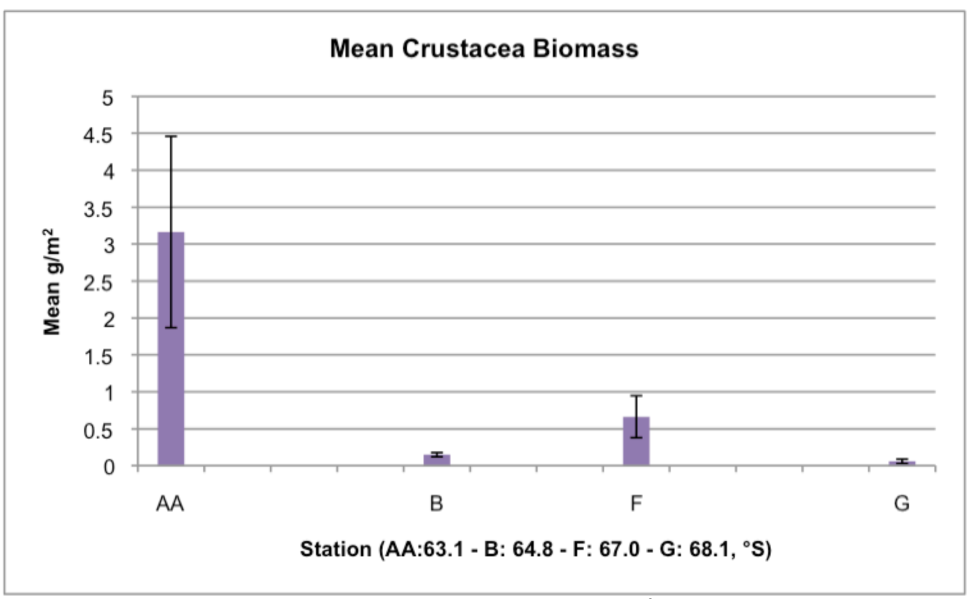


Figure 18: Mean mollusca biomass per square meter (g/m^2) for stations, AA, B, F, and G. Error bars reflect the standard error at each station.

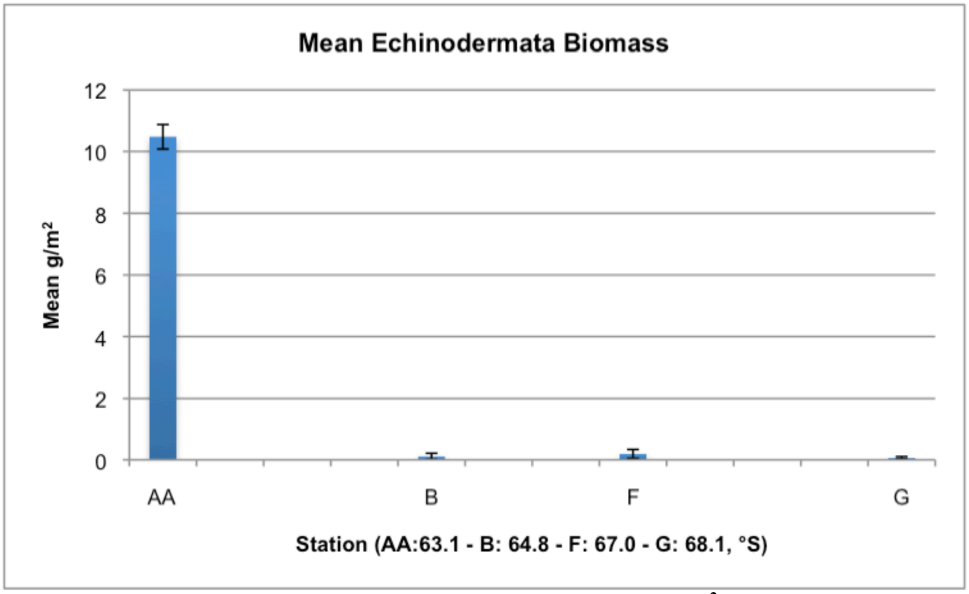


Figure 19: Mean echinodermata biomass per square meter (g/m^2) for Station, AA, B, F, and G. Error bars reflect the standard error at each station.

In addition, relative biomass (g/m^2) per subregion of the WAPcs was also generated (Figure 20 & 21) for comparison against relative biomass (g/m^2) per subregion compiled by Mühlenhardt-Siegel (1988) (Figure 22).

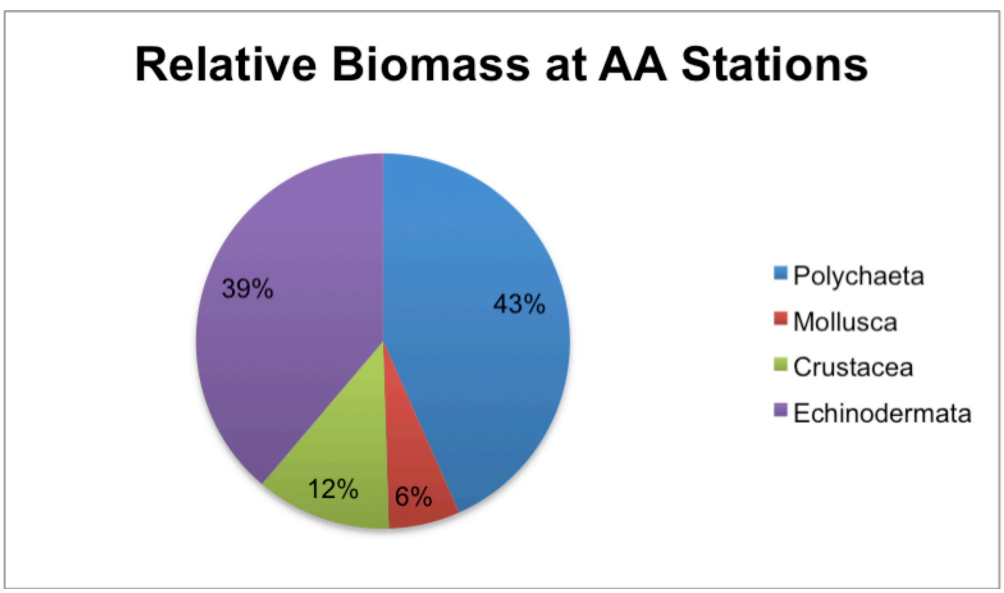


Figure 20: Relative biomass of macrofauna (g/m^2) for AA Stations, reflecting the nsWAPcs. Polychaeta: 43%, Crustacea: 12%, Mollusca: 6%, Echinodermata: 39%. Total mean g/m^2: 27.01.

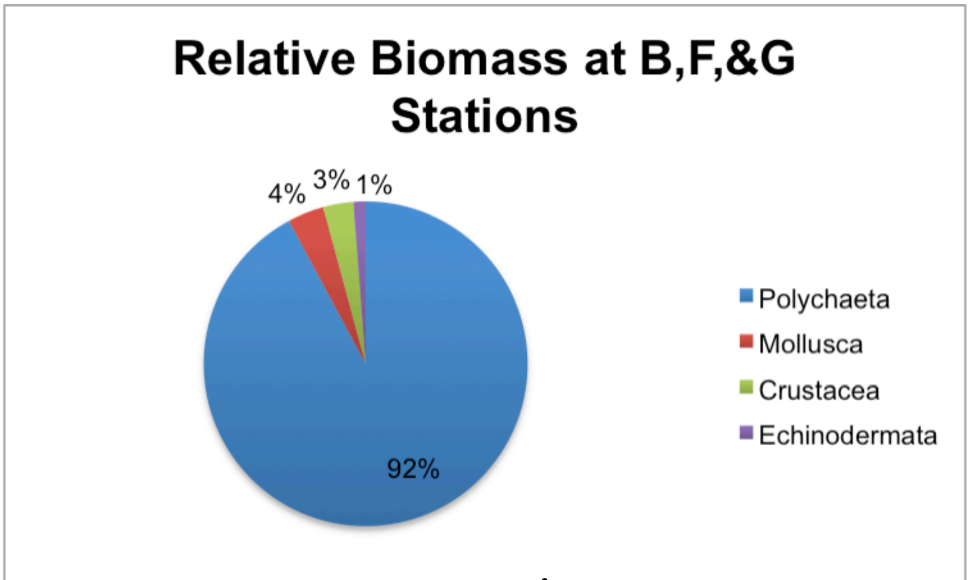


Figure 21: Relative biomass of macrofauna (g/m^2) for B, F, and G Stations, reflecting the ssWAPcs. Polychaeta: 92%, Crustacea: 3%, Mollusca: 4%, Echinodermata: 1%. Total mean g/m^2: 10.19.

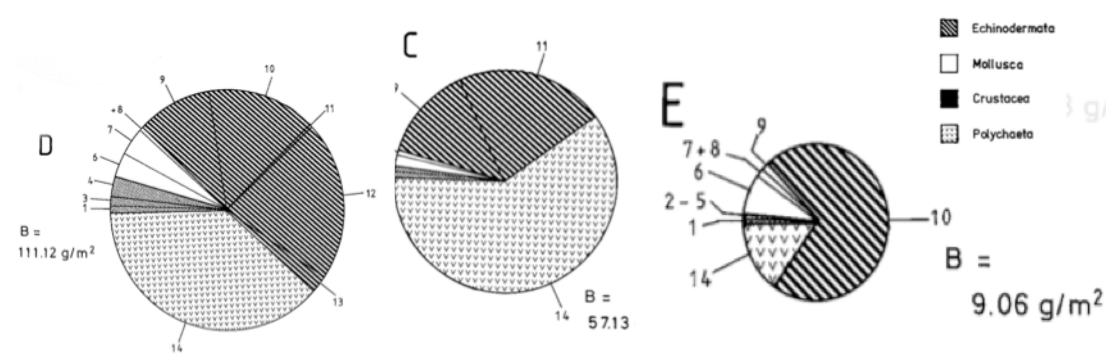


Figure 22: Relative macrofaunal biomass (g/m^2) per region. Region "D," the "northern Antarctic Peninsula" with a mean g/m^2 of 111.12 and Region "C," the "South Shetland Islands" with a mean g/m^2 of 57.13 combined reflect the nsWAPcs. Region "E" reflects the ssWAPcs with a mean g/m^2 of 9.06 g/m^2. Legend provides thatching type associated with broad taxonomic group. From Mühlenhardt-Siegel (1988).

Finally, latitudinal variation of total macrofaunal biomass (g/m^2) both along the WAPcs (Table 9) and between the nsWAPcs and the ssWAPcs (Table 10) was tested for statistical significance via Kruskal-Wallis tests, as described in the Methods: Statistical Analyses of FOODBANCS 2 Data. Results indicate significant variation along the WAPcs and between the nsWAPcs and the ssWAPcs ($P < 0.05$).

Table 9: Kruskal-Wallis Test on total macrofaunal g/m^2 vs. latitude. P-value of 0.004 indicates that macrofaunal biomass per square meter does significantly vary between latitudinal stations.

Kruskal-Wallis Test on g/m^2 vs. Latitude				
Latitude	N	Median	Average Rank	Z
63.1	12	7.6845	33.3	3.4
64.8	8	0.2548	19.1	-0.82
67	12	0.5064	22	-0.17
68.1	12	0.1312	14.5	-2.52
Overall	44		22.5	
H = 13.58	DF = 3	P = 0.004		
H = 13.59	DF = 3	P = 0.004 (adjusted for ties)		

Table 10: Kruskal-Wallis Test on variation of total macrofaunal g/m^2 between the nsWAPcs (represented by macrofaunal g/m^2 of station AA) and the ssWAPcs (macrofaunal g/m^2 of stations B, F, and G with average latitude of 66.6° S). P-value of 0.001 indicates significant variation in total macrofaunal g/m^2 between the nsWAPcs and the ssWAPcs

Kruskal-Wallis Test on nsWAPcs g/m^2 vs. ssWAPcs g/m^2				
Latitude	N	Median	Average Rank	Z
63.1	12	7.6845	33.3	3.40
66.6	32	0.2260	18.5	-3.40
Overall	44		22.5	
H = 11.56	DF = 1	P = 0.001		
H = 11.56	DF = 1	P = 0.001 (adjusted for ties)		

Discussion of Biomass

Our first question asks whether total or taxon biomass varies as a function of latitude. The results from the Kruskal-Wallis test indicate that total biomass values (g/m^2) vary between latitudes (Table 9) at a significance value of $P = 0.004$. Spearman's ranked correlation coefficient also show that the total macrofaunal biomass (g/m^2) varies as a function of latitude (r_s of -0.642 and P-Value of 0.033, Row 2, Table 15). In addition, a Kruskal-Wallis test of macrofaunal biomass (g/m^2) indicates a very significant variation (P-value of 0.001) between the nsWAPcs and the ssWAPcs (Table 10).

Analysis reveals that biomass (g/m^2) of every taxon, including mollusca (Figure 17; r_s of -0.820, P-value of 0.002, Row 9, Table 15), crustacea (Figure 18; r_s of -0.829, P-value of 0.002, Row 10, Table 15), and echinodermata (Figure 19; -0.609, P-value of 0.047, Row 11, Table 15) with the exception only of the polychaeta (Figure 16; r_s of -0.356, P-value of 0.282 Row 8, Table 15) significantly declines with increasing latitude. These total and taxon biomass values are also negatively correlated with mean annual sea-ice cover from (Figure 25) suggesting an association with a latitudinal decrease in primary productivity.

Compared to the results of Mühlenhardt-Siegel (1988), both data sets reveal a significant difference in biomass (g/m^2) between the nsWAPcs and the ssWAPcs. Mühlenhardt-Siegel (1988) found an average biomass of 57.13 g/m^2 in the South Shetland Islands and 111.12 g/m^2 in the northern Antarctic Peninsula (Figure 22). Mühlenhardt-Siegel (1988) also found an average biomass of 9.06 g/m^2 in the ssWAPcs (Figure 22). In comparison, we found a mean biomass of 27.01 g/m^2 in the nsWAPcs (Figure 20) and of 10.19 g/m^2 in the ssWAPcs (Figure 21). These regional differences suggest the persistence of a latitudinal gradient in biomass over the past 26 years between the northern and southern subregions of the WAPcs.

When further examining which taxonomic group dominates the biomass measurements, we found many more polychaeta taxonomically dominating the biomass of the ssWAPcs (92%, Figure 21) compared to the biomass data of the ssWAPcs (~16%, "E," Figure 22) from Mühlenhardt-Siegel (1988). The biomass of the ssWAPcs from Mühlenhardt-Siegel (1988) is dominated by echinodermata, whereas our data from the ssWAPcs show the echinodermata contributing only 1% to biomass (Figure 21). Such a drastic shift in the taxonomic composition of the biomass of the ssWAPcs could be the result of either a low-probability sampling error (eight samples were taken both in the FOODBANCS-2 and Mühlenhardt-Siegel (1988) study region of the ssWAPcs), or the result of a major ecological shift in the macrobenthic community structure of the ssWAPcs. It should be noted that in comparison, the taxonomic composition of the nsWAP looks similar to that of 26 years ago (Figure 20, "D and C" Figure 22).

This brings us to one important difference in comparing average biomass data from the FOODBANCS 2 project of 2008 with the average biomass from Mühlenhardt-Siegel (1988). In 1984 -'85 the average biomass of the nsWAP is over twice as large as that of measured in 2008, whereas the average biomass of the ssWAP is lower (9.06 g/m^2 compared to 10.19 g/m^2) and taxonomically much different (Figure 21, "E" Figure 22). Such a difference suggests the presence of a persisting latitudinal decline in macrobenthic biomass with increasing latitude along the WAPcs, but a decrease in the "steepness" of the cline since 1985. One explanation may be that the macrobenthic biomass parameter is responding heavily to the overlying primary productivity, which has decadally decreased in the nsWAPcs and increased in the ssWAPcs as a function of decreased mean annual sea-ice cover (Montes-Hugo et al., 2009).

To test whether these sub-regional changes were present, i.e., that the slope of the macrobenthic decrease in biomass with increasing latitude was lessening, we statistically tested the sampling of Mühlenhardt-Siegel (1988) for any significant regressions between latitude, depth, and biomass (see Statistical Analyses of Mühlenhardt-Siegel (1988)). After performing a multiple regression of biomass (response) with latitude and depth (predictors) on all sampling stations (which are most heavily concentrated in the nsWAP, Figure 4) from Mühlenhardt-Siegel (1988), we found a significant regression (P-value = 0.05) and the equation "Biomass = 2275.43 – 31.8192*(Latitude) – 0.381964*(Depth)" (Figure 27). Using this equation we would predict a biomass of 46.86 g/m^2 from 26 years ago at the exact location (63.1° S) and depth of station AA (578m), which is almost twice our value of 27.01 g/m^2. The equation fails to accurately predict the biomass at the ssWAP from 26 years ago, but given that the equation is based on sampling that occurs primarily in the nsWAP (only four sampling stations from Mühlenhardt-Siegel (1988) are located in the ssWAP) this is not surprising.

Overall, the shift in taxonomic composition and minor increase in biomass (g/m^2) of the ssWAP from 1985 to 2008 (Figure 21, "E" Figure 22) are accompanied by a large suspected decrease in biomass (g/m^2) in the nsWAP from 1985 to 2008 (46.86g/m^2 to 27.01g/m^2). Thus, while certainly not conclusive, there is evidence for a change in the slope of the latitudinal gradient in biomass (g/m^2) corresponding to a decadal increase in primary productivity in the ssWAPcs and decrease in the nsWAPcs, and further homogenization of the macrobenthic community along the WAPcs (Montes-Hugo et al., 2009) similar to trends in abundance (N/m^2).

Finally, our last question: "how does the macrobenthic biomass (g/m^2) vary as a function of mean annual sea-ice cover?" Our results show significant variation of total macrofaunal biomass (g/m^2) between stations (Kruskal Wallis test, Table 9) and between the nsWAPcs and ssWAPcs (Table 10), as well as the significant correlations of decreasing mollusc, crustacean, echinoderm, and total macrofaunal biomass (g/m^2) with increasing latitude (Row 2, 9 – 11, Table 15) and increasing mean annual sea-ice cover (Figure 25). This significant correlation of biomass (g/m^2) is driven by overlying primary productivity, which is itself a function of mean annual sea-ice cover (Clarke, 1985; Eicken et al, 1992, Dayton, 1990; Arntz et al., 1994; Smith et al., 2006). In conclusion, macrofaunal biomass (g/m^2) does significantly vary as a function of mean-annual sea-ice cover.

Mean Body Size (g/N) Results

Mean body size (g/m^2) for each particular taxa (Table 2) were compiled to broad taxonomic group (Table 11). The mean body size (g/N) per taxon for each station was also determined (Table 12) and graphed (Figure 23 - 24).

Table 11: Mean body size (g/N) for polychaeta, mollusca, crustacea, and echinodermata per station. Total g/N was calculated for each sample (CRS#) at for each station (last column). Undf (undefined), means no organisms of a particular taxon were present in the sample (CRS#).

CRS# - Station	Polychaeta (g/N)	Mollusca (g/N)	Crustacea (g/N)	Echinodermata (g/N)	Totals per sample (g/N)
934-AA	0.002644	0.002226	0.003135	0.285786	0.293791
942-AA	0.001537	0.001584	0.002195	0.517925	0.523241
950-AA	0.001722	0.009516	0.007524	0.202311	0.221073
962-B	0.001549	0.002123	0.000148	0.026800	0.030621
968-B	0.001305	0.001118	0.000168	undf	0.002591
994-F	0.003011	0.001524	0.000424	0.020033	0.024993
999-F	0.001878	0.000484	0.001924	0.010600	0.014887
1001-F	0.001726	0.002558	0.001359	0.001500	0.007143
1013-G	0.001508	0.000427	0.000115	0.003680	0.005731
1017-G	0.001905	0.000846	0.000477	undf	0.003228
1021-G	0.001570	0.000847	0.005760	0.002900	0.011077

Table 12: Mean body size (g/N) at each individual of polychaeta, mollusca, crustacea, echinodermata, along with the standard error (S.E) associated with each taxa. The mean values of mean body size (g/N) ranged from 0.00001 – 0.05451 g/N. Undf (undefined), meaning no organisms of a particular taxon were present in the sample (CRS#).

Station	Polychaeta (g/N)	Polychaeta S.E.	Mollusca (g/N)	Mollusca S.E.	Crustacea (g/N)	Crustacea S.E.	Echinodermata (g/N)	Echinodermata S.E.
AA	0.00197	0.00020	0.00444	0.00147	0.00428	0.00095	0.33534	0.05451
B	0.00143	0.00009	0.00162	0.00036	0.00016	0.00001	0.02680	undf
F	0.00221	0.00023	0.00152	0.00035	0.00124	0.00025	0.01071	0.00309
G	0.00166	0.00007	0.00071	0.00008	0.00212	0.00105	0.00329	0.00028

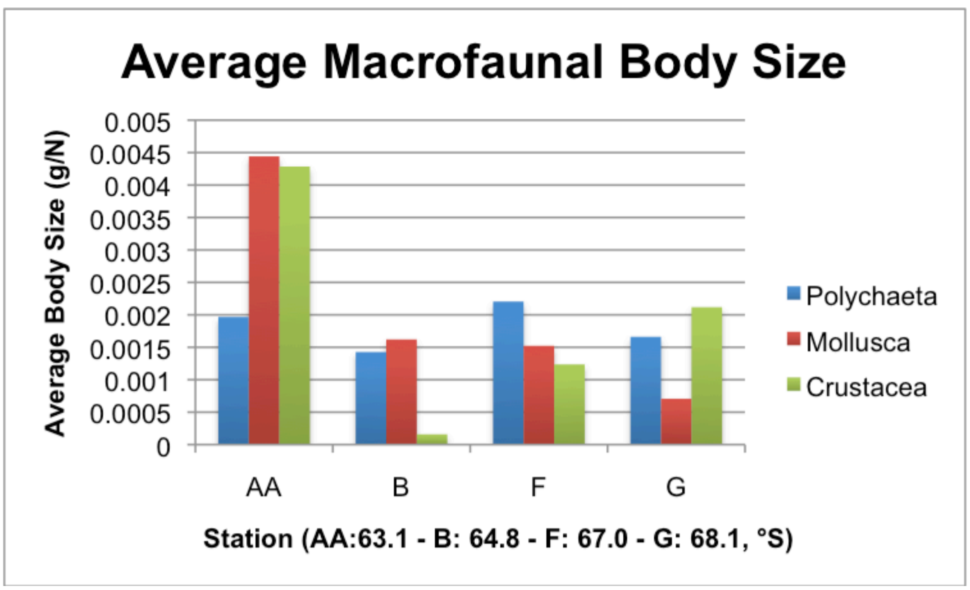


Figure 23: Average macrofaunal body size (g/N) of polychaeta, mollusca, and crustacea by station (note: echinodermata were ommited due to scale).

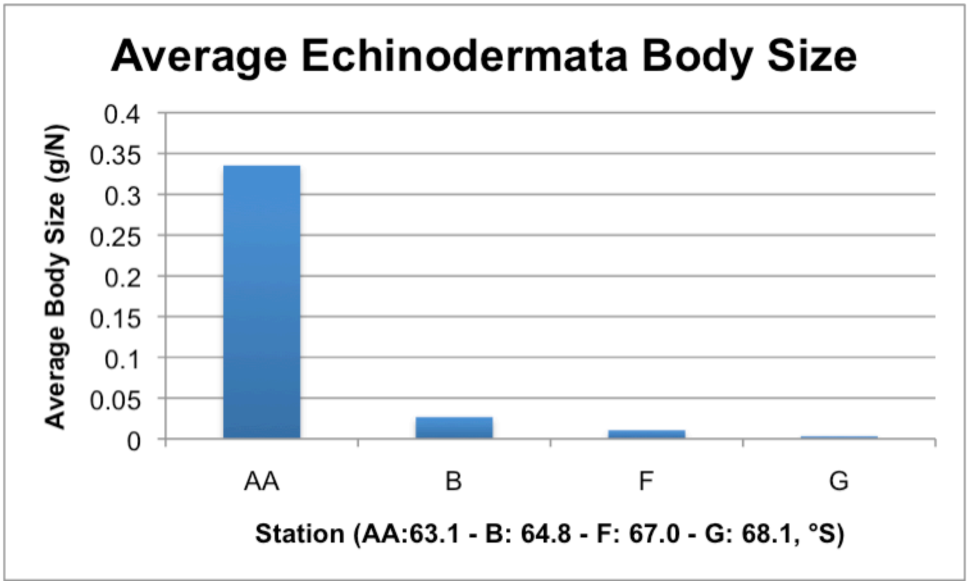


Figure 24: Average echinodermata body size (g/N) per station.

In addition, latitudinal variation of total macrofaunal mean body size (g/N) both along the WAPcs (Table 13) and between the nsWAPcs and the ssWAPcs (Table 14) were tested for statistical significance via Kruskal-Wallis tests, as described in the Methods: Statistical Analyses of FOODBANCS 2 Data. Results indicate significant variation along the WAPcs and between the nsWAPcs and the ssWAPcs ($P < 0.05$).

Table 13: Kruskal-Wallis Test on total macrofaunal g/N vs. latitude. P-value of 0.021 indicates that macrofaunal mean body size does significantly vary between latitudinal stations.

Kruskal-Wallis Test on g/N vs. Latitude				
Latitude	N	Median	Average Rank	Z
63.1	12	0.002890	30.3	2.92
64.8	7	0.001305	15.3	-1.47
67	12	0.001802	21	-0.17
68.1	11	0.001508	16.5	-1.59
Overall	42		21.5	
H = 9.78	DF = 3	P = 0.021		

Table 14: Kruskal-Wallis Test on variation of total macrofaunal g/m^2 between the nsWAPcs (represented by macrofaunal g/N of station AA) and the ssWAPcs (macrofaunal g/N of stations B, F, and G with average latitude of 66.6° S). P-value of 0.003 indicates significant variation in total macrofaunal g/N between the nsWAPcs and the ssWAPcs

Kruskal-Wallis Test on nsWAPcs g/N vs. ssWAPcs g/N				
Latitude	N	Median	Average Rank	Z
63.1	12	0.002890	30.3	2.92
66.6	30	0.001537	18.0	-2.92
Overall	42		21.5	
H = 8.55	DF = 1	P = 0.003		

Discussion of Mean Body Size

Mean body size, measured in mass per individual, reflects the average body "size" (g/N) of the entire population of individuals. Our results show that total macrofaunal mean body size varied significantly between latitudes (P-value of 0.021, Table 13) as well as between the nsWAPcs and the ssWAPcs (P-value of 0.003, Table 14). Furthermore, we also found a significant negative correlation of decreasing total macrofaunal mean body size with latitude (r_s of -0.727, P-value of 0.013, Row 3 Table 9) as well as significant negative correlations of decreasing mean body size within the mollusca (Figure 23; r_s of -0.726, P-value of 0.011, Row 13, Table 15) and echinodermata (Figure 24; r_s of -0.877, P-value of 0.002, Row 15, Table 15). In contrast, there was no significant variation of mean body size of the polychaeta (Figure 23; Row 12, Table 15) or crustacea (Figure 23; Row 14, Table 15).

While Mühlenhardt-Siegel (1988) did not list taxon abundances (N/m^2), total abundances (N/m^2) were provided for each sampling station. Via simple calculations, a comparison of g/N between samples "C" (South Shetland Islands) and "E" (southern

Antarctic Peninsula) reveals differences in the nsWAP (57.13 $g/m^2 \not/ 8642$ N/m^2 = 0.006611 g/N, South Sheltand Islands, 111.12 $g/m^2 / 13599$ N/m^2 = 0.008171 g/N, northern Antarctic Peninsula) and the ssWAP (9.06 $g/m^2 / 2050$ N/m^2 = 0.004390 g/N). These calculations show a similar decreasing trend in mean body size with increasing latitude. Unfortunately the total mean macrofaunal body size values from Mühlenhardt-Siegel (1988) are not significant, but when compared to our data, the values suggest a decreasing trend of macrofaunal mean body size with increasing latitude that has been preserved from 1985 – 2008. Similar to the results of biomass per m^2, this decreasing trend of mean body size with increasing latitude is negatively correlated with increasing mean annual sea-ice cover (Figure 25) and a decrease in primary production in the ssWAPcs (Montes-Hugo et al., 2009).

Conclusion

Our results demonstrate significant latitudinal and decadal variations in multiple macrobenthic parameters along the continental shelf of the Western Antarctic Peninsula (WAPcs). Our data from 2008 show no significant variation in macrofaunal abundance (N/m^2) along the WAPcs (Table 5), nor between the nsWAPcs and the ssWAPcs (Table 6). In contrast, Mühlenhardt-Siegel (1988) found significant variation in macrofaunal abundance (N/m^2) between the northern and southern subregions of the WAPcs (nsWAPcs and ssWAPcs, respectively) in 1984 - 1985 (D vs. E, Abundance, Table 17). The drastic decadal shift in macrofaunal community composition may be in response to the homogenization of overlying primary production on the WAPcs, which is a result of decreased sea-ice cover and other physical factors (Figure 1, Montes-Hugo et al., 2009).

Our results also reveal statistically significant variations in macrofaunal biomass (g/m^2) and mean body size (g/N) along the WAPcs and between the nsWAPcs and ssWAPcs (Tables 9 & 13, Tables 10 & 14, respectively). Significant variation in macrofaunal biomass (g/m^2) was also detected between the nsWAPcs and ssWAPcs in 1984 -'85 by Mühlenhardt-Siegel (1988) (D vs. E, Biomass, Table 17). This suggests that a latitudinal gradient in overlying primary productivity and sea-ice extent, as well as a benthic-pelagic coupling, has persisted over the WAPcs for over the past 25 years.

Further analysis reveals a temporal decrease in the nsWAPcs biomass (g/m^2) from 57.01g/m^2 (South Sheltand Islands, 1984 – '85) and 111.12 g/m^2 (northern Antarctic Peninsula, 1984' – '85) to 27.01 g/m^2 (Station AA, 2008) and an increase in the ssWAPcs biomass (g/m^2) from 9.01 g/m^2 (1984 – 1985) to 10.19 g/m^2 (2008). In addition, the taxonomic composition of the biomass in the ssWAP in 2008 has been dramatically altered (Figure 21) compared to that of 1985 (Figure 22) demonstrating a succession of echinodermata and mollusca by the polychaeta in this region. These temporal and taxonomic changes within the subregional biomass of the WAPcs could be further responses to a diminishing latitudinal gradient in overlying rates of primary productivity and decreased mean annual sea-ice cover on the WAPcs (Montes-Hugo et al., 2009).

In conclusion, the macrobenthic ecosystem along the WAPcs has been dramatically altered over the past 25 years as a function of altered overlying primary productivity and decreased mean annual sea-ice cover. We hypothesize that these changes along the WAPcs are in response to regional warming driven by climate change. Monitoring the changes of the entire benthic community of the Antarctic continental shelf in response to climate change will remain an important research area for years to come.

APPENDIX

Table 15: Pearson (parametric) and Spearman's Ranked (non-parametric) correlation coefficients of latitude with total and taxon abundance (N/m^2), biomass (g/m^2), and mean body size (g/N). P-values are also included with each correlation.

Row	Correlation Factors	Pearson Correlation Coefficient	Spearman's Ranked Correlation Coefficient
1	Latitude, Total N/m^2 per CRS#	r_p = -0.518, P-Value = 0.103	r_s= -0.445, P-Value = 0.170
2	Latitude, Total g/m^2 per CRS#	r_p = -0.795, P-Value = 0.003	r_s= -0.642, P-Value = 0.033
3	Latitude, Total g/N per CRS#	r_p = -0.772, P-Value = 0.005	r_s= -0.717, P-Value = 0.013
4	Latitude, Polychaete N/m^2 per CRS#	r_p = -0.399, P-Value = 0.224	r_s= -0.370, P-Value = 0.262
5	Latitude, Mollusca N/m^2 per CRS#	r_p = -0.629, P-Value = 0.038	r_s= -0.666, P-Value = 0.025
6	Latitude, Crustaca N/m^2 per CRS#	r_p = -0.741, P-Value = 0.009	r_s= -0.831, P-Value = 0.002
7	Latitude, Echinodermata N/m^2 per CRS #	r_p = -0.409, P-Value = 0.212	r_s= -0.346, P-Value = 0.297
8	Latitude, Polychaete g/m^2 per CRS#	r_p = -0.309, P-Value = 0.355	r_s= -0.356, P-Value = 0.282
9	Latitude, Mollusca g/m^2 per CRS#	r_p = -0.621, P-Value = 0.041	r_s= -0.820, P-Value = 0.002
10	Latitude, Crustaca g/m^2 per CRS#	r_p = -0.660, P-Value = 0.027	r_s= -0.829, P-Value = 0.002
11	Latitude, Echinodermata g/m^2 per CRS #	r_p = -0.625, P-Value = 0.040	r_s= -0.609, P-Value = 0.047
12	Latitude, Polychaeta g/N per CRS#	r_p = -0.012, P-Value = 0.972	r_s= -0.061, P-Value = 0.859
13	Latitude, Mollusca g/N per CRS#	r_p = -0.554, P-Value = 0.077	r_s= -0.726, P-Value = 0.011
14	Latitude, Crustacea g/N per CRS#	r_p = -0.323, P-Value = 0.332	r_s= -0.361, P-Value = 0.276
15	Latitude, Echinodermata g/N per CRS#	r_p = -0.818, P-Value = 0.007	r_s= -0.877, P-Value = 0.002

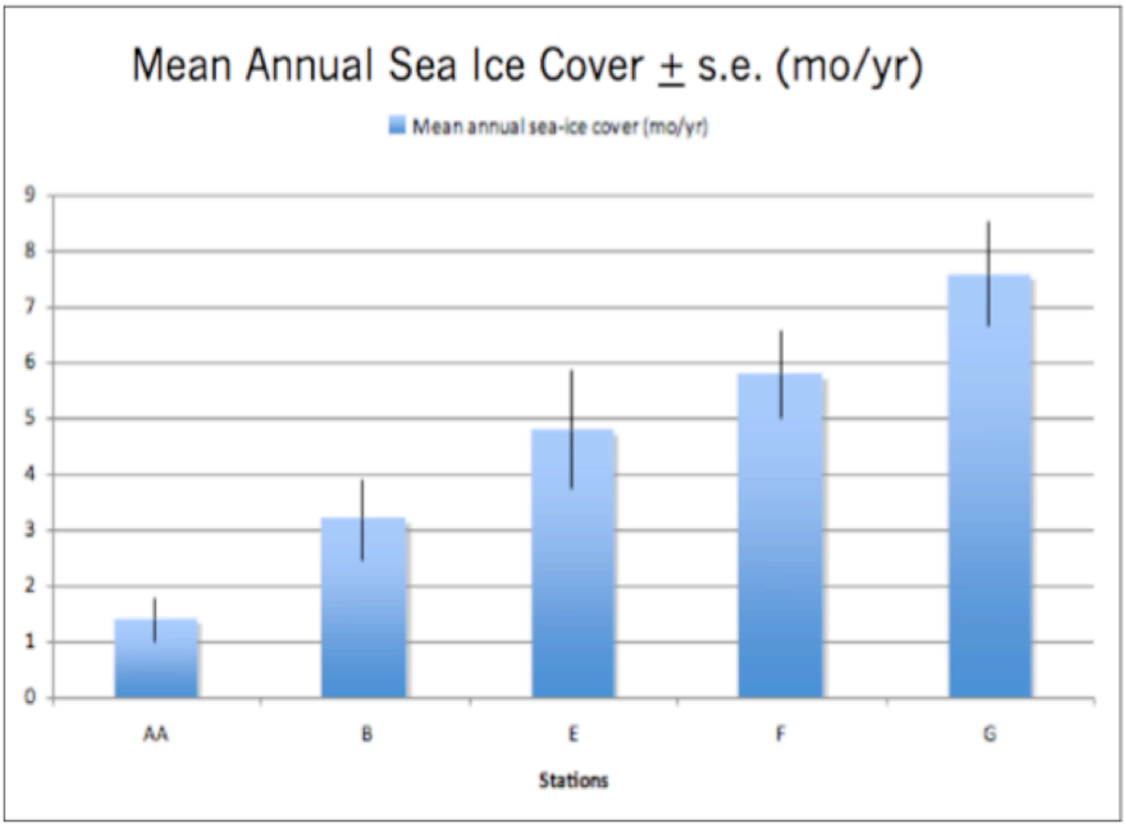


Figure 25: Mean annual sea-ice cover (in months/year) plotted with +/- standard error bars for each sampling station of FOODBANCS 2, based on satellite data from the National Snow and Ice Center. Data was compiled from monthly averages from 2004 – 2008. If a station during any month was covered by sea-ice more than 50% of the month, it was considered "ice-covered" for that month, and if less than 50% it was characterized as "ice-free." Note: station "E" was not used in this study due to lack of box-corer data. From Srsen et al. (unpublished).

Table 16: Spearman's Ranked (non-parametric) correlation coefficients of mean annual sea-ice cover per station with mean total and taxon abundance (N/m^2), mean biomass (g/m^2), and mean body size (g/N). P-values are also included with each correlation. Mean annual sea-ice data from Srsen et al. (unpublished).

Row	Correlation Factors	Spearman's Ranked Correlation Coefficient
1	Mean Annual Sea-Ice Cover, Mean Total N/m^2	r_s= -0.800, P-Value = 0.200
2	Mean Annual Sea-Ice Cover, Mean Total g/m^2	r_s= -0.800, P-Value = 0.200
3	Mean Annual Sea-Ice Cover, Mean Total g/N	r_s= -1.00, P-Value = 0.000
4	Mean Annual Sea-Ice Cover, Mean Polychaete N/m^2	r_s= -1.00, P-Value = 0.000
5	Mean Annual Sea-Ice Cover, Mean Mollusca N/m^2	r_s= -0.800, P-Value = 0.200
6	Mean Annual Sea-Ice Cover, Mean Crustaca N/m^2	r_s= -0.800, P-Value = 0.200
7	Mean Annual Sea-Ice Cover, Mean Echinodermata N/m^2	r_s= -0.800, P-Value = 0.200
8	Mean Annual Sea-Ice Cover, Mean Polychaete g/m^2	r_s= -0.400, P-Value = 0.600
9	Mean Annual Sea-Ice Cover, Mean Mollusca g/m^2	r_s= -1.00, P-Value = 0.000
10	Mean Annual Sea-Ice Cover, Mean Crustaca g/m^2	r_s= -0.800, P-Value = 0.200
11	Mean Annual Sea-Ice Cover, Mean Echinodermata g/m^2	r_s= -0.800, P-Value = 0.200
12	Mean Annual Sea-Ice Cover, Mean Polychaeta g/N	r_s= -0.000, P-Value = 1.00
13	Mean Annual Sea-Ice Cover, Mean Mollusca g/N	r_s= -1.00, P-Value = 0.000
14	Mean Annual Sea-Ice Cover, Mean Crustacea g/N	r_s= -0.200, P-Value = 0.800
15	Mean Annual Sea-Ice Cover, Mean Echinodermata g/N	r_s= -1.00, P-Value = 0.000

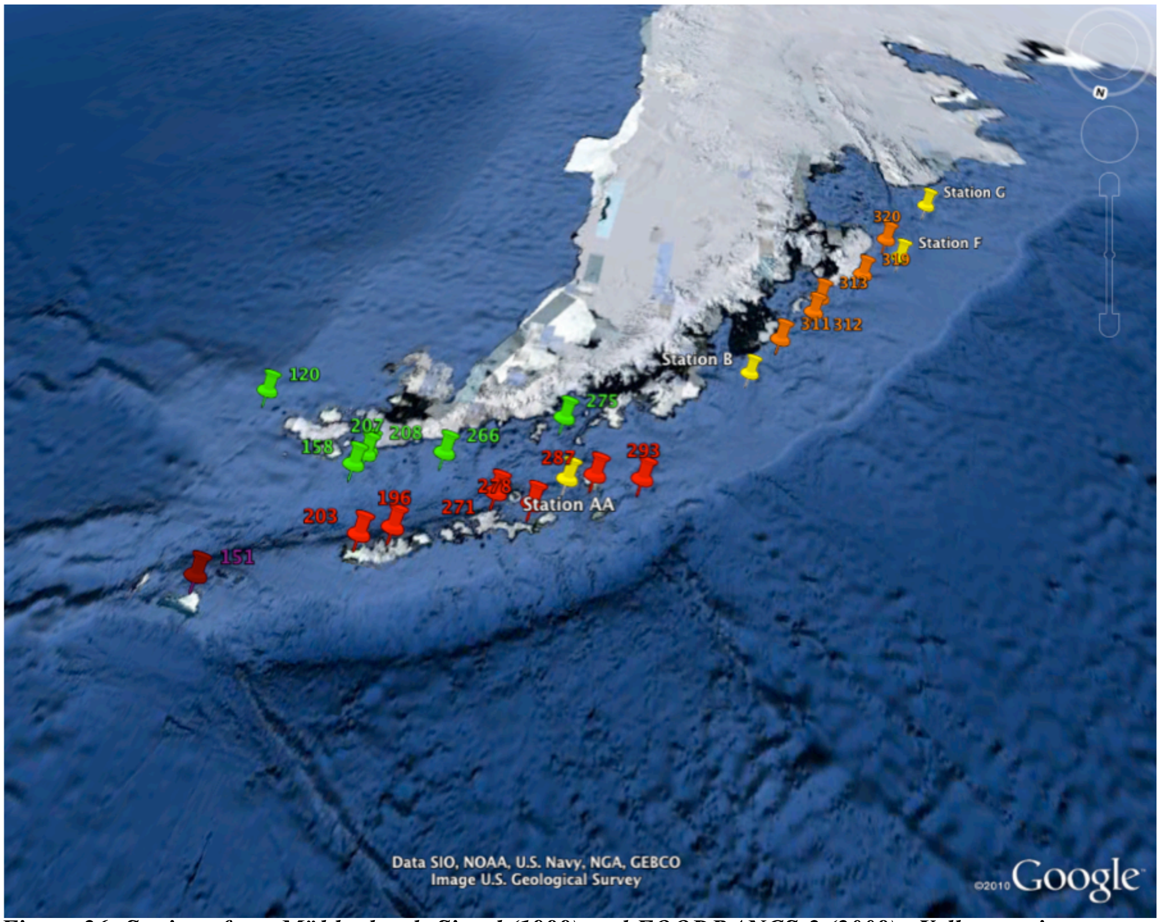


Figure 26: Stations from Mühlenhardt-Siegel (1988) and FOODBANCS-2 (2008). Yellow stations, from this study, include station AA, B, F, and G. Orange stations represent the "southern Antarctic Peninsula" or "region E," red stations represent "the South Shetland Islands" or "region C," the green stations represent the "northern Antarctic Peninsula" or "region D," and the lone purple station, 151, is one station used to represent "Elephant Island" or "region B" in Figures 3, 4, 13, 22 and Table 17, from Mühlenhardt-Siegel (1988). Image constructed in Google Earth (2010).

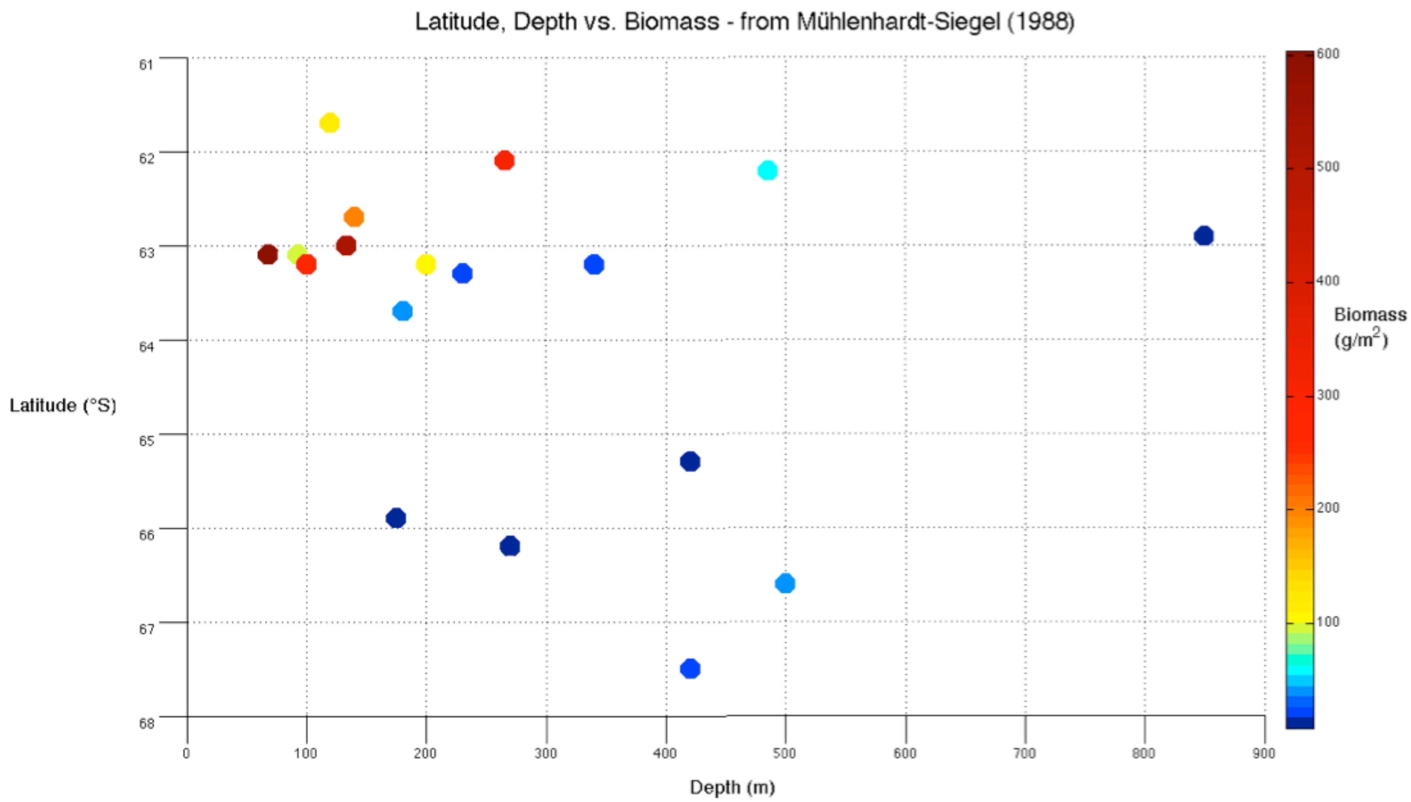


Figure 27: 3D Scatter plot of latitude (°S) and depth (m) and total biomass (g/m^2) per sample along the Antarctic Peninsula from Mühlenhardt-Siegel (1988). Multiple regression of latitude and depth yields a P-value of 0.05 and the equation "Biomass = 2275.43 – 31.8192*(Lat) – 0.381964*(Depth)."

Table 17: Comparison of the differences in abundance (N/m^2) and biomass (g/m^2) between regions of the WAPcs with the Mann-Whitney-U-test. A "+" indicates a significant difference between regions ($P < 0.05$) and "-" indicates no significant difference between regions. From Mühlenhardt-Siegel (1988).

Table 2. Comparison of the different regions with Mann-Whitney-U-test. + = significant ($P = 0.05$) difference; – = no significant difference. A = Elephant Island, *Polarstern*; B = Elephant Island, *Walther Herwig*; C = South Shetland Islands excluding Elephant Island; D = northern part of the Antarctic Peninsula; E = southern part of the Antarctic Peninsula; F = South Orkney Islands

Regions to be tested		Number of individuals						Biomass					
		n1	n2	U1	U2	$U_{crit.}$	diff.	n1	n2	U1	U2	$U_{crit.}$	diff.
WHC vs.	PsC	6	3	4	14	1	–	6	3	4	14	1	–
WHD	PsD	4	7	22	6	3	–	4	7	17	7	3	–
WHC	WHD	6	4	9	15	2	–	6	4	6	18	2	–
PsC	PsD	3	7	17	4	1	–	3	7	15	6	1	–
A	B	2	25	41	9	3	–	2	25	4	46	3	–
A	C	2	9	16	2	0	–	2	9	4	14	0	–
A	D	2	11	20	2	0	–	2	11	11	11	0	–
A	E	2	8	6	10	0	–	2	8	0	16	0	+
A	F	2	13	22	4	1	–	2	13	2	24	1	–
B	C	25	9	99	126	62	–	25	9	148	77	62	–
B	D	25	11	135	140	80	–	25	11	240	35	80	+
B	E	25	8	38	162	53	+	25	8	52	148	53	+
B	F	25	13	155	170	98	–	25	13	122	203	98	–
C	D	9	11	60	39	23	–	9	11	73	26	23	–
C	E	9	8	17	55	15	–	9	8	9	63	15	+
C	F	9	13	62	55	28	–	9	13	29	88	28	–
D	E	11	8	10	78	19	+	11	8	5	83	19	+
D	F	11	13	62	81	37	–	11	13	15	128	37	+
E	F	8	13	21	83	24	+	8	13	42	62	24	–

Figure 28: The RV Nathaniel B. Palmer (A) and the RV Laurence M. Gould (B); the research vessels used in the FOODBANCS-2 projects. Images courtesy of Craig Smith.

Figure 29: The box-corer device used to quantitatively sample the macrobenthos during FOODBANCS-2 research program. In operation (left), and after an overnight freeze (right). Images courtesy of Craig Smith.

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