FACTORS INFLUENCING PATTERNS IN DISTRIBUTION, ABUNDANCE AND DIVERSITY OF SEDIMENTARY MACROFAUNA IN DEEP, MUDDY SEDIMENTS OF PLACENTIA BAY, NEWFOUNDLAND AND THE ADJACENT SHELF

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Factors influencing patterns in distribution, abundance and diversity of sedimentary macrofauna in deep, muddy sediments of Placentia Bay, Newfoundland and the adjacent shelf

by

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Abstract

A nested sampling design and multivariate analyses were used to examine the community structure and spatial distribution of macrofauna on muddy substrates in Placentia Bay, Newfoundland and the adjacent shelf. The goal was to determine how macrofaunal communities are related to water column (e.g., surface productivity) and sediment characteristics (e.g., carbon and nitrogen content). Box core samples were collected at 10 sites (June & July of 1998) that were distributed from the head of the bay through the Eastern and Western Channels to the edge of the continental shelf. This is the first comprehensive study of Placentia Bay infauna and it is divided into three main components. Chapter 1 examines broad-scale patterns in community composition, diversity and abundance along an inshore/offshore gradient. Results indicate that the bay contains distinct inshore and offshore regions and benthic patterns are largely influenced by surface oceanography. Chapter 2 focuses on finer-scale patterns of distribution and abundance within the inshore region of the bay and reveals spatial patterns that were not evident in the analyses of broad-scale patterns in the previous chapter. Sediment-related factors and depth were important in explaining variation in inshore benthic patterns. Thus, contrasting the results of these two chapters suggests that different variables structure these communities at different scales. Because little biological sampling for benthos has been undertaken in this area, Chapter 3 provides a guide to the polychaetes, which are the dominant group of infauna in the study. Digital photographs of the key characteristics used to identify each species are provided to help bridge identification guides developed for other areas.

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Introduction and Overview

Declines in fisheries (e.g. Williams 1998) and renewed interest in marine biodiversity (e.g. Norse 1993; Snelgrove et al. 1997) have created the importance of generating marine species inventories and gaining a better ecosystem-level understanding of marine systems. In general, the marine environment surrounding Newfoundland has been poorly sampled, despite of its economic importance to the province. Although commercial taxa have received considerable attention (e.g. Lawson and Rose 1999; Bradbury et al. 2000), information concerning other ecosystem components, such as benthic communities, is limited to a handful of studies (e.g. Nesis 1965; Carter et al. 1979; Houston and Haedrich 1984; Kennedy 1985; Schneider et al. 1987; Gilkinson et al. 1998; Prena 1999).

The concept of marine infaunal communities has grown out of initial studies by Petersen (1913) and over the years, benthic patterns of community composition and diversity have been shown to be influenced by a variety of physical and biological factors. Examples of such factors include sediment composition and organic content (Gray 1974; Rhoads 1974), water column production (Davis and Payne 1984; Grebmeier et al. 1988; Ambrose and Renaud 1995), disturbance (Rhoads and Young 1970; Woodin 1978), predation and competition (Peterson 1979; Wilson 1989), depth (Houston and Haedrich 1984) and bottom currents (Butman 1987; Snelgrove and Butman 1994). However, the relative importance of these factors in regulating community patterns can vary with spatial scale (Menge and Olson 1990) and the critical variables and scales are not well understood (Josefson and Conley 1997). In general, broad patterns (kilometres–1000's km) in distribution and abundance are thought to be influenced by large-scale differences in temperature, salinity, depth, surface production, topography, sediment dynamics and circulation. By contrast, smaller-scale patterns (millimetres–tens of metres) are usually regulated by a complexity of smaller-scale physical processes and biological interactions (Snelgrove 1999).

The present work is the benthic component of a larger study on spatial and temporal variability in the Placentia Bay ecosystem (e.g. Lawson and Rose 1999; Robichaud and Rose 1999; Bradbury et al. 2000). The availability of complementary data on surface oceanography from these related studies provides an opportunity to study benthic patterns of diversity and abundance in relation to a suite of relatively large-scale oceanographic variables, that are expensive and time consuming to collect, and therefore are often unavailable for most benthic studies.

This study describes the community structure and spatial distribution of sedimentary macrofauna on muddy sediments of Placentia Bay and the adjacent shelf in relation to environmental variables and is divided into three main components. Chapter 1 examines how water column characteristics, such as surface production (chl *a*), and sediment characteristics, such as carbon and nitrogen content, influence broad-scale patterns of community compostion, diversity and abundance along an inshore/offshore gradient that extends from the head of the bay to the continental shelf. Although coupling between benthic and pelagic communities has most commonly been shown to occur at much larger scales than that of the Placentia Bay and shelf area (e.g. Mills 1975; Rowe 1981; Ambrose and Renaud 1995), multiple surveys of Placentia Bay indicate strong spatial variation in phytoplankton and zooplankton communities (Snelgrove et al., unpublished data), suggesting variation in surface oceanography. Thus, it is hypothesised that if sediment composition and depth are similar among sites, then faunal patterns will be influenced by surface production. Chapter 2 focuses on finer-scale patterns of distribution and abundance within the inner bay that may be masked by the greater variability in the analysis of broad-scale patterns presented in the previous chapter. Because greater decoupling between benthic and pelagic communities is expected at smaller scales, it is predicted that sediment-related factors such as grain size, sedimentary organic and nitrogen content will be important in influencing pattern. In the third Chapter, documentation is provided to aid in identification of polychaete species sampled within Placentia Bay and on the shelf. Digital photographs are included of the key characteristics used to identify each species along with references to identification guides that are useful to the Placentia Bay area.

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Co-Authorship Statement

All manuscripts in this thesis were co-authored with Paul Snelgrove. In all instances, I was the principal contributor to project design and proposal, implementation of the field research component, analysis of data and manuscript preparation.

Chapter 1. Does surface oceanography influence faunal patterns in coastal and shelf sedimentary communities on the south coast of Newfoundland?

1.1 Introduction

Marine benthic infanal communities are characteristically patchy in distribution of abundance and diversity (e.g. Volchaert 1987; Morrisey et al. 1992). This patchiness has been long recognised (Petersen 1913; Jones 1950) and the causes of patchiness have been examined in a number of studies that have shown that infaunal communities are influenced by a variety of environmental and biological factors. Examples of such factors include sediment composition and organic content (Gray 1974; Rhoads 1974), water column production (Davis and Payne 1984; Grebmeier et al. 1988; Ambrose and Renaud 1995), disturbance (Rhoads and Young 1970; Woodin 1978), predation and competition (Peterson 1979; Wilson 1989), depth (Houston and Haedrich 1984) and bottom currents that bring food and new recruits to the community (Butman 1987; Snelgrove and Butman 1994).

Although many factors have been shown to be related to patterns of composition and diversity, it has proven difficult to determine which of these variables are most important in creating and maintaining structure within benthic communities. This difficulty is mainly because of the co–variation of environmental factors and the extreme patchiness of infauna (Whitlatch 1980). Moreover, the lack of appropriate spatial replication of samples within study sites can confound interpretation of pattern (Morrisey et al. 1992), which prevents valid comparisons of abundance and diversity between different sites at larger scales. It has been suggested by Morrisey et al. (1992) that this problem of confounding can be overcome by the use of nested sampling designs.

There is little doubt that many different processes can potentially influence diversity and local patterns of community composition. However, the relative importance of these factors in regulating patterns can vary with spatial scale (Menge and Olson 1990) and the critical variables and scales are not well understood (Josefson and Conley 1997). In general, broad patterns (kilometres-1000's km) in distribution and abundance are influenced by larger-scale (10's-100's km) oceanographic features such as temperature, salinity, depth, surface production, topography and circulation and it is these processes that set the stage for smaller-scale (<1 km) physical processes and biological interactions to operate and define smaller-scale (millimetres-tens of metres) patterns in distribution and abundance (for review of smaller-scale processes see Chapter 2).

Temperature, salinity and depth often delimit broad distributions in terms of physiological constraints (Snelgrove 1999). Many species have specific tolerances to these variables that are related to osmotic balance and enzyme function. Circulation patterns can influence benthic communities in many ways. Most importantly they modify other water column processes such as near-bottom flow, which largely determines sediment type and food supply to the benthos. Circulation also affects larval supply to benthic habitats because larval supply to benthic habitats is thought to be passive over broad scales (Butman 1987; Bradbury and Snelgrove 2001). However, the link between larval supply and benthic pattern is a subject of much debate (Snelgrove and Butman 1994; Ólafsson et al. 1994). Circulation is also closely linked to topographic features such as islands and banks, which can create enhanced larval retention through eddies (Lobel and Robinson 1986; Tremblay et al. 1994). Topography may also influence larval transport and survival in highly productive areas associated with upwelling. Benthic communities that occur below the photic zone are dependant on sinking water column production as a major food source and thus, the quality and quantity of sinking organic matter to the sea-bed is likely to be a very important factor in influencing benthic community structure, biomass and metabolism (Mills 1975; Jørgensen 1983; Smetacek 1984). Central to this linkage, is the role of herbivory and how decoupling between herbivory and primary production can result in greater export of production to the bottom as a result of lowered zooplankton grazing rates (Ambrose and Renaud 1995).

Most benthic-pelagic coupling studies have examined infaunal response to organic matter input (i.e., phytodetritus) using methods involving oxygen or carbon dioxide exchange (Smith et al. 1983; Witbaard et al. 2000; Duineveld et al. 2000), heat or nutrient release (Smith et al. 1983) or changes of ATP-biomass (Drazen et al. 1998). Such measures are only useful as indicators of the response of the entire sedimentary community and do not differentiate between various infaunal groups and individuals. Limited attention has been given to specific infaunal groups and studies that have focused on bacteria (Lochte and Turley 1988; Pfannkuche 1993), meiofauna (Gooday et al. 1996; Pfannkuche 1993) or macrofauna (Grebmeier et al. 1988; Long and Lewis 1987; Pfannkuche 1993; Ambrose and Renaud 1995) have shown a variety of community responses to the input of organic matter.

Macrofaunal studies have often found a positive relationship between benthic abundance and biomass and enhanced flux of organic carbon to the sea-bed (Davies and Payne 1984; Elmgren 1978). Others have linked water column production to benthic biomass and abundance. For example, Grebmeier et al. (1988) found a significantly greater mean benthic biomass in the highly productive Bering Shelf-Anadyr Water, on the shelf of the northern Bering and Chukchi Sea than in less productive Alaska Coastal Water. C/N ratios for the Bering Shelf-Anadyr Water were low, suggesting a higher quality, nitrogen rich marine carbon supply than in the northern Bering and Chukchi Sea where higher C/N ratios indicated lower quality carbon in the sediments. In the Northeast Water Polynya on the northeast Greenland continental shelf, Ambrose and Renaud (1995) found benthic pigment concentration was the most important predictor of infaunal density and polychaete biomass. Benthic pigment concentrations were strongly related to concentrations of water column pigments, suggesting that water column productivity was closely linked to flux to the bottom and was subsequently transmitted to fauna.

Data on relatively broad-scale (100's of km) oceanographic variables do not exist for most benthic studies, and their collection can be expensive and time consuming. The present work is part of a larger study that has focused on the Placentia Bay ecosystem, with particular emphasis on cod and other commercial taxa (e.g. Lawson and Rose 1999; Robichaud and Rose 1999; Bradbury et al. 2000). Thus, the availability of complementary data on surface oceanography provides an opportunity to study benthic patterns of diversity and abundance in relation to a suite of relatively large-scale oceanographic variables. Although studies that have linked surface production to benthic biomass and abundance are typically at larger scales than the Placentia Bay study, multiple surveys of Placentia Bay indicate strong spatial variation in phytoplankton and zooplankton communities (Snelgrove, unpublished data), suggesting variation in surface oceanography.

The present study describes the community structure and spatial distribution of sedimentary macrofauna on muddy substrates in Placentia Bay, Newfoundland and the adjacent shelf environment in relation to environmental variables. Specifically, water column characteristics, such as surface production (chl *a*) and sediment characteristics, such as carbon and nitrogen content, are examined to determine how they influence infaunal community composition and diversity along an inshore/offshore gradient that extends from the head of Placentia Bay to the edge of the continental shelf. It is hypothesized that if sediment composition and depth are similar among sites, then faunal patterns of diversity and abundance will be related to surface production.

1.2 Materials and Methods

1.2.1 *Study Site*

Placentia Bay is a large embayment on the south coast of Newfoundland (Fig. 1.1), measuring ~132 km long (oriented NNE–SSW) and 100 km wide at its southerly directed mouth, which links it to the adjacent shelf environment. Bottom depths range from shallow areas, including those created by several banks, to holes greater than 200 m in depth. The inner part of the bay is divided longitudinally into three channels by several islands. These channels join just south of the islands to form the large outer bay that opens onto the shelf. Circulation patterns within the bay are characterised by northerly flow on the eastern side and southerly flow on the western side (see Bradbury et al. 2000).

1.2.2 *Sampling Design*

Infaunal box core samples were collected in June and July 1998 from ten sites that were distributed from the head of the bay, through the Eastern and Western Channels, to the edge of the continental shelf (Fig. 1.1). One site was located at the head of the Bay (6 replicates per site), five in the inner bay (6 replicates per site), another was located in the outer bay (3 replicates), and the remaining three were located offshore, along a transect across the continental shelf (2-3 replicates per site) toward the shelf edge. Initial site selection was primarily based upon similarity in sediment composition (muddy areas) as determined by examining local charts and a geological map constructed by Stehman

(1976). For most stations, depth was similar ($\bar{x}$=184–232 m) although two sites were more extreme in range ($\bar{x}$=67 m and 286 m respectivly).

A nested, hierarchical sampling design was used where each of a series of successively smaller spatial scales was nested within larger scales (Morrisey et al. 1992). Two sampling areas were nested within each of 3 subsites, nested within each site (Fig. 1.2). Subsite locations were randomly chosen within a 500 m radius of the approximate center of each site. This pattern was achieved by generating random compass bearings and distances between 0–360 ° and 0–500 m respectively. These values were then used to calculate subsite co-ordinates (i.e., latitude and longitude) originating from the initial center of each site. Thus, each subsite location extended in a random direction at a random distance from the original site. Sampling locations were randomly chosen within a 100 m radius of each subsite location as outlined above, except that map co-ordinates were obtained relative to the subsite co-ordinates. This approach produced 3 subsites x 2 sampling sites for a total of 6 replicates per site. All 6 replicates were collected from sites in the inner bay however, because of ship time contraints only 2-3 replicates were collected from sites located between the outer bay and shelf edge. In some instances alternate sampling sites were randomly generated, using the same method described above, because bottom substrate at some of the initial sites was not appropriate for the sampling gear.

1.2.3 *Infaunal Sampling*

The box corer was subdivided into six subcores that were each 10 cm x 10 cm wide and 30 cm deep. This design allowed several variables to be sampled simultaneously. Four of the subcores were processed through a 500 μm screen to evaluate the macrofaunal community, another subcore was processed through a 100 μm screen to sample for recently settled individuals (not reported here), and the surface (~1 cm) of the sixth subcore was used for CHN and grain size analysis. Because macrofauna generally present occur within the top 6-8 cm of sediment and are usually concentrated in the well-oxygenated top 3 cm, subcores for macrofaunal analysis were sectioned into 0–3 cm and 3–10 cm vertical increments; this strategy facilitated processing later. Macrofaunal samples were initially preserved in 4% buffered formalin and then promptly transferred to 70% ethanol with rose bengal. Organisms were enumerated and identified to species where possible.

1.2.4 *Environmental Data*

Vertical casts for salinity and temperature were collected with a Seabird 25 CTD concurrently with box core samples at 1 of the replicate sampling areas at each site within the inner bay, outer bay and shelf edge and at 2 of the 3 sites on the shelf (S_1 and S_2). The depth at each replicate sampling area within each site was recorded. Mixed-layer temperatures and salinities were determined by averaging the upper 40 m from each profile, and bottom temperatures and salinities were taken from approximately 5 m above the bottom. Chlorophyll *a* samples were collected from a grid of stations throughout

Placentia Bay during June and August 1998 and analysed by methods outlined by Bradbury et al. (2000). Chlorophyll measurements for April, July and September were taken from satellite imagery of sea surface color (SeaWiFS, Sea-viewing Wide Field of View Sensor, see http://dfomr.mar.dfo-mpo.gc.ca/science/ocean/seawifs/seawifs_1.html). Distances of each site from the nearest shoreline and from the head of the bay were determined using the program Mapinfo.

1.2.5 *Sediment Analyses*

For grain size analysis, a 50:50 water/peroxide solution was added to each sediment sample, and heated to 300°C to remove organics. Samples were then placed in a drying oven at 200°C prior to resuspension and disaggregation using 0.1 % calgon solution and a magnetic stirrer. Following this treatment, samples were wet sieved through a 63 μm sieve into a bucket which separated them into a coarse (sand) and fine fraction (silt and clay). The coarse fraction was re-sieved through nested sieves (350, 250, 177, 125, 88, and 62.5 μm). Dry weights were then calculated.

The fine fraction was left to settle for 24–48 h, after which a 50–60 ml subsample was obtained for sedigraph analysis (5100 Particle Size Analyser). The sedigraph collects data on sedimentation velocity of settling particles by measuring the concentration of particles remaining in suspension as a function of time. For this analysis, the particle size ranged from 62.5 to 0.49 μm. Percentages of sand, silt and clay at each site were then calculated for this data. For CHN analysis, frozen samples were thawed, transferred to small vials, and freeze dried at –60 °C prior to analysis in a Perkin Elmer Model 2400. Sediment samples were not treated with acid to remove carbonate because sediment samples from other Newfoundland Bays (e.g. Conception Bay) have shown that carbonate concentrations are not high and do not affect carbon values (E. Hatfield, Memorial University, personal communication).

1.2.6 *Data Analyses*

The four subcores used to evaluate the macrofaunal community were not considered to be independant replicates because they were not completely separated from each other (no spacing between cores) and thus were considered to be one large core for community composition analysis. This pooling yielded six replicate samples (each with 400 cm^2 surface area) at each site within the bay, with fewer replicates in the outer bay and shelf. Shannon–Weiner diversity, richness, evenness and density (total macrofauna) were compared at each site by plotting means and 95% confidence intervals. To determine whether there was a significant difference in these measures between inshore and offshore areas of the bay, an independent samples t-test was performed. Homogeneity of variance tests indicated that with the exception of species evenness, no data transformation was necessary. Species evenness data was root transformed, however, after transformation homogeneity tests still indicated unequal variance and therefore a non-parametric test (Mann-Whitney U) was used. Comparisons were made of the distribution of macrofauna among vertical fractions (i.e., percentage of total macrofauna in 0-3 fraction compared to the 3-10 fraction). A t-test was also performed on root transformed data to determine if there was a significant difference in macrofaunal abundance among the 3-10 vertical fraction between different areas of the bay. Average densities of the dominant taxa were compared at each site by plotting means and 95% confidence intervals for replicate samples. Dominant taxa were defined as the four most abundant taxa in terms of individuals·400 cm^{-2} at each site.

Community composition was compared among sites using CNESS (Chord Distance Normalised Expected Species Shared) as described by Trueblood et al. (1994). CNESS is an extension of Orloci's (1978) chord distance and Grassle and Smith's (1976) NESS (Normalised Expected Species Shared). CNESS is a faunal index that produces a dissimilarity matrix from a sample x species matrix, and is based upon the number of expected species shared in a random draw of *n* individuals from two samples. This particular index was chosen because it is sensitive to rare as well as abundant species. Distribution patterns were clustered using unweighted, pair–group mean average sorting of CNESS dissimilarities (COMPAH 90–E.D. Gallagher). To provide a more complex and informative presentation of the data, a metric scaling of CNESS was performed in Matlab (programs written by E.D. Gallagher).

The metric scaling of CNESS converts the sample–by–species matrix to a normalised hypergeometric probability matrix, (H), which describes the probability of sampling each species in each sample with a random draw of ten individuals. This hypergeometric matrix is then analysed by principal components (PCA–H). The first two scores from

PCA–H provide a two dimensional metric scaling of CNESS distances among samples representing the best least–squares fit for the data. This plot is very similar to that produced by non-metric multidimensional scaling (NMDS), (Trueblood et al. 1994; Snelgrove et al., submitted), however, the advantage of metric scaling is that CNESS distances among samples are preserved. The species that contribute to CNESS variation among samples can then be displayed in a Gabriel Euclidean distance biplot overlay (Gabriel 1971; Ter Braak 1983), where the length and angle of species vectors indicate the contribution of the species to the PCA–H axes.

Determining which species drive pattern from the biplots alone is somewhat subjective because biplots capture within-site as well as between-site variation. In order to provide a more objective interpretation, discriminant function analysis (SPSS 8.0) was also performed with site grouping designated as factor. The site groupings were obtained from the PCA–H analysis. This analysis was not used for formal hypothesis testing, and instead it was used as a relative yardstick to evaluate which species were responsible for between-site differences that were observed in the PCA–H plots. Taxa with a p-value less than 0.05 were used as a screening criterion and were designated as most important. The percentage of total individuals contributed by each of these species was calculated using the same site groupings determined in the discriminant function analysis. Stacked bar graphs were then constructed for those species that made up at least 5% of the total density at any one site.

PCA (Principal Components Analysis) determined differences among the 10 sampling sites based on environmental variables, including abiotic and biotic water column variables and sediment-related measures (SPSS 8.0). Prior to analysis, variables were converted to standardised Z-scores with a mean of zero and standard deviation of one; this standardisation reduces the degree to which any one variable with a larger mean value sways the result. For the majority of environmental variables, individual data values were only collected for 2 or 3 of the replicate sampling locations at each site. Therefore, replication of environmental variables was not as great as it was for species data, however, given the close proximity of replicates within each site, variation for most of these variables was observed to be small. Correlation analysis was conducted between the environmental variables and dominant biotic variables (i.e., diversity, abundance, evenness and species richness). To account for error due to the large number of contrasts the Dunn-Šidák method was used to adjust the p-value, resultingin a critical p-value of 0.0002. A multiple regression with adjusted F ratios and p-values was also run separately with diversity, richness and density as the dependant variable(s) and environmental variables as the independent variables. Since many of the environmental variables in this study are interelated, only 9 were used in this analysis including depth, % organic carbon, mixed layer temperature, bottom temperature, bottom salinity, mixed layer salinity, distance from the head of the bay, Chl *a* in June and % very-fine to medium silt. Chlorophyll *a* in June was selected because benthic samples were collected in July and very-fine to medium silt was common among sites. A plot of best fits and residuals showed trends that defied the assumptions for this analysis.

1.3 Results

1.3.1 *Overview: Placentia Bay Infauna*

A total 15,120 individuals were collected from 10 stations encompassing 118 different species of molluscs, echinoderms, crustaceans, polychaetes, cnidarians, hemichordates, nemerteans, scaphopods and sipunculids. Many species were present in low abundance and at few sites; of the 118 taxa, 35 were present at only one site. A complete list of taxa and their abundance is found in appendix 3.1. Polychaetes were the most abundant group, comprising 88% of the total infauna collected. Bivalves and amphipods constituted 4% and 2% respectively. The dominant taxa in Placentia Bay (Figs. 1.3 A and B) included eleven different polychaetes, a bivalve (*Thyasira* sp.), Nemertea spp., and an amphipod. The single most abundant species was the polychaete *Cossura longocirrata*, which comprised 54% of the total infauna (63% of polychaetes). The polychaetes, *Prionospio steenstrupi* (8% of total infauna), Dorvilleidae spp. (together 3% of total infauna), and *Nephtys neotena* (3% of total infauna) were the next most abundant taxa.

A comparison of the distribution of macrofauna among vertical fractions revealed that the majority of individuals (>70%) were found in the top 0–3 cm of sediment, however, significantly fewer organisms ($n=47$, $t=6.58$ $p=<0.001$) were found in the 3-10 portion of samples from the head and inner bay (inshore), ($\bar{x}=23.0$ individuals·400 cm^{-2}, $se=4.2$, $n=36$) than those from the outer bay and shelf (offshore), ($\bar{x}=110.2$ individuals·400 cm^{-2}, $se=19.9$, $n=11$), (Fig. 1.4).

1.3.2 *Species Abundance and Diversity*

C. longocirrata was the most abundant species overall, with average densities ranging from 33–50 individuals·400 cm^{-2} , (Fig. 1.3 A); it was most abundant in the Eastern Channel, lower Western Channel (W_2, southern portion of Western Channel) and, outer bay. *P. steenstrupi*, *N. neotena*, Dorvilleidae spp., Nemertea spp., *Chaetozone setosa*, and *Lumbrineris* spp. were present at each site but abundances differed greatly. *P. steenstrupi* (3-132 individuals·400 cm^{-2}) and *N. neotena* (0.33-38 individuals·400 cm^{-2}) were most abundant in the outer bay and on the shelf (S_1 and S_2), with lower densities at the head of the bay, inner bay (channel sites) and at the shelf edge (Fig. 1.3 A). Capitellidae spp. (0–27 individuals·400 cm^{-2}), *C. setosa* (1-26 individuals·400 cm^{-2}) and Nemertea spp. (1-17 individuals·400 cm^{-2}) were greater in abundance in the area between the outer bay and the shelf edge compared to the head and inner part of the bay (Fig. 1.3 B). Dorvilleidae spp. (0.33-38 individuals·400 cm^{-2}) densities were higher in the Eastern Channel and lower Western Channel (W_2), compared to other areas (Fig. 1.3 A), and *Lumbrineris* spp. (0.50-42 individuals·400 cm^{-2}) were most abundant in the outer bay (Fig. 1.3 A). *Thyasira* sp. (0-14 individuals·400 cm^{-2}) was most abundant in the Central Channel, lower Western Channel (W_2) and in the outer bay (Fig. 1.3 B). *Gyptis* sp. (0-14 individuals·400 cm^{-2}) was present at all sites, except the shelf edge, and was abundant at the head, inner and outer parts of the bay (Fig. 1.3 B). *Pectinaria granulata* (0-41 individuals·400 cm^{-2}) was found at very low densities in the inner and outer bay, however it, was the second most abundant taxon at the head of the bay (Fig. 1.3 A). *Byblis gaimardi* (0-35 individuals·400 cm^{-2}) and *Nereimyra punctata* (0-23 individuals·400 cm^{-2}) were only encountered at three sites. Both species were present at the head of the bay but *B. gaimardi* was most abundant at S_2 and *N. punctata* was most abundant in the upper Eastern Channel (E_1, northern portion of Eastern Channel), (Fig. 1.3 A and B respectively). *Aricidea quadrilobata* (0-31 individuals·400 cm^{-2}) was only encountered at the edge of the continental shelf, where it was the second most abundant taxon (Fig. 1.3 A).

Overall density was relatively high, ranging between 2717 and 17, 725 individuals m^{-2}, (Fig. 1.5). The highest densities were observed in the outer bay, whereas the lowest densities were found at the head of the bay, in the Central Channel and in the upper Western Channel (W_1). Shannon diversity indices for Placentia Bay and the adjacent shelf ranged from very low to moderate (1.3-3.1), (Fig. 1.6). Diversity was lowest in the Eastern Channel, lower Western Channel (W_1) and S_1 and was greatest at the shelf edge. Species richness ranged from 18 to 45 taxa per sample (Fig. 1.7) and evenness varied between 0.42 and 0.82 (Fig. 1.8).

1.3.3 *Cluster & PCA-H Analysis*

At a dissimilarity of 66%, cluster analysis of infaunal cores showed six somewhat distinct groups. These included the head (H), Central Channel (C), outer bay (O), combined Eastern and Western Channels ($E_{1\ \&\ 2}$ and $W_{1\ \&\ 2}$), shelf sites (S_1 and S_2) and shelf edge (S_3), (Fig. 1.9). There was evidence of further substructure within the inner bay samples that will be discussed in Chapter 2.

PCA-H analysis showed a less ambiguous grouping of sites (Fig. 1.10), with distinct communities at the head of the bay (H), in the Central Channel (C) and at the edge of the continental shelf (S_3). The Eastern and Western Channels formed a grouping (with the exception of a few Western Channel samples), and the outer bay (O) and shelf sites (S_1 and S_2) formed another grouping. Thus, the inner bay channel samples ($E_{1\,\&\,2}$ & $W_{1\,\&\,2}$) were generally similar to one another and the outer bay samples were more similar to those collected from the shelf. Moreover, unlike the pattern observed for the inner bay, the individual sites from the outer bay (O, S_1, S_2) were distinct from one another, and the shelf edge site (S_3) was distinct from each of these. Thus, benthic composition is continually changing and becoming more distinct spatially with increased distance from the inner bay. The first PCA–H axis suggests an inshore/offshore trend in community differences, whereas the second axis describes differences in communities located within the inner part of the bay.

Gabriel biplots indicate that the polychaetes *C. longocirrata* and an unidentified dorvilleid played a greater role in the community structure within the inner part of the bay, whereas Capitellidae spp. and *P. steenstrupi* played a greater role on the shelf and at the shelf edge (Fig. 1.10). *C. longocirrata* makes up 27.5%, 51% , 67% and 40% of total densities at the head of the bay, Central Channel, combined Eastern/Western Channels and outer bay/shelf respectively (Fig. 1.11 A). On average it comprised less than 10% of the total density at the shelf edge. The outer bay/shelf is also dominated by *P. steenstrupi*, which comprises an average of 22.5% of total densities (Fig. 1.11 A). Dorvilleidae spp.

attained their highest density in the inner bay (channel sites) whereas capitellid polychaetes densities were highest at the head (6% of total density) of the bay and at the shelf edge (6.5% of total density), (Fig. 1.11 A and B). At the head of the bay, the polychaete *P. granulata* was important, comprising 25% of total densities (Fig. 1.11 A).

1.3.4 *Discriminant Function Analysis:*

Discriminant function analysis, conducted on the above site groupings, found the same taxa to be important in describing the observed patterns, however, it also identified forty others as being important. Of these, five polychaetes including *Chaetozone setosa*, *N. neotena*, *A. quadrilobata*, *Terebellides stroemi*, and an unidentified Paraonid along with several nemerteans and the bivalve, *Thyasira* sp., were relatively abundant (species with densities ≥5% of the total density at any one site), (Fig. 1.11 B). Nemertea spp. and *Thyasira* sp. were important in the Central Channel, where densities were elevated compared to other areas. No single species dominated at the shelf edge, however, *A. quadrilobata* was unique to this area and the highest densities of Paraonidae sp., *C. setosa* and *T. stroemi* were encountered here. Thirty-three rare taxa (species with densities <5% of total density) were also found to differ between these different sites (Table 1.1). These included 18 polychaetes, 5 gastropods, 4 amphipods, 2 bivalves, 2 echinoderms, tanaids and cumaceans.

1.3.5 *Environmental Data*

On average, total organic carbon present in the sediments ranged between 1.0-8.0% (C·mg^{-1}), (Table 1.2) and a t-test showed that carbon was significantly higher (n=43 , t=7.0, p=<0.001) in sediments within the inner bay ($\bar{x}_{inshore}$=6.6, se=0.22, n=33) compared to the outer bay and shelf ($\bar{x}_{offshore}$=2.0, se=0.61, n=10). C/N ratios remained relatively low and constant in the inner bay ($\bar{x}$=8.8, s.d=0.30, n=33) compared to the outer bay and shelf ($\bar{x}$=8.3, s.d=0.36, n=8), and were much higher at the shelf edge ($\bar{x}$=19.4, s.d=1.42, n=2); (Table 1.2). Grain size analysis indicated that sediment in the inner bay was dominated by clay and very fine to medium silt sized particles, whereas samples collected between the outer bay and shelf edge contained higher amounts of coarse silt to very fine sand (Table 1.2). Mixed layer temperatures were between 9.0–10.1 °C in the inner bay and between 6.0 and 9.2 °C in the outer bay, shelf and shelf edge. Bottom temperatures in the inner bay were low and ranged from –0.32 to -0.81 °C, with the exception of the head of the bay which was 3.43 °C. Outer bay and shelf bottom temperature ranged between -0.41 and -0.66 °C but was much higher at the shelf edge (7.0 °C), (Table 1.3). Chl *a* extractions showed that chlorophyll *a* concentrations were high at the head of the bay (June and August) and in the Western Channel (August) and ranged from 0.23 µg·l^{-1} to 1.2 µg·l^{-1} (Table 1.3). These spatial and temporal patterns in chlorophyll *a* were similar to the distribution observed at the sea surface in SeaWiFS images for the same time period (http, dfomr.mar.dfo-mpo.gc.ca/science/ocean/seawifs/seawifs_1.html).

Spatial pattern in PCA analysis of sampling sites based upon the environmental data showed some similar spatial groupings to those observed in the PCA-H analysis of species data. Factors 1 and 2 account for 50 and 23% of the variance in the data respectively (Fig.1.12 A and B). Factor 1 clearly separates the head and inner bay samples, with positive factor loadings, from outer bay and shelf samples, which have negative factor loadings. Factor 2 separates the shelf edge samples from the outer bay and remaining shelf samples. There is also some evidence that the head of the bay is different from the inner bay samples. Unlike the PCA-H analysis of species data, the center of the bay site groups with the rest of the inner bay and therefore is more similar to the inner bay than the outer bay and shelf in terms of environmental variables. Factor 1 has positive loadings for productivity-related variables (average C/mg, chl *a*, average N/mg), abiotic water column variables (mixed layer temperature) and fine sediment (average clay to very fine to medium silt) and negative loadings for average C/N, medium sediment (average coarse silt to medium sand), abiotic water column variables (average depth, mixed layer and bottom salinity and bottom temperature) and distance from head of bay and shoreline. Factor 2 is heavily weighted positively for bottom temperature and average C/N. Factor loadings are summarised in Table 1.4. Correlation analysis showed that chlorophyll *a* (April, July and August) were significantly correlated positively with sediment organic carbon (Appendix 1.1). Although not significant, sediment organic carbon was negatively correlated with abundance and species richness and positively correlated with diversity. In addition, mixed layer temperature was significantly correlated with both chlorophyll a (April and July) and organic carbon (Appendix 1.1).

Multiple regression analysis showed that all of the overall models developed to predict infaunal denisty, species richness and diversity were significant. Sediment organic carbon was shown to be the most important predictor of infaunal density with a significantly negative relationship (Table 1.6). Sediment organic carbon, mixed layer temperature and salinity were significant predictors of species richness (Table 1.7). Organic carbon was negatively related to species richness. No single environmental variable was important in predicting diversity (Table 1.8).

1.3.6 *Inshore/offshore: Species Diversity and Abundance*

Because multivariate analyses suggested an inshore/offshore difference, where the outer bay was more similar in terms of species composition and environmental variables to the shelf samples, these samples were grouped as offshore, and the inner bay and head of the bay as inshore for diversity comparisons. Although there was some varibility in diversity among inshore and offshore sites a t-test indicated that inshore diversity was significantly less than offshore (Table 1.5). Species richness was found to be significantly higher in the offshore samples than in the inshore (Table 1.5) however, it should be noted that species richness was highly variable within the offshore. Despite some overlap, density was also significantly higher offshore than inshore (Table 1.5). A Mann-Whitney test showed no significant difference in species evenness between the inshore and offshore regions of the bay at the 0.05 level (n=47, inshore mean rank=22.53, offshore mean rank=28.82 , Mann-Whitney U= 145.00 and p=0.183).Although the statistical power of non-parametric tests is weaker than for parametric tests, the result was consistant with a t-test comparison.

1.4 Discussion

1.4.1 *Introduction*

Benthic ecologists have long appreciated the fact that marine sedimentary communitites are patchily distributed (Petersen 1913; Jones 1950). Much research has focused on addressing why this spatial variation exists and what factors are most important in maintaining structure within these communities. Nonetheless, this question is still largely unanswered and remains at the forefront of benthic ecological research. Sedimentary macrofauna play an essential role in the dynamics of marine systems (Mills 1975; Snelgrove 1999), and recent ecological studies have stressed the vital need to understand the dynamic processes structuring these communities (e.g. Osolinish 1990; Snelgrove et al. 1997). This study describes the community structure and spatial distribution of sedimentary macrofauna on muddy substrates in Placentia Bay and the adjacent shelf environment. Specifically it examines how water column and sediment characteristics influence infaunal communities along an inshore/offshore gradient.

1.4.2 *Spatial patterns: Species and Environmental Data*

Cluster analysis of box core samples combined with ordination suggests that changes in community composition may be related to broad-scale differences in the bay's oceanography. Distinguishable communities occur at the head of the bay, Central Channel and on the continental shelf. Sites within the Eastern and Western Channels are generally similar to one another whereas those from the outer bay to the continental shelf are continually changing with increased distance from the inner bay. One of the most interesting observations from these analyses was that the outer bay site is more similar in terms of species composition to the shelf; suggesting an inshore/offshore difference (with the inner bay and head of the bay collectively the inshore and the outer bay and shelf as offshore). However, more sites within the outer bay should to be sampled to be confident that all areas of the outer bay are more similar to the shelf.

1.4.3 *Species Composition and Abundance*

Community analyses showed that species composition patterns varied among different areas of Placentia Bay. *C. longocirrata* and Dorvilleidae spp. were important components of the community structure inshore where they were most abundant. Sediments inshore were primarily composed of clay and high amounts of organic carbon, and studies have found *C. longocirrata* to be typically abundant on muddy to silt substrates in organically enriched areas (Blake and Hilbig 1994; Volckaert 1987). Dorvilleids can be found in all sublittoral environments, including heavily polluted areas (Fauchald and Jumars 1979). Several species of capitellids and *P. steenstrupi* played a greater role offshore where densities were higher and abundance of *C. longocirrata* was reduced. *P. steenstrupi* is a eurybathic species and is one of the numerically dominant polychaetes found on the Grand Banks (Hutcheson et al. 1981) east of Newfoundland and in Nain Bay, Labrador (Bousfield 1981). *P. granulata* was a dominant member of the infaunal community at the shallow site at the head of the bay, where sediments contained elevated amounts of fine sand compared to other inshore sites. *P. granulata* is usually found on sandy substrates at shallow to sublittoral depths. Abundances of this species were highly variable in this area and a large proportion of juveniles in the early stages of tube building were present. *P. granulata* displays remarkable selectivity in grain size when tube building (Pocklington, unpublished) and high variability in fine sand deposits at this site may explain variability in abundance.

Grain size offshore consisted of a larger proportion of coarse silt to medium sand. Seven polychaete species were shared between the head of the bay and the offshore, which are both areas with coarse sediments and all of these species including *S. armiger*, *P. plumosa* (Hughes et al. 1972), *Spio filicornis* (Appy et al. 1980), *Syllides longocirrata*, *G. maculata* (Pocklington, unpublished) are usually found on coarse sediments. Snelgrove and Butman (1994) have argued that sediment grain size may often be a surrogate for correlated variables such as larval supply. In this system, however, discontinuity in benthic pattern with larval supply (the complete absence or single occurrence of the above species from the inner bay sites with finer sediments even though they are present at the head of the bay as well as offshore where sediments are coarser) suggests that grain size or organic content is important.

A. quadrilobata was only found at the shelf edge where bottom temperature was higher than any other area, which is most likely a result of intrusion of Gulf Stream water. Sediments also contained the largest proportion of fine sand. *A. quadrilobata* typically inhabits muddy sand, and Placentia Bay is towards its most northern limit. The highest densities of *C. setosa*, *T. stroemi* and an unidentified paraonid species were also found at the shelf edge.

The communities within Placentia Bay were very different from that found by Kennedy et al. (1985) and Scheibe (unpublished thesis) in nearby Conception Bay, Newfoundland, even though both bays contained polychaete dominated assemblages with species characteristic of coastal areas in eastern Canada. In shallow areas (62-75 m) predominantly composed of silt, Kennedy found *Maldane sarsi* to be the most abundant polychaete, making up 55% of all annelids collected. *M. sarsi* builds tubes of mud and silt and has been encountered at great depths on the Newfoundland slope and rise (Pocklington, unpublished data). In Placentia Bay, *M. sarsi* was not encountered and species assemblages were dominated by *C. longocirrata* (63% of polychaetes), which was not encountered in Kennedy's study. *C. longocirrata* is a burrower common in deep slope and abyssal muds (Appy et al. 1980), although it is also known from organic rich areas as discussed earlier. *N. punctata* (5% of polychaetes), *Nephtys incisa* (4% of polychaetes) and *G. maculata* (4% of polychaetes) were found to be the next most abundant and relatively widespread species in Conception Bay and of these, only *N. punctata* was among the dominant taxa in Placentia Bay. At areas of similar depth and substrate type as Placentia Bay, Scheibe (1991) found *M. sarsi*, *P. steenstrupi*, *Lumbrineris latreilli*, *Spiophanes wigleyi*, *C. setosa*, *E. longa*, *Yoldia hyperborea* to be among the four most dominant species at any one site. *M. sarsi*, *S. wigleyi*, and *N. incisa* were not sampled in Placentia Bay and although the others were present, only *C. setosa* was among the dominants; other species accounted for less than 1% of the total infauna. Moreover, *C. longocirrata* was $\leq 0.8\%$ of total infaunal abundance.

It is likely that high amounts of organic carbon within Placentia Bay sediments ($\bar{x}_{inshore}=6.5\%$) play a role in influencing the macrofaunal assemblages. Many of the common species in Placentia Bay are typically abundant in organic rich areas. For example, Rygg (1985) showed *C. longocirrata* and *C. setosa* in Norwegian fjords to be very tolerant to pollution. *C. setosa* was also found to occur along a pollution gradient in organically enriched Oslofjord (Mira and Gray 1981) and *P. steenstrupi* occurred in relatively high numbers after pollution abatement on the Atlantic coast of Nova Scotia–Canso Strait (Pocklington, unpublished). *N. neotena* was the dominant species found in the Miramichi River where the sediments contained a high amount of wood pulp and was also present in the Bay of Chaleur (Belledune Harbor) at an area previously used as a dump site (Pocklington, unpublished). It is important to note that such findings are not limited to pollution studies. In St. Margaret's Bay, Nova Scotia (Volchaert 1987), where organic-carbon content in sediments rivalled those of Placentia Bay ($\bar{x}=4.1$), *C. longocirrata* was the most abundant species present and *A. neotenus*, *A. quadrilobata*, *E. incolor*, *P. steenstrupi* were among the numerically dominant species. In a Spitsbergen fjord, Kendall (1994) found *C. longocirrata* and *C. setosa* to be among the characteristic species found at a shallow site that appeared to be influenced by seasonal sediment deposition from an adjacent stream. High amounts of organic carbon in Placentia Bay sediments may be a result of high rates of sedimentation or slowed degradation of organic material due to cold temperatures (Pomeroy and Deibel 1986), and low oxygen concentrations below the first few centimetres of sediment (discussed below). In contrast, organic carbon in Conception Bay was much lower ($\bar{x}$=1.7 %: Kennedy 1985) than in Placentia Bay, and of the three dominant taxa in Conception Bay that were not encountered in Placentia Bay, *M. sarsi* and *N. incisa* have been described as sensitive or non–tolerant to organic pollution (Mirza and Gray 1981: *M.sarsi*; Pearson et al. 1983: *N. incisa*). Although Placentia Bay and Conception Bay differ in terms of oceanographic influences (i.e., the amount of influence each receives from the Labrador Current and Gulf Stream), broad-scale oceanography is unlikely to be important in this case because both of these species are commonly found around the coast of Nova Scotia as well as north of Conception Bay to the eastern Arctic.

1.4.4 *Species Richness, Evenness and Diversity*

Areas with highest levels of surface chlorophyll in Placentia Bay were also shown to contain correspondingly high amounts of sedimentary organic carbon, namely the head of the bay (June and August) and the inshore compared to offshore. The inshore contained significantly higher amounts of sedimentary carbon and species richness and diversity were generally lower. Low levels of diversity inshore were largely due to the dominance of the polychaete *C. longocirrata*, which far outnumbered any other taxon. Certain polychaetes are noted for their opportunistic response to organic enrichment in shallow waters where they are more numerous and dominate the community (Pearson and Rosenberg 1978; Levin et al. 1996), and *C. longocirrata* has been described by Olsgard and Hasle (1993) as a typical opportunistic species. On the continental slope off Cape Hatteras, where there is an unusually high influx of organic carbon, a similar situation occurred. Infaunal assemblages were found to be strikingly different from other locations along the U.S. Atlantic coast (Blake and Hilbig 1994), *C. longocirrata* was one of the dominant species, and infaunal assemblages were characterized by lower species richness, and diversity (Blake et al. 1987; Blake and Grassle 1994). Although organic carbon peaked at the head of Placentia Bay, species richness was similar throughout the inshore. One explanation for this similarity is that variation in organic carbon between the head of the bay and the remainder of the inshore sites may not have been great enough to cause variation in species richness. However, lower density of *C. longocirrata* at the head of the bay resulted in higher species evenness and greater diversity.

Species richness and diversity are often compared between different studies to examine community structure in different areas and environments. However, such measures can be influenced by a variety of artificially imposed factors such as the type of sampling gear, sampling effort and the degree of taxonomic resolution, which limits their usefulness and should be interpreted with caution. For example, Stewart et al. (1985) found macrofaunal diversity at most sampling stations in the Canadian eastern arctic had a moderate Shannon-Wiener diversity ranging from 3.65 to 4.96 whereas in Placentia Bay diversity at most sites ranged from 1.31 to 2.48. In the arctic study, up to ten Van Veen Grab samples ($0.1m^{-2}$) were collected at each station and samples were sieved through a 0.42 mm screen. It is very difficult to determine how much of this variation in diversity is due to differences in sampling and processing procedures or if the arctic generally does have a higher diversity of macrofauna than Placentia Bay. In the Gulf of St. Lawrence, Long and Lewis (1985) found diversity to be very low ranging from 0.75 to 1.29, however, in their study Shannon-Wiener diversity was calculated at the family level which may help explain why diversity was so low and prevents valid comparisons with other studies where this calculation is done at the species level.

1.4.5 *Infaunal Density*

There is evidence in support of a deeper living fauna offshore, where significantly more organisms were found in the 3-10 cm core portion compared to inshore. This may be a result of reduced oxygen concentrations below the first few centimetres of sediment of inshore cores. Sedimentary organic carbon content inshore was very high, ranging on average from 4.8 to 9.1%. Valderhaug and Gray (1984) reported that relatively high values of 4.0% were typical for areas receiving high sewage input into an enclosed area. High organic-carbon in sediments has been associated with reduced pore-water oxygen content (Levin and Gage 1998) and oxygen deficiency, which can result in accumulation of hydrogen sulfide as a result of intense degradation of organic carbon. Both of these variables can limit the abundance and biomass of macrofaunal communities (Lopez-Jumar 1981; Levin et al 1991). Several observations suggest that low pore water oxygen was an important factor in Placentia Bay. Inshore cores smelled strongly of hydrogen sulphide and were noticeably black directly below the top 2.5-3.0 cm of sediment, however, blackness was not encountered until much deeper in the offshore cores.

Despite the presence of hydrogen sulfide at depth in cores, macrofaunal densities inshore (2717 to 12,600 individuals·m^{-2}) were high compared to other muddy, coastal areas at similar depths. Long and Lewis (1987) found macrofaunal densities in the Gulf of St. Lawrence to be very low, ranging between 330 individuals·m^{-2} and 3425 individuals·m^{-2} and densities were 20 to 37 times higher in Placentia Bay compared to those found in nearby Conception Bay (100μm sieve: 134.8 to 337.6 individuals·m^{-2}), (Schiebe, unpublished thesis). In contrast, density in Nain Bay, Labrador was 11,200 individuals·m^{-2} (see Mills 1975), which corresponds to some of the higher densities observed in Placentia Bay. High densities of macrofauna in Placentia Bay were not unexpected, given that Placentia Bay is known to be a relatively productive area. Low C/N ratios ($\bar{x}$=8.9) for this area indicate that relatively fresh (Banse 1974) and easily degradable (Parsons et al. 1977) organic material from the plankton reaches the benthos; C/N ratios have been commonly used in studies to indicate food quality in the benthic environment (Mills 1975; Grebmeier et al. 1988; Levin et al. 1991). Much higher ratios (e.g. values between 14 and 30) are expected for lower quality refractory or terrestrial sources (Godell 1972). Freshwater sources entering Placentia Bay are small, and supply of allochthonous particulate material is likely of little influence, however, there was some evidence of terrestrial debris at the head of the bay (discussed in greater detail in Chapter 2). Low C/N ratios, along with the observation that areas with highest levels of surface chlorophyll also were shown to have correspondingly high amounts of sedimentary organic-carbon, suggests that water column productivity is received on the bottom (e.g. Ambrose and Renaud 1995), and not advected out of the bay before it reaches the bottom.

Surface chlorophyll concentrations were also found to be significantly correlated with organic carbon in the sediments. Within the inshore, surface production (chl *a*) was greatest at the head of the bay where sedimentary organic carbon content also peaked. Surface production (chl *a*) and organic carbon were also greater inshore than offshore.

A number of studies, typically at larger scales than Placentia Bay study, have linked surface production to benthic biomass and or abundance (Grebmieir et al. 1988; Ambrose and Renaud 1995). A positive relationship has been found between benthic biomass/abundance and surface production (chl *a*), (Ambrose and Renaud 1995). However, when all areas Placentia Bay were considered, a negative relationship was found between surface chlorophyll and abundance. A significantly negative relationship was also found between organic carbon and abundance, and organic carbon was shown to be the most important predictor of infaunal abundance. Abundance was significantly higher in the less productive offshore and within the inshore some of the lowest densities were found at the head of the bay. Ambrose and Renaud (1995) noted some decoupling of surface production and benthic biomass in the Southern Trough of Greenlands' Northeast Water Polynya, where no relationship was found between water column and benthic pigment concentrations (chl *a* and phaeopigments) and benthic biomass/density was lower than in areas where a positive relationship existed between these variables. This decoupling was attributed to zooplankton grazing. Decoupling was probably not the mechanism in Placentia Bay because areas with highest levels of surface chlorophyll were also shown to have correspondingly high amounts of relatively fresh sedimentary organic-carbon, and this relationship was statistically significant.

The negative relationship found between surface production and infaunal abundance in Placentia Bay is likely a result of two confounding factors. Within the inshore, relatively low densities at three sites greatly reduced mean density. Organic carbon was higher at these sites and low densities may be a result of lower oxygen concentrations within the first few centimetres of sediment or poorer food quality (variation inshore will be discussed in detail in chapter 2). Densities at one site in the outer bay, located near Oderin Bank, were much greater than at any other site, which greatly increased mean density offshore. Oderin Bank is known to be a relatively productive area with considerable upwelling. Upwelling areas have been associated with high macrofaunal abundance (Levin and Gage 1998), except when hypoxia confounds the pattern (Sanders 1969; Levin et al. 1997). When the three sites with similar low density inshore and the site at Oderin Bank were removed, mean density inshore ($\bar{x}$=518 individuals·400cm^{-2}) was greater than offshore ($\bar{x}$=354 individuals·400cm^{-2}), supporting a positive relationship between surface production and abundance.

1.5 Summary

Spatial patterns of community composition and environmental variation indicate that Placentia Bay can be broadly divided into an inshore and offshore region. The head of the bay and continental shelf were distinct, inner bay sites were generally similar, whereas offshore sites were highly variable. Greater mixed layer temperatures, higher surface production (chl *a*), and large amounts of relatively fresh organic carbon characterized the inshore portion of the bay. High levels of organic carbon inshore influenced the macrofaunal assemblages, and many of the common species are known to be abundant in organic rich areas elsewhere, corresponding to somewhat reduced species richness, and diversity. Generally speaking, high amounts of organic carbon in Placentia Bay sediments may be a result of high rates of sedimentation or slowed degradation of organic material resulting from cold temperatures and potentially low oxygen concentrations below the first few centimetres of sediment. Low diversity was caused by dominance of *C. longocirrata*, an opportunistic species capable of establishing high densities in sediments with high amounts of organic carbon. Offshore, lower organic carbon corresponded to somewhat greater species richness, and diversity and reduced densities of *C. longocirrata*.

Different variables appear to opperate at different scales. At smaller scales (e.g. head of the bay and within the offshore), grain size was particularly important even though areas of high surface production (chl *a*) had correspondingly elevated amounts of organic carbon. It is likely that variation in organic carbon between the head of the bay and the remainder of the inshore sites may not have been great enough to cause variation in species richness. In terms of abundance patterns, some of the lowest densities were found at the head of the bay, and significantly higher densities were found in the less productive offshore. This pattern suggested a negative relationship between surface production and abundance. Most benthic pelagic coupling studies have found a positive relationship between benthic abundance and biomass and enhanced flux of organic carbon to the sea bed (Davies and Payne 1984; Elmgren 1978; Ambrose and Renaud 1995) and closer inspection revealed that this negative relationship was likely confounded by low abundance patterns at three sites within the inshore (discussed in chapter 2), along with elevated densities offshore at Oderin Bank. In conclusion broad-scale patterns (inshore vs offshore) of community composition and abundance in Placentia Bay are largely influenced by surface oceanography as seen by the importance of surface water characteristics and sedimentary carbon (which tracts surface production).

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Table 1.1. Results of discriminant function analysis. Rare species with densities <5% at any of the site groupings presented as present (+) or absent (–). Groupings based on those obtained in PCA-H analysis

Taxa	**Head**	**Central Channel**	**Eastern & Western Channels**	**Outer & Shelf**	**Shelf edge**
Polychaeta					
Syllides longocirrata	+	-	+	-	+
Maldane glebifex	+	+	-	+	-
Spio filicornis	+	-	-	-	+
Pherusa plumosa	+	-	+	+	+
Lumbrineris spp.	+	+	+	+	+
Pholoë longa	+	-	+	+	-
Euchone incolor	+	-	+	+	+
Scoloplos armiger	+	+	-	-	+
Brada villosa	+	-	+	+	+
Ampharete acutifrons	-	-	-	+	-
Diplocirrus sp.	-	-	-	-	+
Tharyx sp. *A*	-	-	-	+	+
Polydora sp.	-	-	-	+	-
Goniada maculata	+	-	-	+	+
Apistobranchus typicus	-	-	+	+	+
Lysilla loveni	-	+	+	-	-
Filibranchus roseus	-	-	-	-	+
Terebellides spp.	-	-	-	-	+
Gastropoda					
Retusa obtusa	+	+	+	+	+
Propebela rugulata	-	-	-	+	-
Naticidae	-	-	-	-	+
Curitotoma sp.	-	-	-	-	+
Frigidoalvania pelagica	+	-	+	+	+
Amphipoda					
Bathymedon sp.	+	+	+	+	+
Monoculodes sp.	+	-	-	-	-
Byblis gaimardi	+	-	-	+	-
Hippomedon sp.	+	+	-	+	+
Bivalvia					
Nuculana pernula	-	+	+	+	-
Yoldia sp.	+	-	+	+	+
Echinodermata					
Brisaster fragilis	-	-	-	-	+
Synapitidae	-	-	-	-	+
Tanaidacea	+	+	-	+	+
Cumacean	+	+	+	+	+

Table 1.2. Summary of site location, depth, sediment related variables and grain size with 95% confidence intervals.

Site	Location	Depth (m)	n	%C/mg	%N/mg	C/N	n	% clay (<3.9-0 µm)	% m-f - silt (31-3.9 µm)	% coarse-silt (<62.5-31 µm)	% vf-sand (<125-62.5 µm)	% fine sand (<250-125 µm)	% m-sand (>350-250 µm)
Head (H)	47° 45.26′ 54° 14.07′	67±3.7 n=6	3	8.07 ±0.6	1.33 ±0.2	8.51 ±0.2	6	36.0 ±5.6	45.0 ±8.9	11.0 ±1.2	3.9 ±2.3	3.9 ±4.8	0.24 ±0.5
Central C)	47° 34.82′ 54° 7.48′	210±5.1 n=6	3	6.57 ±0.3	0.91 ±0.1	9.11 ±0.1	6	38.4 ±9.0	48.3 ±9.0	10.4 ±6.3	1.6 ±0.5	1.0 ±.0.2	0.16 ±0.2
West (W_1)	47° 38.69′ 54° 15.96′	214±2.1 n=6	3	7.82 ±0.1	1.15 ±0.1	8.79 ±0.1	6	55.0 ±16.8	41.6 ±6.8	0.50 ±0.4	1.3 ±1.2	1.2 ±0.9	0.27 ±0.5
West (W_2)	47° 26.89′ 54° 19.79′	283±11.7 n=6	3	5.31 ±0.3	0.64 ±0.1	9.05 ±0.2	5	41.0 ±7.6	47.4 ±7.6	8.2 ±2.9	2.6 ±1.0	0.86 ±0.7	0.0 ±0.0
East (E_1)	47° 44.85′ 54° 3.81′	225±6.7 n=6	3	6.15 ±0.2	0.77 ±0.1	8.60 ±0.2	5	33.8 ±16.6	60.4 ±13.9	3.3 ±3.8	1.3 ±1.0	0.91 ±0.9	0.0 ±0.0
East (E_2)	47° 33.80′ 54° 2.57′	217±6.5 n=6	3	4.83 ±0.4	0.61 ±0.1	9.23 ±0.4	5	45.2 ±4.6	46.7 ±4.2	5.4 ±1.1	1.6 ±1.2	1.1 ±1.9	0.0 ±0.0
Outer (O)	47° 10.8′ 54° 22.4′	230±0.0 n=3	3	1.26 ±023	0.15 ±0.04	8.26 ±0.57	3	11.6 ±2.7	23.5 ±3.5	43.3 ±5.7	21.1 ±2.7	0.42 ±0.2	0.06 ±0.1
Shelf (S_1)	47° 43.5′ 54° 47.8′	229±6.9 n=2	2	2.70 ±0.0	0.33 ±0.0	8.00 ±0.3	2	25.7 ±4.0	41.8 ±2.9	24.6 ±1.3	7.7 ±8.4	0.20 ±0.1	0.0 ±0.0
Shelf (S_2)	46° 13.5′ 54° 50.4′	184±0.0 n=3	3	0.91 ±0.1	0.14 ±0.0	8.42 ±0.2	3	6.8 ±1.9	12.4 ±1.9	19.1 ±3.0	24.1 ±6.8	18.2 ±13.2	19.4 ±14.1
Shelf edge (S_3)	45° 5.0′ 54° 48.7′	231±11.8 n=3	3	5.27 ±0.1	0.23 ±0.5	19.44 ±2.0	2	27.7 ±0.9	22.7 ±2.9	5.4 ±2.0	11.3 ±1.6	32.5 ±1.7	0.46 ±0.3

Table 1.3. Summary of site environmental variables with 95% confidence intervals for mixed layer temperature, bottom temperature, mixed layer salinity and bottom salinity where applicable.

Site	**Distance shore (m)**	**Distance head (m)**	**Mixed Temp. (°C) n=2**	**Bottom Temp. (°C) n=2**	**Mixed Salinity (‰) n=2**	**Bottom Salinity (‰) n=2**	**Chl *a* April (µg/l)**	**Chl *a* June (µg/l)**	**Chl *a* July (µg/l)**	**Chl *a* August (µg/l)**	**Chl *a* Sept. (µg/l)**
Head (H)	600	12000	9.4	3.4	31.8	32.2	10	0.46	1.00	0.76	1.62
Central C)	1000	26000	8.5	-0.3	32.0	32.7	10	0.25	1.00	0.39	1.56
West (W_1)	4000	23000	9.7	-0.3	31.9	32.7	10	0.35	1.00	0.64	1.68
West (W_2)	1000	45000	9.2	-0.8	31.9	32.8	10	0.26	1.00	0.26	1.02
East (E_1)	2500	8000	10.1	-0.7	31.8	32.8	10	1.28	1.00	0.23	1.57
East (E_2)	3000	29000	9.1	-0.6	31.9	32.8	10	0.37	1.00	0.58	1.66
Outer (O)	23000	74000	6.9	-0.7	32.1	32.9	8	0.13	0.65	0.23	1.75
Shelf (S_1)	42000	132000	6.0±0.0	-0.4±0.0	32.2±0.0	33.0±0.0	1	0.19	0.65	0.01	1.00
Shelf (S_2)	85000	186000	6.4±0.0	-0.5±0.0	32.4±0.0	33.0±0.0	7	0.10	0.65	0.01	1.00
Shelf edge (S_3)	200000	316000	9.2	7.0	32.8	32.8	10	0.10	0.65	0.01	1.00

Table 1.4. Factor loadings for the PCA of environmental variables. Heavily weighted loadings (+/- 0.70) are shown in bold.

Variable	Factors	
Productivity-related variables	**1**	**2**
C/mg (percent/site)	**.815**	.531
chl *a* april (chlorophyll *a* April (μg/l))	.558	.449
chl *a* june (chlorophyll *a* June(μg/l))	.587	-.024
chl *a* july (chlorophyll *a* July(μg/l))	**.955**	.064
chl *a* aug (chlorophyll *a* August(μg/l))	**.842**	.015
chl *a* sept (chlorophyll *a* September(μg/l))	.656	-.284
N/mg (percent/site)	**.907**	.166
C/N (carbon/nitrogen mg)	-.213	**.947**
Grain size (%)		
m-sand (medium sand >350-250 μm)	-.565	-.112
f-sand (fine sand <250-125μm)	-.639	**.737**
v-fine sand (very fine sand <125-62.5 μm)	**-.858**	-.234
c-silt (coarse silt <62.5-31 μm)	-.554	-.651
v-f-med silt (very fine to medium silt <31– 3.9 μm)	**.853**	-.075
clay (<3.9-0 μm)	**.829**	.287
Abiotic water column		
depth (depth/site)	-.242	-.133
temp ML (mixed layer temperature °C)	**.753**	.548
temp BT (bottom temperature °C)	-.217	**.868**
salinity ML (mixed layer salinity ‰)	**-.862**	.487
salinity BT (bottom salinity ‰)	-.677	-.377
Distance		
distance shore (distance from shoreline m)	**-.742**	.655
distance head bay (distance from head of bay m)	**-.851**	.516

Table 1.5. T-tests for differences in diversity, species richness, and abundance between the inshore and offshore regions of Placentia Bay (∝=0.05 & * indicates a significant difference).

Biotic Variables	**Inshore n=36**		**Offshore n=11**		**T-tests n=47**	
	$\bar{x}$	se	$\bar{x}$	se	t	p value
Diversity H'	1.76	0.10	2.39	0.16	3.06	*0.004
Species Richness	24.17	0.90	38.73	3.18	6.15	*0.001
Abundance (#/m^{-2})	282.19	33.38	451.00	63.63	2.42	*0.020

Table 1.6. Multiple regression of environmental variables with density (#/m^{-2}). The overall model is significant (p=0.009) with df(total)=18 and F=3.99. Environmental variable(s) that contributed significantly to the model are shown in bold.

Environmental Variables	**Standardized Regression Coefficients**	**p-values**
V-f-med-silt	0.176	0.599
Depth	0.727	0.188
Salinity ML	0.921	0.686
Temperature ML	0.909	0.109
Temperature BT	-0.798	0.359
Salinity BT	-1.494	0.221
Distance fr. headbay	-0.160	0.934
Chlorophyll *a* June	-0.146	0.662
% C/mg	-1.770	**0.005**

Table 1.7. Multiple regression of environmental variables with species richness. The overall model is significant (p=0.001) with df(total)=18 and F=6.43. Environmental variable(s) that contributed significantly to the model are shown in bold.

Environmental Variables	**Standardized Regression Coefficients**	**p-values**
V-f-med-silt	0.032	0.907
Depth	-1.590	0.558
Salinity ML	0.265	**0.027**
Temperature ML	1.319	**0.010**
Temperature BT	4.587	0.064
Salinity BT	-1.412	0.065
Distance fr. headbay	-1.949	0.131
Chlorophyll *a* June	-2.517	0.847
% C/mg	0.054	**0.003**

Table 1.8. Multiple regression of environmental variables with diversity H'. The overall model was significant (p=0.021) with df(total)=18 and F=3.25. None of the environmental variables contributed significantly to the model.

Environmental Variables	**Standardized Regression Coefficients**	**p-values**
V-f-med-silt	-0.369	0.311
Depth	0.316	0.593
Salinity ML	-.070	0.903
Temperature ML	0.065	0.910
Temperature BT	1.740	0.480
Salinity BT	-0.600	0.518
Distance fr. headbay	-0.873	0.498
Chlorophyll *a* June	-0.531	0.797
% C/mg	-0.065	0.855

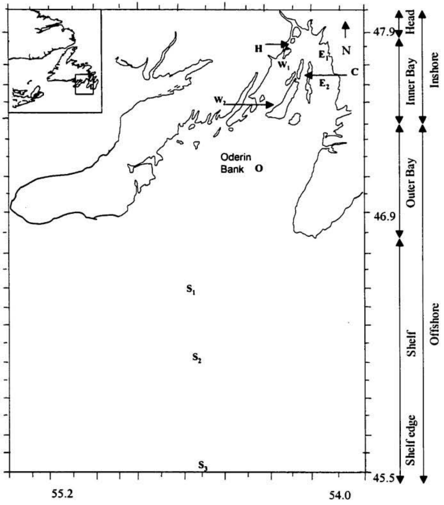

Figure 1.1. Chart of Placentia Bay and location of sampling sites. Capital letters indicate sampling sites. H denotes head of bay, C denotes Central Channel, E_1 and E_2 are upper and lower Eastern Channel, W_1 and W_2 are Western Channel, O is outer bay, S_1 and S_2 are shelf, and S_3 is the edge of the shelf. Arrows on the right indicate different parts of the bay including the head, and inner bay (collectively the inshore), and the outer bay and shelf (collectively the offshore). Inset shows Placentia Bay in relation to Newfoundland.

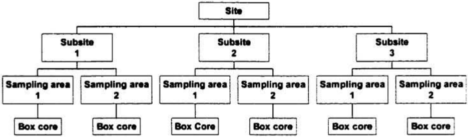

Figure 1.2. Nested hierarchical sampling design where a series of successively smaller spatial scales is nested within the scale above: distance between-site locations (10's to 100's of km), radial distance between subsites ≤500 m, and radial distance between sampling areas ≤100 m.

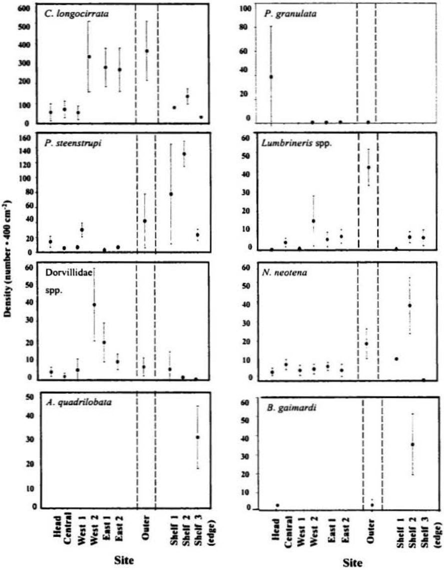

Figure 1.3. A. Plot showing mean densities and 95% confidence intervals of dominant taxa, with n=6 (Head, Central, West 1, West 2, East 1, and East 2); n=2 (Shelf 1) and n=3 (Outer, Shelf 2 and Shelf 3). Note, scale on y-axis differs among taxa.

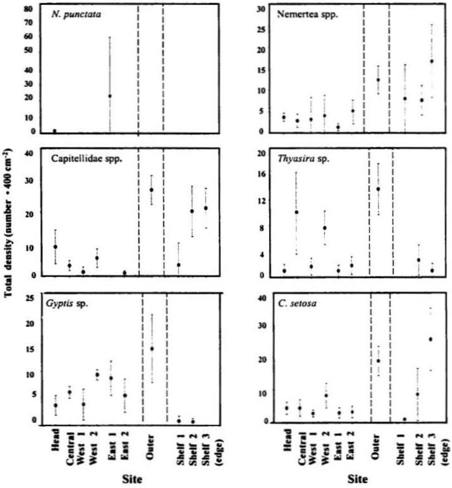
Total density (number • 400 cm^{-2})
N. punctata
80
70
60
50
40
30
20
10
0
Nemertea spp.
30
25
20
15
10
5
0
Capitellidae spp.
40
30
20
10
0
Thyasira sp.
20
16
12
8
4
0
Gyptis sp.
25
20
15
10
5
0
C. setosa
40
30
20
10
0
Head
Central
West 1
West 2
East 1
East 2
Outer
Shelf 1
Shelf 2
Shelf 3
(edge)
Site
Head
Central
West 1
West 2
East 1
East 2
Outer
Shelf 1
Shelf 2
Shelf 3
(edge)
Site

Figure 1.3. B.

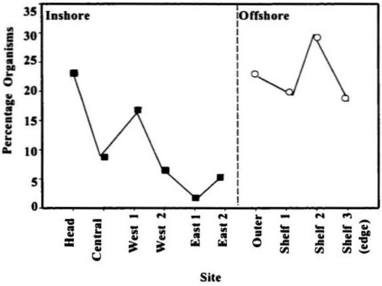

Figure 1.4. Percentage of organisms in the 3-10 core portion from samples collected inshore (head and inner bay, with n=36) compared to offshore (outer bay and shelf, with n=11).

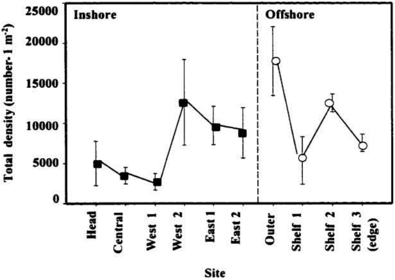

Figure 1.5. Plot showing means and 95% confidence intervals for total density of macrofauna at each site, with n=6 (Head, Central, West 1, West 2, East 1, and East 2); n=2 (Shelf 1) and n=3 (Outer, Shelf 2 and Shelf 3).

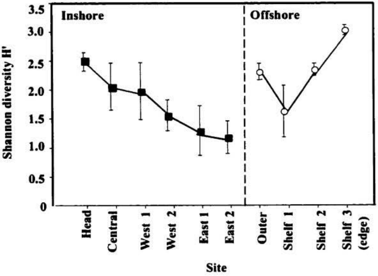

Figure 1.6. Plot showing means and 95% confidence intervals for Shannon diversity at each site, with n=6 (Head, Central, West 1, West 2, East 1, and East 2); n=2 (Shelf 1) and n=3 (Outer, Shelf 2 and Shelf 3).

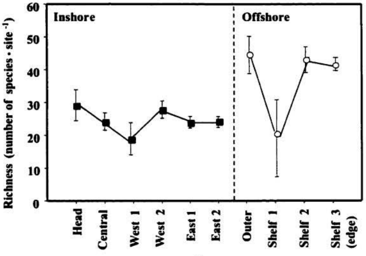

Figure 1.7. Plot showing means and 95% confidence intervals for the species richness present at each site, with n=6 (Head, Central, West 1, West 2, East 1, and East 2); n=2 (Shelf 1) and n=3 (Outer, Shelf 2 and Shelf 3).

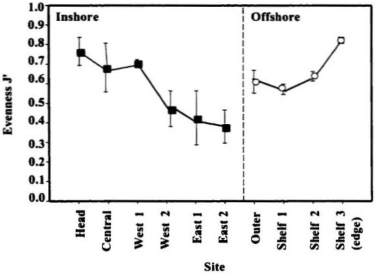

Figure 1.8. Plot showing means and 95% confidence intervals for species evenness at each site. A value of 1.0 indicates the same number of individuals for each species are present, with n=6 (Head, Central, West 1, West 2, East 1, and East 2); n=2 (Shelf 1) and n=3 (Outer, Shelf 2 and Shelf 3).

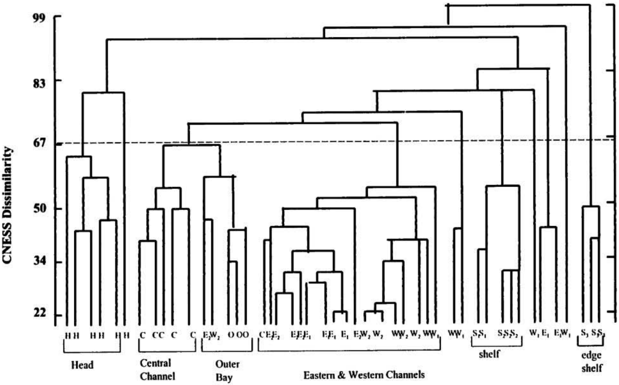

Figure 1.9. Cluster analysis of the10 site (47 box core samples) by 118 species matrix based on CNESS dissimilarity. Capital letters stand for sites sampled. H (head bay), E_1 and E_2 (upper and lower Eastern Channel), W_1 and W_2 (upper and lower Western Channel), C (Central Channel), S_1 and S_2 (shelf), and S_3 (edge of shelf).

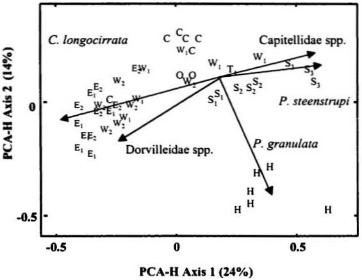

Figure 1.10. PCA-H metric scaling ordination in two dimensions of box core spatial patterns based on CNESS (NESSm = 10 individuals). The first two axes explain 24% and 14% of the variance in the data respectively. Species vectors (Gabriel Euclidean distance biplot) have been overlaid on community ordination to show which species contribute to CNESS variation among samples and therefore drive spatial patterns.

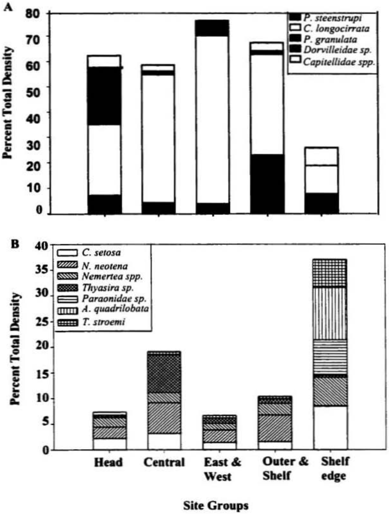

Figure 1.11 Stacked bar graphs showing the percentage of total individuals contributed by each species to the site groupings. A. Includes species that were identified as important by Gabriel biplots. B. Additional species designated as important by discriminant function analysis. Site groupings conform to those obtained from the PCA-H analysis and only those species making up at least 5% of the total density at any one site are included. Proportions were determined by pooling the replicates with each grouping. Note that scales on the y-axis differ for A and B.

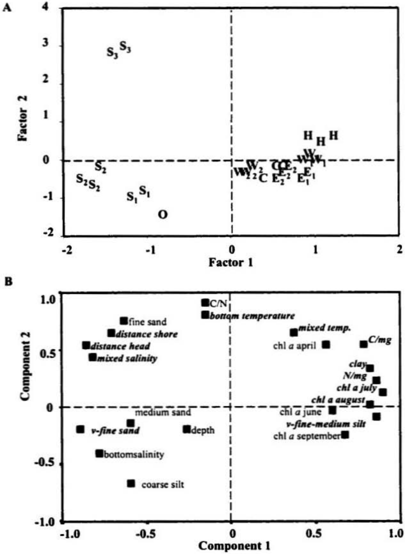

Figure 1.12 A and B.. Plotted factor loadings for the PCA of environmental variables (A) Heavily weighted loadings (+/- 0.70) are shown in bold and italics in the bottom figure.

Appendix 1.1

Correlation matrix of environmental variables and dominant biotic variables. Significant correlations are shown in bold and are significant at 0.0002 using the Dunn-Šidák method (Ury, 1976).

	C/mg									
N/mg	.883 **<.0001**	N/mg								
v-f-sand	-.821 **<.0001**	-.692 **<.0001**	v-f-sand							
m- sand	-.581 .002	-.424 .035	.664 **<.0001**	m-sand						
c-silt	-.711 **<.0001**	-.515 .008	.630 .001	.204 .328	c-silt					
v-f-m- silt	.629 .001	.531 .006	-.790 **<.0001**	-.579 .002	-.455 .022	v-f-m-silt				
Clay	.766 **<.0001**	.692 **<.0001**	-.796 **<.0001**	-.563 .003	-.641 .001	.394 .051	Clay			
Depth	-.241 .245	-.472 .017	-.073 .730	-.127 .544	-.050 .811	.060 .775	-.241 .245	Depth		
Sal-ML	-.547 .005	-.702 **<.0001**	.641 .001	.393 .052	.241 .246	-.701 **<.0001**	-.547 .005	-.702 **<.0001**	Sal-ML	
Temp ML	.851 **<.0001**	.651 **<.0001**	-.725 **<.0001**	-.534 .006	-.756 **<.0001**	.600 .002	.851 **<.0001**	.651 **<.0001**	-.499 .011	Temp ML
Temp BT	.243 .241	.058 .784	.051 .810	-.140 .503	-.164 .433	-.223 .283	.243 .241	.058 .784	.526 .007	.244 .240
Sal-BT	-.748 **<.0001**	-.825 **<.0001**	.459 .021	.352 .084	.335 .102	-.336 .101	-.748 **<.0001**	-.825 **<.0001**	.467 .018	-.603 .001
N-shore	-.400 .048	-.610 .001	.544 .005	.307 .135	.087 .678	-.622 .001	-.449 .024	.107 .611	.969 **<.0001**	-.287 .165
Headbay	-.550 .004	-.713 **<.0001**	.633 .001	.388 .055	.210 .313	-.688 **<.0001**	-.524 .007	.169 .419	.994 **<.0001**	-.462 .020
Chl *a* June	.392 .052	.350 .087	-.433 .031	-.267 .197	-.357 .080	.688 **<.0001**	.121 .565	-.122 .561	-.544 .005	.562 .003
Chl *a* Aug	.755 **<.0001**	.868 **<.0001**	-.602 .001	-.396 .050	-.406 .044	.424 .035	.676 **<.0001**	-.503 .010	-.740 **<.0001**	.622 .001
Chl *a* Sept	.582 .002	.658 **<.0001**	-.475 .016	-.394 .051	-.185 .376	.437 .029	.457 .022	-.351 .085	-.692 **<.0001**	.518 .008
Chl *a* April	.656 **<.0001**	.502 .011	-.444 .026	-.280 .176	-.592 .002	.307 .135	.473 .017	-.068 .747	-.379 .062	.856 **<.0001**
Chl *a* July	.804 **<.0001**	.797 **<.0001**	-.811 **<.0001**	-.469 .018	-.621 .001	.735 **<.0001**	.729 **<.0001**	-.097 .646	-.867 **<.0001**	.788 **<.0001**
Richness	-.542 .005	-.568 .003	.759 **<.0001**	.579 .002	.331 .106	-.699 **<.0001**	.660 **<.0001**	-.045 .832	.677 **<.0001**	-.334 .102
Abundance	-.611 .001	-.568 .003	.455 .022	.338 .099	.259 .212	-.303 .141	-.388 .056	.453 .023	.226 .227	-.290 .159
Diversity H'	.028 .893	-.013 .950	.392 .053	.232 .264	.156 .456	-.517 .008	-.247 .234	-.417 .038	.496 .012	-.091 .666
Evenness	.202 .332	.183 .380	.200 .338	.090 .669	.092 .662	-.361 .076	-.069 .713	-.473 .017	.323 .115	-.016 .940

	Sal-BT							
N-shore	.335 .101	N-shore						
Headbay	.461 .020	.977 **<.0001**	Headbay					
Chl *a* June	-.258 .213	-.411 .041	-.513 .009	Chl *a* June				
Chl *a* Aug	-.795 **<.0001**	-.642 .001	-.742 **<.0001**	.246 .236	Chl *a* Aug			
Chl *a* Sept	-.520 .008	-.608 .001	-.723 **<.0001**	.440 .028	.915 **<0001**	Chl *a* Sept		
Chl *a* April	-.521 .008	-.198 .342	-.361 .077	.306 .137	.566 .003	.510 .009	Chl *a* April	
Chl *a* July	-.584 .002	-.767 **<.0001**	-.857 **<.0001**	.505 .010	.786 **<.0001**	.638 .001	.691 **<.0001**	Chl *a* July
Richness	.257 .214	.679 <.0001	.685 **<.0001**	-.367 .071	-.501 .011	-.435 .030	-.202 .924	-.627 .001
Density	.517 .008	.185 .376	.265 .200	-.209 .317	-.438 .029	-.380 .061	-.065 .757	-.305 .138
Diversity H'	-.255 .219	.528 .007	.477 .016	-.376 .064	-.057 .787	-.146 .488	.024 .911	-.392 .053
Evenness	-.375 .065	.351 .086	.298 .148	-.309 .132	.107 .612	-.018 .930	.006 .976	-.242 .244

Richness	Richness		
Density	.475 .016	Density	
Diversity H'	.574 .003	-.298 .148	Diversity H'
Evenness	-.298 .148	-.507 .010	.951 **<.0001**

Chapter 2: Factors influencing patterns in distribution, abundance and diversity of sedimentary macrofauna in deep, muddy sediments of inshore Placentia Bay, Newfoundland

2.1 Introduction

Declines in fisheries (e.g. Williams 1998), recent interest in marine biodiversity (e.g. Norse 1993; Snelgrove et al. 1997) and increasing pressure from scientists to design and implement marine reserves (e.g. Botsford et al. 1997) have stressed the need to generate marine species inventories and gain a better ecosystem level understanding of marine systems. In general the marine environment surrounding Newfoundland has been poorly sampled, in spite of its importance to the province. Although commercial taxa have received considerable attention, other ecosystem components, including the benthos, have received only limited attention (e.g. Nesis 1965; Carter et al. 1979; Houston and Haedrich 1984; Kennedy 1985; Schneider et al. 1987; Gilkinson et al. 1998; Prena 1999).

The present work is a subset of the benthic component of a larger study on spatial and temporal variability in the Placentia Bay ecosystem (e.g. Lawson and Rose 1999; Robichaud and Rose 1999; Bradbury et al. 2000) that provides a unique opportunity to link pelagic processes to benthic community structure. Placentia Bay is an economically important area and contains a (sporadically) reopened cod fishery, an oil refinery and a large transhipment facility. This, along with the fact that few studies on benthic communities have been conducted within Placentia Bay (e.g. Dooley 1991; Swiss and Osborn 1976; Chapter 1), provide strong motivation for benthic research.

Chapter 1 provided the first comprehensive study on sedimentary macrofauna on muddy substrates in Placentia Bay, Newfoundland and the adjacent shelf environment. It showed that many of the common species were typically abundant in organic rich areas, and based on community composition and environmental variation, there are distinct inshore and offshore regions. Alhough there was some evidence of further substructure inshore, communities in inner bay areas were shown to be similar to one another, relative to the strong inshore and offshore differences. The goal of the present chapter is to examine inshore patterns in greater detail.

Physical and biological factors both influence benthic pattern in sedimentary communities (Chapter 1). However, the relative importance of these factors in regulating community patterns can vary with spatial scale (Menge and Olson 1990). In general, broad patterns in distribution and abundance are influenced by large–scale differences in temperature, salinity, depth, surface production, topography, sediment dynamics and circulation. In recent years, the coupling between pelagic and benthic systems has received increased attention (Graf 1992). Although it is well accepted that benthic communities are fueled by sinking water column production from the overlying water column (e.g. Grebmeier et al 1988; Ambrose and Renaud 1995), coupling between benthic and pelagic communities in terms of critical variables and scales are not well understood (Josefson and Conley 1997).

Surface productivity has been shown to be most important in influencing broad-scale patterns in community structure, usually at much larger scales than that observed between the inshore and offshore regions of Placentia Bay (e.g. Rowe 1981; Mills 1975; Ambrose and Renaud 1995), and decoupling is expected at smaller scales but in Chapter 1 surface production was indeed important in differentiating inshore/offshore areas. At smaller-scales however, other variables may be important.

In general, smaller-scale patterns are usually regulated by a complexity of smaller-scale physical processes and biological interactions (Snelgrove 1999). Macrofaunal patterns of diversity and abundance have been related to several sediment characteristics including grain size, sorting and organic content (Rhoads and Young 1970; Gray 1974; Grebmeier et al 1989). Hughes et al. (1972) used multivariate techniques to show that sediment characteristics accounted for 46% of the variance in the frequency of occurance of polychaete and echinoderms in St. Margaret's Bay, Nova Scotia. The role of predators in subtidal areas has produced ambiguous results (e.g. Blegvad 1928; Virnstein 1977; Peterson 1979; Ambrose 1984; Holland et al. 1980) and the driving forces in regulating community structure in these areas are not as clear. In general, studies suggest that competition is probably not a major structuring force but predation may be important (see Peterson 1979).

This chapter focusses on spatial patterns within the inshore region of the bay and examines which factors (i.e., water column productivity-related variables and sediment characteristics) are important in influencing inshore patterns of community composition, diversity and abundance. This finer-scale analysis has the potential to reveal spatial patterns within the inshore that were not evident in the analyses of broad-scale patterns. It is hypothesized that the factors which influence benthic patterns are scale dependent. Specifically, water column productivity-related variables, which were important in influencing broad-scale patterns between the inshore and offshore areas discussed in chapter 1, are not important in explaining the distribution and abundance of macrofauna among inshore sites, where variability in water column parameters is limited. Instead, sediment-related factors such as grain size, sedimentary organic carbon and nitrogen will be important.

2.2 Materials and Methods

2.1.1 *Study Site*

Placentia Bay is a large embayment on the south coast of Newfoundland that is divided into three main regions including the head of the bay, inner bay (collectively the inshore) and the outer bay (Fig. 2.1). The inner part of the bay is divided longitudinally into three channels by several islands and is characterised by northerly flow on the eastern side and southerly flow on the Western side (see Bradbury et al. (2000)). A more complete description of the bay is given in Chapter 1.

2.2.2 *Sampling Design*

Infaunal box core samples were collected during July of 1998 from six inshore sites distributed among the head of the bay, Central Channel and the Eastern and Western Channels (Fig. 2.1). Initial site selection was primarily based upon similarity in sediment composition (muddy areas) as determined by examining local charts and a geological map constructed by Stehman (1976). For most stations, depth was similar ($\bar{x}$=210–225 m) although two sites were more extreme in range ($\bar{x}$=67 m and 286 m respectively), (Table 2.1). A nested, hierarchical sampling design was used where each of a series of successively smaller spatial scales was nested within the scale above (Morrisey et al. 1992; Chapter 1), for a total of six replicates per site.

2.2.3 *Infaunal Sampling*

The box corer was subdivided into six subcores (10 cm x 10 cm width and 30 cm deep). Four subcores were processed through a 500 μm screen for macrofauna, another was processed through a 100 μm sieve (not reported here), and the sixth subcore was used for CHN and grain size analysis. Subcores for macrofaunal analysis were sectioned into 0–3 cm and 3–10 cm vertical increments and fixed in 4% buffered formalin prior to being transferred to 70% ethanol with rose bengal. Organisms were enumerated and identified to the lowest taxonomic level (usually species) possible.

2.2.4 *Environmental Data*

Vertical casts for salinity, temperature and depth were collected with a SeaBird 25 CTD at 1 of the 6 replicate box core sampling areas at each site. Temperature and salinity for April were obtained from a complementary study in the same area (Bradbury et al. 2000). From these data, mixed layer and bottom temperature and salinity were determined as described in Chapter 1. Chlorophyll *a* samples were collected from a grid of stations throughout Placentia Bay during June and August 1998 (Bradbury et al. 2000). Surface chlorophyll measurements for April, July and September were taken from SeaWiFs (Sea-viewing wide field of view sensor) images, (http://dfomr.mar.dfo-mpo.gc.ca/science/ocean/seawifs/seawifs_1.html). A brief summary of procedures for CHN and grain size analysis are outlined in Chapter 1.

2.2.5 *Data Analysis*

The four subcores used to evaluate the macrofaunal community were pooled for community composition analysis to yield six replicate samples (each with 400 cm^2 surface area) at each site in the inner bay. Shannon–Weiner diversity, richness, evenness and density (total macrofauna) were compared by plotting means and 95% confidence intervals for each site. Average densities of the most dominant taxa (defined as the six most abundant taxa at each site) were compared in a similar way. ANOVA was also performed for density, species richness, diversity and evenness to determine if there was a significant difference among the the PCA-H site groupings, Tukey's tests were used to determine which sites differed. Homogeneity of variance tests indicated that no transformation of data was necessary for density, however, tests for diversity, species richness and evenness indicated unequal variance even after data transformation. Therefore, a non-parametric test (Mann-Whitney) was employed for these three measures.

Community composition among sites was analyzed using CNESS (Chord–Distance Normalized Expected Species Shared) as described by Trueblood et al. (1994). CNESS is a faunal index that is based upon the number of expected species shared in a random draw of *n* individuals from two samples. Distribution patterns were clustered using unweighted, pair–group mean average sorting of CNESS dissimilarities (COMPAH 90– E.D. Gallagher). To provide a more complex and informative presentation of the data, a metric scaling of CNESS (see Chapter 1) was performed in Matlab (programs written by E.D. Gallagher), and Gabriel Euclidean distance biplots (Gabriel 1971; ter Braak 1983) were overlaid to indicate the relative importance of individual species in creating observed patterns. Only those species that contributed more than 5% to CNESS variation were displayed in the biplots. The percentage of total individuals contributed by each of these species to site groupings was calculated and displayed as stacked bar graphs. A multivariate ANOVA and Tukey test was also performed for each of these species to determine if there was a significant difference in abundance among the three PCA-H site groupings. With the exception of *Pectinaria granulata*, homogeneity of variance tests indicated that no transformation of data was necessary. Data for *P. granulata* was root transformed, however, a homogeneity of variance test indicated that variance was unequal and therefore a non-parametric test (Mann-Whitney) was used.

Determining which species drive patterns from biplots alone is somewhat subjective because biplots capture within-site as well as between-site variation. To provide a more objective interpretation, discriminant function analysis (SPSS 8.0) was also performed with site designated as factor (site groupings were obtained from Principal Components Analysis of Hypergeometric Probabilities (PCA-H) axes 1 and 2). This analysis was not used for formal hypothesis testing and p-values were not reported. Instead p-values of 0.05 were used as a screening criterion to evaluate which species were responsible for the between-site differences that were observed in the PCA-H plots. As with CNESS, the percentage of total individuals contributed by each species was calculated, using the same site groupings determined in the discriminant function analysis, and displayed as stacked bar graphs (only those species that made up at least 1% of the total density at any one site were included).

PCA (Principal Components Analysis) of standardized data (see Chapter 1) determined differences among sampling sites based on abiotic and biotic water column variables and sediment-related measures (SPSS 8.0). For the majority of environmental variables, data values were only collected from 1 of the 6 replicate sampling locations at each site (with the exception of the upper Eastern Channel which only had data for 2 replicate locations). Thus, replication of environmental variables was not as great as it was for species data, however, given the close proximity of replicates within each site, variation for the most of these variables was observed to be small (Chaper 1). A multiple regression with adjusted F ratios and p-values was also run separately with diversity, species richness, and density as the dependant variable and environmental variables as the independants. Because many of the environmental variables in this study are interrelated, only 10 were used in this analysis including depth, % organic carbon, mixed layer temperature (July), mixed layer salinity (July), distance from the head of the bay, Chl *a* concentrations in June, ichthyoplankton concentrations in June and very fine to medium silt (see Chapter 1). Ichthyoplankton was included as a measure of secondary production in the absence of a complete zooplankton data set. The choice of June sampling for ichthyoplankton and surface chlorophyll was based on it being the closest sampling time to the July benthos sampling period. A plot of best fits and residuals showed no trends that defied the assumptions for this analysis.

2.3 Results

2.3.1 *Overview: Inshore Macrofauna*

A total of 10,159 individuals were collected from 6 inshore stations encompassing 65 taxa (level of identification varies). Polychaetes were the most abundant group sampled, comprising 87% (by number) of the total infauna collected, followed by bivalves that comprised 4.6%. Dominant taxa included representatives from four phyla including Polychaeta (11 species/taxa), Bivalvia (3 species), Scaphopoda (1 species) and Cnidaria (1 taxon), (Fig. 2.2 A & B). The majority of dominant taxa were relatively widespread, occurring at all sites, however, the single most abundant species was the polychaete *Cossura longocirrata* which comprised 63% of total infauna. The next most abundant taxa included the polychaetes *Prionospio steenstrupi* (4% of total infauna), *P. granulata* (2.5% of total infauna), *Gyptis* sp. (2.2% of total infauna), *Nepthys neotena* (2.2% of total infauna), *Lumbrineris* spp. (1.9% of total infauna) and *Chaetozone setosa* (1.6% of total infauna).

2.3.2 *Species diversity and Abundance*

C. longocirrata was the most abundant species present at each site, attaining densities as high as 655 individuals·400 cm^{-2}, (Fig. 2.2 B). Its greatest densities were observed in Eastern Channel and lower Western Channel (W2, southern portion of Western Channel), (268-341 individuals·400 cm^{-2}) and relatively lower densities were present at the head of the bay, Central Channel and upper Western Channel (W1, northern portion of Western Channel), (54-70 individuals·(400 cm^{-2}). Similar patterns in abundance were observed for *Lumbrineris* spp. (0.50-15.0 individuals·400 cm^{-2}), Dorvellidae spp. (1.83-37.5 individuals·400 cm^{-2}) and *Gyptis* sp. (3.5-9.3 individuals·400 cm^{-2}), (Fig. 2.2 A.). *Nereimyra punctata* (0-23.0 individuals·400 cm^{-2}) and *P. granulata* (0-40.67 individuals·400 cm^{-2}) were absent from most areas, however, very high densities were present at the head of the bay (Fig. 2.2 B). For the remainder of the dominant taxa, mean density generally peaked at one site inshore, and was relatively constant elsewhere (Fig. 2.2 A & B). For example, abundance of Capitellidae spp. (0-9.17 individuals·400 cm^{-2}), *Aricidea nolani* (0.50-7.83 individuals·(400 cm^{-2}), and *Macoma calcarea* (0.50-8.83

individuals·400 cm^{-2}) were highest at the head of the bay and abundance of *N. neotena* (4.5-10.33 individuals·400 cm^{-2}) and *Thyasira* sp. (1-10.33 individuals·400 cm^{-2}) were highest in the Central Channel. *C. setosa* (2.83-8.33 individuals·400 cm^{-2}) and *P. steenstrupi* (2.83-29.50 individuals·400 cm^{-2}) attained their greatest abundance in the lower Western Channel (W2) whereas abundances of *Nuculana pernula* (0-4.17 individuals·400 cm^{-2}) and *Antalis entale* (0-4.5 individuals·400 cm^{-2}) were greatest in the upper Western Channel (W1).

Shannon diversity indices for Placentia Bay were moderately low ($\bar{x}$=1.76), (Fig. 2.3). Species richness ranged from 33 to 12 taxa per sample and average values ranged from 17 to 29 taxa per site (Fig. 2.4). A Mann-Whitney test indicated that diversity was significantly different among the three site groupings established by the PCA-H axes 1 and 2 (i.e., head of bay vs Central Channel/upper Western Channel group; head of the bay vs lower Western Channel/Eastern Channel group; Central Channel/upper Western Channel group vs lower Western Channel/Eastern Channel group), (Table 2.8). A Mann-Whitney test also indicated that species richness significantly differed among these three site groupings (Table 2.8). Evenness values ranged from 0.47 to 0.76. A Mann-Whitney test indicated that evenness was significantly different between the head of the bay and upper Western Channel/Eastern Channel as well as between the Central Channel/upper Western Channel group and the lower Western Channel/Eastern Channel group (Table 2.8). The contrast between the head of the bay and the Central Channel/upper Western Channel group was ambiguous because the parametric and non-parametric tests gave a conflicting result. Infaunal densities ranged between 2,716.67 and 12,600.00 individuals·m^{-2} (Fig. 2.6). ANOVA p-values indicated that total density was significantly different among the three site groupings indicated by the PCA-H (axes 1 and 2), (n=36, F=14.52, p=<0.0001). A Tukey test showed significant differences between all three groups

2.3.3 *Cluster & PCA-H Analysis*

At a dissimilarity level of 73% cluster analysis of infaunal cores showed three relatively distinct geographic groups, although there were several outliers. These groups included the head of the bay, Central Channel (with the exception of two samples from the northern portion of the Western Channel) and combined Eastern and Western Channels (Fig. 2.7). PCA-H axes 1 and 2 indicated similar groupings and accounted for 27% and 19% of the variation in the data respectively (Fig. 2.8). The community at the head of the bay (H) was distinct. The Central Channel (C) and most samples from the upper Western Channel (W_1) grouped together, and samples from the Eastern Channel (E_1 (northern portion of Eastern Cahnnel) & E_2 (southern portion of Eastern Channel) and lower Western Channel (W_2) formed another group. Gabriel biplots for axes 1 and 2 indicate that the polychaete *C. longocirrata* and Dorvilleidae spp. played a greater role in the community structure in the Eastern/lower Western Channel group. *C. longocirrata* made up 28% of the total abundance at the head of the bay, 50% in the combined Central/upper Western Channels, and 72% in the combined Eastern/lower Western Channels. Dorvilleidae comprises <5% of each group (Fig. 2.9). ANOVA p-values indicated that abundance of C. *longocirrata* was significantly different among the three site groupings indicated by the PCA-H (axes 1 and 2), (n=36, F=23.08, p=0.000). A Tukey test showed significant differences between the Eastern/lower Western Channel group and head of the bay as well as between the Eastern/lower Western Channel group and the Central Channel/upper Western Channel group. ANOVA p-values also indicated that abundance of Dorvilleidae spp. differed significantly between the PCA-H groups (n=36, F=13.90, p=0.000) and a Tukey test showed this difference to be significant for the same groups as *C. longocirrata*. Capitellid polychaete densities were highest at the head of the bay (5% of total density) and combined Central/upper Western Channels (2% of total abundance). ANOVA p-values indicated that abundance of Capitellidae spp. also differed significantly between the PCA-H groups (n=36, F=7.32, p=0.012). A Tukey test showed significant differences between the head of the bay and the Eastern/lower Western Channel group as well as between the head of the bay and Central Channel/upper Western Channel group. *P. granulata* was important at the head of the bay (20% of total abundance) and the bivalve *Thyasira* sp. was important in the Central Channel/upper Western Channel (5% of total abundance). However, ANOVA for *Thyasira* sp. showed that differences in abundances between these groups were not significant (n=36, F=2.5, p=0.098).

PCA-H axes 1 and 3 (27% and 10% of the variation respectively) showed evidence of further substructure within the bay, indicating differences between communities in the Eastern and lower Western Channel (Fig. 2.10). As in PCA-H axes 1 and 2, distinct communities were also located at the head of the bay and combined Central and upper Western Channels. Gabriel biplots for axes 1 and 3 (Fig. 2.10), indicate that *C. longocirrata* is more important in the Eastern Channel where it is abundant (74% of total abundance) whereas Dorvilleidae was more important in the Western Channel (7% of total abundance) where it attained its greatest numbers (Fig. 2.11). *P. steenstrupi* played an important role in the community structure at the head of the bay (7% of total abundance) and in the Western Channel (6% of total abundance) whereas *P. granulata* and Capitellidae sp. were both important at the head of the bay.

2.3.4 *Discriminant Function Analysis*

Discriminant function analysis conducted on the site groupings indicated by PCA-H axes 1 and 2, showed the same taxa to be important along with twenty others. Seven of these were relatively common (species with densities >1% of total abundance) including four polychaetes (*Maldane glebifex*, *Syllides longocirrata*, *A. nolani*, *Lysilla loveni*), two bivalves (*M. calcarea*, and *N. pernula*), and a Scaphopod (*A. entale*), (Fig. 2.12). *M. glebifex* and *Syllides longocirrata* were important at the head of the bay, where they made up 2.0 and 2.7% of the total density respectively. Although *A. nolani*, and *M. calcarea* were present at all three areas, they were more important at the head of the bay where they occurred in greatest abundance (4.0 and 4.4% of total density respectively). In the combined Central and upper Western Channels *N. pernula* (2.4% of total density), *L. loveni* (1.0% of total density) and *A. entale* (2.3% of total density) were important. The remainder of taxa identified in the discriminant function analysis were less abundant (species with densities <1% of total density) and included 6 polychaetes, 1 bivalve, 2 amphipods, 1 scaphlopod, 1 hemichordate, tanaids and actiniarians (Table 2.2).

In comparing the Eastern and lower Western Channels, *C. setosa*, *Thyasira* sp., *L. loveni*, *Lumbrineris* spp. and *A. nolani* occurred in higher density in the Western Channel, whereas *Yoldia* sp., and *M. calcarea* were more abundant in the Eastern Channel (Table 2.3). In addition, *N. punctata* and *Retusa obtusa* were not present in the lower Western Channel samples and *Sphaerodoropsis minuta* was not found in the Eastern Channel.

2.3.5 Environmental Data

On average, total organic carbon present in inshore sediments was high, ranging between 4.83 and 8.07 % ($C{\cdot}mg^{-1}$), (Table 2.4) with higher amounts at the head of the bay, ($\bar{x}$=8.07 $C \cdot mg^{-1}$) upper Western Channel, ($\bar{x}$=7.82 $C{\cdot}mg^{-1}$) and Central Channel ($\bar{x}$=6.57 $C{\cdot}mg^{-1}$) compared to other areas. Average nitrogen ranged between 0.61 and 1.33 $N{\cdot}mg^{-1}$ and was also higher at the head of the bay ($\bar{x}$=1.33 $N{\cdot}mg^{-1}$), upper Western Channel ($\bar{x}$=1.15 $N{\cdot}mg^{-1}$) and Central Channel ($\bar{x}$=0.91 $N{\cdot}mg^{-1}$) relative to other sites. C/N ratios were relatively low and constant ($\bar{x}$=8.51-9.23%) throughout the inshore. Grain size in inshore sediments was dominated by clay ($\bar{x}$=33.8-55.0%) and medium to fine silt ($\bar{x}$=41.6-60.4%), (Table 2.4). Clay content was greatest in the upper Western Channel samples, whereas medium to fine silt content was greatest at the upper Eastern Channel. Elevated amounts of coarse silt were present in the Central Channel ($\bar{x}$=10.4%) and lower Western Channel ($\bar{x}$=8.2%). The lower Western Channel also contained elevated amounts of fine sand ($\bar{x}$=2.6%). Coarser sediments were present at the head of the bay, which contained higher amounts of coarse silt ($\bar{x}$=11.0%), very fine sand ($\bar{x}$=3.9%) and fine sand ($\bar{x}$=3.9%) compared to other areas sampled. Mixed-layer temperatures did not vary greatly between sites and ranged between 0.3 and 0.5°C in April and between 9.1 and 10.1°C in July. (Table 2.5). Bottom temperature in July ranged between –0.3 and –0.8°C, with the exception of the head of the bay which was much warmer (3.4°C). Mixed layer salinity (31.9-32.1‰) and bottom salinity (32.2-32.8‰) were relatively constant throughout the inshore (Table 2.5). Chl *a* extractions suggested that concentrations were spatially consistent throughout the inner bay in April (~10 $\mu g \cdot l^{-1}$) and July (~1$\mu g \cdot l^{-1}$) whereas in June they ranged between 0.25 and 1.28 $\mu g \cdot l^{-1}$ and were higher in the upper Eastern Channel (Table 2.5). In August, concentrations ranged between 0.23-0.76 $\mu g \cdot l^{-1}$ and were elevated at the head of the bay (0.76 $\mu g \cdot l^{-1}$) and in the upper Western Channel (0.64 $\mu g \cdot l^{-1}$). Concentrations in September (1.02-1.68 $\mu g \cdot l^{-1}$) were also elevated at these sites (1.62 and 1.68 $\mu g \cdot l^{-1}$ respectively) as well as in the lower Eastern Channel (1.66 $\mu g \cdot l^{-1}$). These temporal and spatial patterns in chlorophyll *a* were similar to the distribution in SeaWiFS (Sea-viewing wide field of view sensor), surface images for the same time frame (http://dfomr.mar.dfo-mpo.gc.ca/science/ocean/seawifs/seawifs_1.html). Total ichthyoplankton concentrations were higher at the head of the bay (10,958·1000 m^{-3}) than in the channels during April, (Table 2.5). Concentrations in June were also highest at the head of the bay (7222·1000 m^{-3}) as well as in the upper Eastern Channel (7052·1000 m^{-3}), whereas August concentrations were higher in the lower Eastern Channel (10,206·1000 m^{-3}) relative to other parts of the bay.

PCA analysis of sampling sites based on the environmental data showed similar spatial groupings to those observed in the PCA-H analysis of species data for axes 1 and 2. Factor 1 and 2 accounted for 39.2 and 20.8% of the variance in the data respectively (Fig. 2.13 A and 2.13 B). Factor 1 separated the head of the bay samples with positive loadings from the remainder of the inner bay samples. Factor 1 also separated the Central Channel and upper Western Channel samples from the lower Western and lower Eastern Channel samples which had more negative factor loadings. Factor 2 separated the upper Eastern Channel samples from the rest of the inshore samples. Factor 1 had positive loadings for productivity-related variables (chl *a*, ichthyoplankton concentrations (April & June), sediment C·mg and N·mg), abiotic water column variables (mixed layer and bottom temperature), and coarse sediment. Negative loadings were observed for average C/N, fine sediment (clay to medium silt), abiotic water column variables (mixed layer and bottom salinity), ichthyoplankton concentration (September), and distance from the head of the bay and shoreline. Factor 1 was heavily weighted positively for N/mg, bottom temperature (July), ichthyoplankton concentration (April and June) and negatively for C/N ratio, depth, mixed layer salinity, bottom salinity in July and distance from the head of the bay. Factor two was heavily weighted positively for ichthyoplankton concentration (August) and negatively for chl *a* (June), very fine to medium silt, and mixed layer temperature and salinity. Factor loadings are summarized in Table 2.6.

Because water column and productivity-related variables are often decoupled from benthic communities, a second PCA analysis was done where only sediment-related variables and depth were included. Spatial patterns were similar to those described above (Fig. 2.14). Factors 1 and 2 accounted for 35.7 and 24.0% of the variability in the data. Factor 1 largely separated the head of the bay samples with high positive loadings from the remainder of the inner bay samples, which formed two groups along this axis, including the combined Central and upper Western Channel samples and combined lower Western and Eastern Channel samples. Factor 2 separated the upper Eastern Channel samples from the remainder of the inner bay samples. Factor 1 had positive loadings for organic carbon, nitrogen, and grain size (clay and coarse silt to medium sand), and negative loadings for C/N and depth. Factor 1 was heavily weighted positively for organic carbon and nitrogen content and negatively for depth. By contrast, Factor 2 was heavily weighted positively for clay content and negatively for very-fine-medium silt content. Factor loadings are summarized in Table 2.7. Multiple regression analysis of species richness and environmental variables showed that the overall model developed to predict species richness was not significant (F=0.453, p=0.858, n=17). Overall models developed to predict infaunal diversity and density were significant. Depth and distance from the head of the bay were shown to be the most important predictors of diversity. Depth had a significant negative relationship whereas distance from the head of the bay had a significant positive relationship (Table 2.9). Depth was a significantly positive predictor of infaunal density (Table 2.10).

2.4 Discussion

In general, the marine environment surrounding Newfoundland has been poorly sampled and benthic communities in particular have been studied in only a few instances, (e.g. Nesis 1965; Carter et al. 1979; Hutcheson et al. 1981; Houston and Haedrich 1984; Schneider et al. 1987; Gilkinson et al. 1998; Prena 1999), despite their essential role in the dynamics of marine ecosystems (Mills 1975; Snelgrove 1999). Chapter 1 described the community structure and spatial distribution of sedimentary macrofauna on muddy substrates in Placentia Bay Newfoundland and the adjacent shelf environment, and found that many of the dominant species in Placentia Bay are characteristic of organic rich areas. Community composition and environmental variation indicated that the bay can be broadly divided into inshore and offshore regions. Community composition and benthic patterns in diversity and abundance at broad scales (i.e., between the inshore and offshore) were shown to be largely influenced by surface oceanography, as seen by the importance of surface water characters and sedimentary carbon. Although communities in the inner bay were shown to be generally homogeneous relative to offshore sites, there was some evidence of further substructure inshore. This chapter describes these spatial patterns and examines which factors (i.e., water column and sediment characteristics) are important in influencing inshore patterns of community composition, diversity and abundance.

Cluster and PCA-H analysis of species data from box core samples collected within the inshore region of the bay revealed spatial patterns that were not evident in the analyses of broad-scale patterns in Chapter 1. Discernable communities occurred at the head of the bay (H), combined Central/upper Western Channels (C and W1 samples formed a cluster), and combined Eastern/lower Western Channels (E1, E2 and W2 samples formed another cluster). Spatial patterns in PCA analysis of sediment-related variables and depth were similar to those observed for the benthic species data (PCA-H) with the exception of the upper Eastern Channel samples differed from all other samples and accounted for 35.7 and 24% of the variance in the data. PCA analysis of water column productivity-related variables bore no resemblance to benthic patterns. Thus, abiotic and biotic water column variables are not as important as sediment-related factors and depth in explaining the distribution and abundance of macrofauna inshore, a very different finding than that described for larger-scale inshore/offshore patterns presented in Chapter 1.

Community analyses showed that species composition patterns differed among different areas inshore and many of these patterns can be related to grain size. The polychaete, *P. granulata*, was a dominant member of the community at the shallow site at the head of the bay, whereas within the inner bay it was either completely absent or present in extremely low numbers. The head of the bay was the shallowest site sampled and contained coarse sediments with higher amounts of coarse silt to fine sand, which is consistent with what is known about the biology of this species. *P. granulata* is usually found on sandy substrates at shallow to sublittoral depths. It is a burrowing, selective deposit-feeder, (Fauchald and Jumars 1979) that displays remarkable selectivity in grain size when building its conical tube (Pocklington, unpublished). Several other polychaete species, important in distinguishing the head of the bay site from the inner bay sites, have also been found on coarse/sandy sediments, including Maldanidae (i.e., *M. glebifex*), (Pocklington, unpublished), *Goniada maculata*, *A. nolani*, *S. longocirrata* (Pocklington, unpublished) and *Spio filicornis* (Appy et al. 1980). Of these, *G. maculata*, *S. filicornis* and *S. longocirrata* were also associated with coarser sediments offshore (Chapter 2). Capitellidae spp. were important at the head of the bay, Central Channel and in the Western Channel, however, densities were higher on coarse sediments at the head of the bay, Central Channel, and lower Western Channel compared to the remainder of the sites. This is consistent with observations in chapter 1, which showed that Capitellidae spp. densities were higher offshore where sediments consisted of a larger proportion of coarse silt to medium sand compared to inshore.

Thyasira sp., an opportunistic, deposit-feeding bivalve, was most abundant in the Central Channel, and was a key taxon in describing Central Channel community structure. Relatively high densities were also found in the lower Western Channel, where sediment composition was very similar. Despite the coarser sediments at the head of the bay, density of this species was as low as that observed for inner bay areas with finer sediments. A similar situation was observed for *M. calcarea*, another deposit-feeding bivalve that was similarly abundant on coarse sediments at the head of the bay and on finer sediments in the Eastern Channel. These patterns suggest that some factor other than grain size may be important in influencing the distributions of these species. Closer observation of density patterns revealed that at any given site, with the exception of the upper Western Channel, high density of one of these species corresponded to lower density of the other. In the upper Western Channel, densities of both species were low and density of another deposit-feeding bivalve, *N. pernula*, was higher than elsewhere in the inshore. These patterns suggest that post-settlement processes such as competition may be important in influencing the relative abundance of these dominant, deposit-feeding bivalves.

Although Dorvilleidae spp. and *C. longocirrata* were present at all sites inshore, they were important components of the community structure in the Eastern and lower Western Channels, where they were more abundant. Dorvillieds are small, free living polychaetes that feed on algae and small invertebrates (Fauchald and Jumars 1979). They can be found in all sublittoral environments, including heavily polluted areas (Fauchald and Jumars 1979). *C. longocirrata* is typically abundant on muddy to silt substrates in organically enriched areas (Blake and Hilbig 1994; Volckaert 1987) and is considered to be an opportunistic species (Olsgard and Hasle 1993). Given the biology of this species, it was not unexpected that patterns in abundance showed no consistent relationship with grain size, however, it was surprising that lower densities were associated with higher amounts of sedimentary organic carbon at the head of the bay, Central Channel and upper Western Channel compared with other areas. Density of *Lumbrineris* spp., *Gyptis* sp. and total macrofauna (discussed later) were also lower at the the head of the bay, Central Channel and upper Western Channel compared with other areas.

Although *C. longocirrata* was identified as being more important in the Eastern and lower Western Channels compared to other areas, this species played a very important role in the community structure of the entire inshore region. Moderately low levels of diversity inshore were largely due to the dominance of this opportunistic species (Chapter 1). *C. longocirrata* was the most abundant species present at each site and densities were far greater than for any other species. Lower densities of *C. longocirrata* at the head of the bay, Central Channel and upper Western Channel also resulted in higher species evenness and relatively higher diversity at these three sites. Depth and distance from the head of the bay were the most significant predictors of species diversity, and diversity was higher at shallower depths with coarser sediments. Although no one environmental variable was shown to be important in predicting species richness it is possible that the coarse component of sediments at the head of the bay created greater particle diversity that resulted in greater richness than would otherwise be observed for fine sediments with high levels of organic carbon (e.g. Etter and Grassle 1992). The upper Western Channel, where fine sediments were combined with high organic carbon, also exhibited the lowest species richness.

Of all the inshore sites macrofaunal densities were much lower at the head of the bay, Central Channel and upper Western Channel ($\bar{x}$=3737.5 individuals ±1077, n=18). Depth was the most important predictor of infaunal density and density was lower at shallower depths with greater amounts of relatively fresh organic carbon (as indicated by low C/N ratios). There are several possible explanations for such a large reduction in densities at these three sites, however, none are conclusive without further study.

One possible explanation is that lower oxygen concentrations occurred within the first few centimetres of sediment at these three relatively shallower sites that contained greater amounts of organic carbon. It is also important to note that bottom temperature, although not significant, was the next most important predictor of infaunal density and bottom temperature was relatively higher at these three sites. All of these factors could contribute to lower oxygen concentrations, however, data on dissolved oxygen concentrations in the sediment were not collected. Nonetheless, there is little evidence in terms of species composition and abundance patterns, or from the vertical distribution of macrofauna, to suggest that low oxygen conditions occurred. For example, at the shallow site at the head of the bay, more organisms were found in the 3-10 core fraction compared to other inshore sites and this same pattern was observed to a lesser degree for the Central Channel (Chapter 1, fig. 1.4).

Biological interactions such as predation (Paine 1966) and competition (Connell 1961) could contribute to density differences at these sites, however, further research is necessary to address this possibility. Predation and competition have been shown to be the primary regulating factors structuring rocky intertidal systems, because food and larval supply often exceed the spatial carrying capacity, resulting in more recruits than can occupy the space available (Grassle and Grassle 1992). However, studies on the role of predators in subtidal areas have produced mixed results (e.g. Blegvad 1928; Virnstein 1977; Peterson 1979; Ambrose 1984; Holland et al. 1980) and the driving forces in regulating community structure in these areas are not as clear. In general, studies suggest that competition is probably not a major structuring force but predation may be important (see Peterson 1979). In addition, many of the common species in Placentia Bay are typically abundant in organic rich areas and some have been described as being tolerant to pollution; thus pollution can not be ruled out as a structuring factor.

The explanation for which there is the most evidence is that the relatively low macrofaunal densities are a result of poorer food quality. Substantial amounts of terrestrial debris in the form of wood pulp, twigs and leaves (all very black in color) were present in samples collected at the head of the bay near Bar Haven, which is near Swift Current, the only major source of freshwater entering the bay (Willey 1976). Very small amounts were also noted in samples from the Central and upper Western Channels. Although C/N ratios for these sites were low and ratios have been commonly used to indicate food quality to the benthos (Mills et al. 1975; Grebmeier et al. 1988; Levin et al. 1991), interpreting food quality based solely on C/N ratios requires caution, especially if detritus is aged. With aging, and thus increased microbial activity, the nitrogen content of detritus increases and C/N ratios can be low (Tenore et al. 1979; 1982). Microbial growth and increased nitrogen levels do not necessarily increase the nutritional quality of detritus because the nitrogen present may not be available to the benthos (Tenore 1982). For example, during aging, non-liable humic nitrogen from terrestrial sources, rather than microbial protein, may represent a significant fraction of the observed nitrogen (Odum et al. 1979; Rice 1982). The presence of terrestrial debris that is black in color and most likely not of recent origin, along with substantial reduction in macrofaunal densities at these three sites, suggests that such a scenario is possible. Sediment C/N ratios in-conjunction with isotopic analyses have been used to assess the origin of sedimentary organic matter (Ostrom 1989) and could resolve this question for Placentia Bay.

2.5 Summary

Analyses of community composition and abundance data for the inshore region of Placentia Bay revealed spatial patterns that were not evident in the analyses of broad-scale patterns described in Chapter 1. Communities at the head of the bay, combined Central and upper Western Channels and combined Eastern and lower Western Channels could be distinguished in terms of species composition. Several of the key species determined to be important by Gabriel biplots (ie. Capitellidae spp., Dorvilleidae spp. , *C. longocirrata*) were significantly different in abundance among these three areas. Analyses of sediment-related variables essentially showed the same spatial patterns as species data, whereas productivity-related variables bore no linkage to benthic patterns. This finding was not unexpected because decoupling of surface productivity and benthic patterns is expected at smaller spatial scales (Barry and Dayton 1991). Community analyses showed that species composition patterns differed among these different areas and that many of these patterns could be related to grain size. This was particularly true for the shallow site at the head of the bay. This area was characterized by coarse sediments consisting of relatively higher proportions of coarse silt to fine sand, which are characteristic of the habitat of several species of polychaetes that were important in distinguishing the head of the bay site from other areas. Species richness was greatest at the shallow site at the head of the bay despite higher amounts of organic carbon in sediments. Although no one environmental variable was shown to be important in predicting species richness, it is possible that the coarse component of sediments at the head of the bay created greater particle diversity that resulted in greater richness than would otherwise be observed for fine sediments with high levels of organic carbon. Species richness was lowest in the upper Western Channel, which was characterized by fine sediments with high organic carbon. The opportunistic polychaete, *C. longocirrata,* played an important role in the community structure of the entire inshore region, where somewhat low levels of diversity were largely due to the dominance of this opportunistic species. *C. longocirrata* occurred in far greater densities than any other species. Lower densities of *C. longocirrata* at the head of the bay, Central Channel and upper Western Channel resulted in higher species evenness and relatively higher diversity at these three sites. Depth and distance from the head of the bay were the most significant predictors of species diversity, which was higher at shallower depths with coarser sediments. In terms of abundance patterns, evidence suggests that the quality rather than quantity of organic material was important in influencing macrofaunal densities among inshore sites. Reduced macrofaunal densities were observed at the head of the bay, Central Channel and upper Western Channel despite higher amounts of organic carbon than at other sites. Terrestrial debris was present in samples collected at these three sites, which were in close proximity to the only major source of freshwater entering the bay (Willey 1976). Although C/N ratios for these sites were low, the nitrogen that was present may have been unavailable to the benthos (see Tenore 1982). Thus, water column productivity-related variables were not as important as sediment-related factors (i.e., grain size and quality of organic material) and depth in explaining the distribution and abundance of macrofauna on muddy substrates within the inshore region of Placentia Bay, which is a very different finding than for larger-scale spatial patterns between the inshore and offshore described in Chapter 1.

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Table 2.1. Distance-related variables with 95% confidence intervals for depth.

Site	Depth (m)	Distance shore (m)	Distance head (m)
Head (H)	67±3.7	600	12000
Central C)	210±5.1	1000	26000
West (W_1)	214±2.1	4000	23000
West (W_2)	283±11.7	1000	45000
East (E_1)	225±6.7	2500	8000
East (E_2)	217±6.5	3000	29000

Table 2.2. Results of discriminant function analysis. Species with densities <1% at any of the site groupings presented as present (+) or absent (–). Groupings are based on those obtained in PCA-H analysis.

Taxa	**Head**	**Central & Upper Western Channel**	**Eastern and Lower Western**
Polychaeta			
Goniada maculata	+	-	-
Spio filicornis	+	-	-
Terebellides stroemi	-	+	+
Apistobranchus typicus	-	+	+
Pherusa plumosa	+	-	+
Pholoë longa	+	-	+
Bivalvia			
Yoldia sp.	+	+	+
Amphipoda			
Monoculodes sp.	+	-	-
Lysianassidae sp.	-	+	-
Mysid	+	-	+
Hemichordata	+	-	-
Tanaidacea	+	+	-
Actiniaria	+	-	+

Table 2.3. General comparison of species abundances in the Eastern and lower Western Channels that were shown to differ in PCA-H axes 1 and 3 ((+) indicates present, (-) indicates absent and (>) indicates greater abundance in one of the channels).

Taxa	**Eastern Channel**	**Lower Western Channel**
Polychaeta		
Lysilla loveni	+	>+
Chaetozone setosa	+	>+
A. nolani	+	>+
Lumbrineris spp.	+	>+
Sphaerodoropsis minuta	-	+
Nereimya punctata	+	-
Bivalvia		
Thyasira sp.	+	>+
Yoldia sp.	>+	+
Macoma calcarea	>+	+
Gastropoda		
Retusa obtusa	+	-

Table 2.4. Summary of sediment-related variables with 95% confidence intervals.

Site	* n	% clay (<3.9-0 μm)	% m-f -silt (31-3.9 μm)	% coarse-silt (<62.5-31 μm)	% vf-sand (<125-62.5 m)	% fine sand (<250-125 μm)	% m-sand (>350-250 μm)	* n	%C/mg	%N/mg	C/N
Head (H)	3	36.0 ±5.6	45.0 ±8.9	11.0 ±1.2	3.9 ±2.3	3.9 ±4.8	0.24 ±0.5	6	8.07 ±0.6	1.33 ±0.2	8.51 ±0.2
Central C)	3	38.4 ±9.0	48.3 ±9.0	10.4 ±6.3	1.6 ±0.5	1.0 ±.0.2	0.16 ±0.2	6	6.57 ±0.3	0.91 ±0.1	9.11 ±0.1
West (W_1)	3	55.0 ±16.8	41.6 ±6.8	0.50 ±0.4	1.3 ±1.2	1.2 ±0.9	0.27 ±0.5	6	7.82 ±0.1	1.15 ±0.1	8.79 ±0.1
West (W_2)	3	41.0 ±7.6	47.4 ±7.6	8.2 ±2.9	2.6 ±1.0	0.86 ±0.7	0.0 ±0.0	5	5.31 ±0.3	0.64 ±0.1	9.05 ±0.2
East (E_1)	2	33.8 ±16.6	60.4 ±13.9	3.3 ±3.8	1.3 ±1.0	0.91 ±0.9	0.0 ±0.0	5	6.15 ±0.2	0.77 ±0.1	8.60 ±0.2
East (E_2)	3	45.2 ±4.6	46.7 ±4.2	5.4 ±1.1	1.6 ±1.2	1.1 ±1.9	0.0 ±0.0	5	4.83 ±0.4	0.61 ±0.1	9.23 ±0.4

Table 2.5. Summary of abiotic and biotic water column variables.

Site	**Mixed Temp. Ap. (°C)**	**Mixed Temp. July (°C)**	**Bottom Temp. July (°C)**	**Mixed Salinity April (‰)**	**Mixed Salinity July (‰)**	**Bottom Salinity July (‰)**	**Chl *a* April (μg/l)**	**Chl *a* June (μg/l)**	**Chl *a* July (μg/l)**	**Chl *a* Aug. (μg/l)**	**Chl *a* Sept. (μg/l)**	**Ich. April (#/1000 m^3)**	**Ich. June (# / 1000 m^3)**	**Ich. August (# / 1000 m^3)**
Head (H)	0.5	9.4	3.4	31.9	31.8	32.2	10	0.46	1.00	0.76	1.62	10 958	7222	7427
Central (C)	0.5	8.5	-0.3	32.1	32.0	32.7	10	0.25	1.00	0.39	1.56	52	843	7059
West (W_1)	0.4	9.7	-0.3	32.2	31.9	32.7	10	0.35	1.00	0.64	1.68	152	978	6019
West (W_2)	0.4	9.2	-0.8	32.2	31.9	32.8	10	0.26	1.00	0.26	1.02	110	905	8678
East (E_1)	0.4	10.1	-0.7	32.2	31.8	32.8	10	1.28	1.00	0.23	1.57	569	7052	2531
East (E_2)	0.3	9.1	-0.6	32.1	31.9	32.8	10	0.37	1.00	0.58	1.66	422	1255	10206

Table 2.6 Factor loadings for the PCA of environmental variables. Heavily weighted loadings (+/-0.70) are shown in bold.

Variable	**Factors**	
Productivity related variables	**1**	**2**
C/mg (%/site)	.621	.142
chl *a* june (chlorophyll *a* June µg/l)	.187	**-.942**
chl *a* aug (chlorophyll *a* Augustµg/l)	.673	.323
chl *a* sept (chlorophyll *a* September µg/l)	.437	-.178
N/mg (%/site)	**.757**	.249
C/N (carbon/nitrogen mg)	**-.727**	.402
Grain Size (%)		
m-sand (medium sand >350-250 µm)	.312	.353
f-sand (fine sand <250-125µm)	.583	.117
v-fine sand (very fine sand <125-62.5 µm)	.535	.132
c-silt (coarse silt <62.5-31 µm)	.310	.371
v-f-med silt (very fine to medium silt <31–3.9 µm)	-.095	**-.752**
clay (<3.9-0 µm)	-.215	.512
Abiotic Water Column		
depth (depth/site)	**-.969**	-.072
temp ML April (mixed layer temperature °C)	.411	.393
temp ML July (mixed layer temperature °C)	.244	**-.741**
temp BT July (bottom temperature °C)	**.964**	.183
salinity ML April (mixed layer salinity ‰)	**-.928**	-.318
salinity ML July (mixed layer salinity ‰)	-.527	**-.714**
salinity BT July (bottom salinity ‰)	**-.963**	-.213
Distance		
distance shore (distance from shoreline m)	-.338	-.323
distance head bay (distance from head of bay m)	**-.731**	.511
Ichthyoplankton		
ichthyoplankton April (#/1000m^3)	**.955**	.108
ichthyoplankton June (#/1000m^3)	**.803**	-.534
ichthyoplankton August (#/1000m^3)	-.047	**.733**

Table 2.7. Factor loadings for the PCA of sediment variables. Heavily weighted loadings (+/-0.70) are shown in bold.

Variable	**Factors**	
Sediment Variable	**1**	**2**
c/mg (%/site)	**.734**	.159
n/mg (%/site)	**.869**	.141
c/n (carbon/nitrogen mg)	-.591	.318
m-sand (medium sand >350-250 µm)	.566	.465
f-sand (fine sand <250-125µm)	.620	-.195
v-fine sand (very fine sand <125-62.5 µm)	.484	-.489
c-silt (coarse silt <62.5-31 µm)	.203	-.463
v-f-med silt (very fine to medium silt <31–3.9 µm)	-.414	**-.724**
clay (<3.9-0 µm)	.123	**.957**
Abiotic water column Variable		
depth (depth/site)	**-.874**	.320

Table 2.8. Mann-Whitney tests for differences in diversity, species richness and evenness between the site groupings designated by the PCA-H analysis (axes 1 &2) of species data, (α=0.05 and significant differences are shown in bold).

Site Group	**Diversity**		**Richness**		**Evenness**	
	Mean Rank	**p-value**	**Mean Rank**	**p-value**	**Mean Rank**	**p-value**
n=18 Head of Bay vs Central Channel	15.50	**<0.001**	14.00	**0.010**	10.67	0.553
vs upper Western Channel group	6.50		7.25		8.92	
n= 30 Head of Bay vs Eastern Channel	21.42	**0.002**	10.67	**0.013**	22.08	**<0.001**
vs lower Western Channel group	11.56		18.72		11.11	
n=24 Central Channel/upper Western Channel group	21.33	**<0.001**	17.58	**0.041**	21.00	**<0.001**
vs Eastern Channel/ lower Western Channel group	9.56		10.81		9.67	

Table 2.9. Multiple regression of environmental variables with species diversity. The overall model is significant (p=0.003) with df(total)=16 and F=8.97. Environmental variable(s) that contributed significantly to the model are shown in bold.

Environmental Variables	**Standardized Coefficients**	**p-values**
Temperature BT (July)	1.204	0.162
Chlorophyll *a* June	1.247	0.089
Depth	-3.424	**0.010**
% C/mg	0.579	0.265
V-f-med-silt	-0.057	0.754
Temperature ML	1.811	0.050
Salinity ML	1.371	0.088
Distance fr. headbay	**2.141**	**0.036**

Table 2.10. Multiple regression of environmental variables with density. The overall model is significant (p=0.027) with df(total)=16 and F=4.31. Environmental variable(s) that contributed significantly to the model are shown in bold.

Environmental Variables	**Standardized Coefficients**	**p-values**
Temperature BT (July)	1.773	0.136
Chlorophyll *a* June	-1.291	0.182
Depth	3.535	**0.035**
% C/mg	-0.430	0.534
V-f-med-silt	0.178	0.480
Temperature ML	-1.714	0.150
Salinity ML	-1.037	0.361
Distance fr. headbay	-1.458	0.246

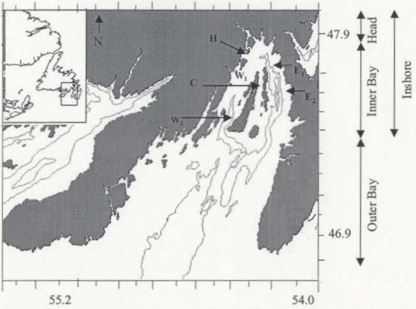


Figure 2.1. Chart of Placentia Bay and location of sampling sites. Capital letters indicate sampling sites. H denotes head of bay, C is Central Channel, E1 and E2 are upper and lower Eastern Channel, W1 and W2 are Western Channel. Arrows on the right indicate different parts of the bay including the head, and inner bay (collectively the inshore), and the outer bay which is considered to be offshore. Inset shows Placentia Bay in relation to Newfoundland. Depth contour line is 200 m.

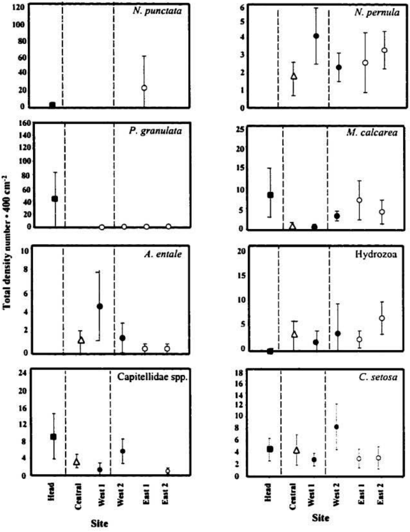


Figure 2.2. Plot showing mean densities and 95% confidence intervals of dominant taxa, with n=6. Note scale on y-axis differs among taxa.

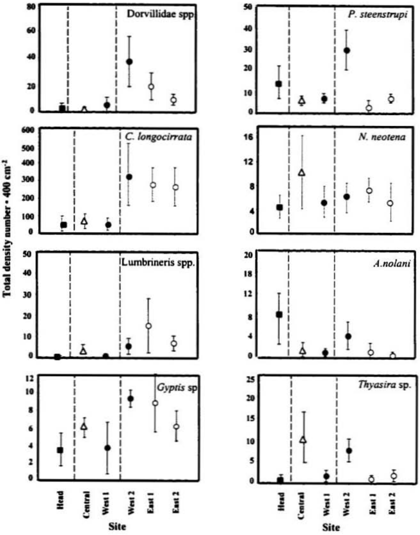

Dorvillidae spp
P. steenstrupi
C. longocirrata
N. neotena
Lumbrineris spp.
A.nolani
Gyptis sp
Thyasira sp.
Total density number • 400 cm-2
80
60
40
20
0
50
40
30
20
10
0
600
500
400
300
200
100
0
16
12
8
4
0
50
40
30
20
10
0
20
18
12
8
4
0
12
10
8
6
4
2
0
25
20
15
10
5
0
Head
Central
West 1
West 2
East 1
East 2
Site
Head
Central
West 1
West 2
East 1
East 2
Site

Figure 2.2. B.

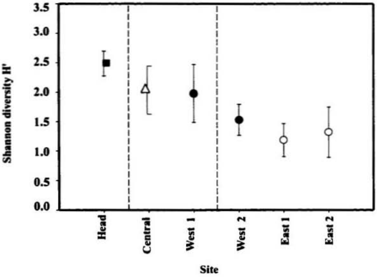


Figure 2.3. Plot showing means and 95% confidence intervals for Shannon diversity at each site (n=6).

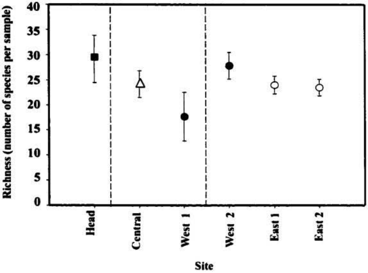


Figure 2.4. Plot showing means and 95% confidence intervals for the number of species present at each site (n=6).

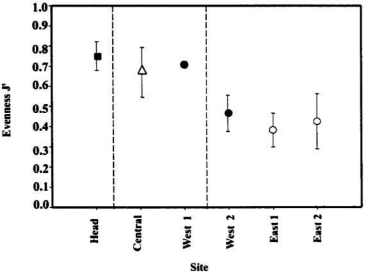


Figure 2.5. Plot showing means and 95% confidence intervals for species evenness at each site (n=6).

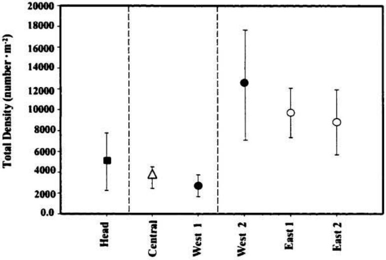


Figure 2.6. Plot showing means and 95% confidence intervals for total density of macrofauna at each site (n=6).

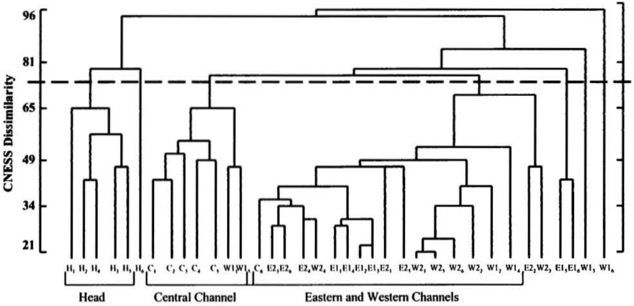


Figure 2.7. Cluster analysis of 6 site (36 box core samples) by 88 species matrix based on CNESS dissimilarity. Capital letters denote sites sampled and subscript denotes replicate box cores (1 to 6), H_1, H_2… (head of bay replicates 1 and 2 respectively), $E1_1$, $E1_2$... (upper Eastern Channel replicates 1 and 2), $E2_1$ (lower Eastern Channel replicate 1), $W1_1$ (upper Western Channel replicate 1), and $W2_1$ (lower Western Channel replicate 1) and C_1 (Central Channel replicate 1).

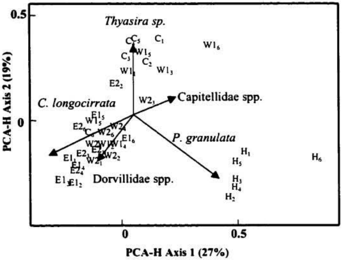


Figure 2.8 PCA-H metric scaling ordination in two dimensions of box core spatial patterns based on CNESS (NESSm = 10 individuals). Species vectors of PCA-H ordination (Gabriel Euclidean distance biplot) have been overlaid on community ordination to show which species contribute to CNESS variation among samples and therefore drive spatial patterns. The first two axes explain 27% and 19% of the variance in the data respectively.

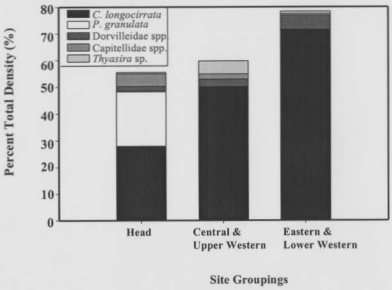


Figure 2.9. Stacked bar graph showing the percentage of total individuals contributed by each species to the site groupings obtained in PCA-H shown in Figure 2.8. Graph only includes species that were identified by Gabriel biplots. Proportions were determined by pooling the replicates within each geographic grouping.

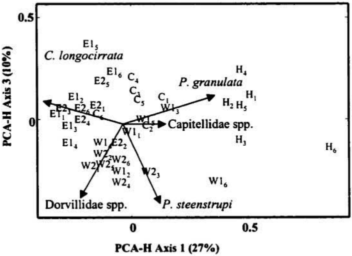


Figure 2.10. PCA-H metric scaling ordination in two dimensions of box core spatial patterns based on CNESS (NESSm=10 individuals). Species vectors of PCA-H ordination (Gabriel Euclidean distance biplot) have been overlaid on community ordination to show which species contribute to CNESS variation among samples and therefore drive spatial patterns. The first two axes explain 27% and 10% of the variance in the data respectively. See Figure 2.7 for site designations.

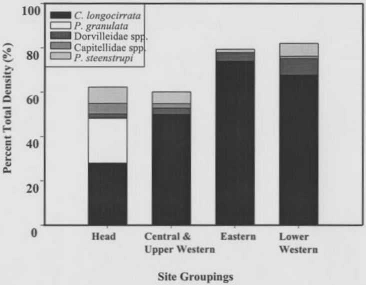


Figure 2.11. Stacked bar graph showing the percentage of total individuals contributed by each species to the site groupings obtained in PCA-H shown in Figure 2.10. Proportions were determined by pooling the replicates within each geographic grouping.

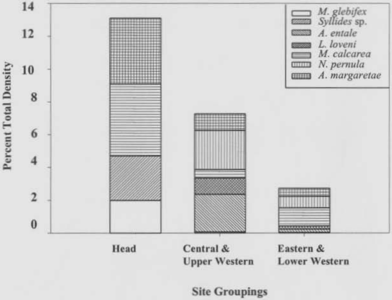


Figure 2.12. Stacked bar graphs showing the percentage of total individuals contributed by each species to the site groupings obtained from PCA-H analysis shown in Figure 2.8. Only includes species designated as important by discriminant function analysis and that make up at least 1% of the total density at any one site.

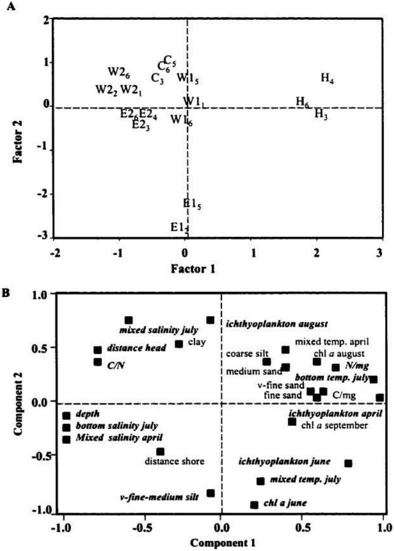


Figure 2.13 A. Spatial patterns defined by Principal Components Analysis of environmental data. B. Plotted factor loadings with heavily weighted loadings (±0.70) shown in bold.

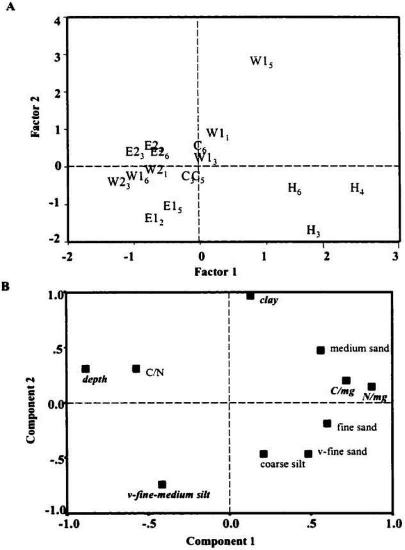


Figure 2.14 A. Spatial patterns defined by Principal Components Analysis of sediment- related variables and depth. B. Plotted factor loadings with heavily weighted loadings (±0.70) shown in bold.

Chapter 3. A guide to the polychaetes of Placentia Bay, Newfoundland

3.1 Introduction

One of the greatest challenges in completing this study was the accurate identification of macroinvertebrates, and this was especially true for the polychaetes. Information concerning subtidal benthic communities in Newfoundland (Carter et al. 1979; Houston and Haedrich 1984; Kennedy 1985; Gilkinson et al. 1998) or the east coast of Canada (e.g. Whiteaves 1901; Treadwell 1948; Bourget and Messier 1983), for that matter, is scant, and taxonomic literature and expertise are largely lacking for this area of the world. In most cases, several identification keys encompassing a wide range of geographical areas including the east coast of Canada, British Columbia, California, and New England to Bermuda were used in order to identify a single species.

Polychaetes are an important part of soft-sediment communities and it is well established that they can be dominant in terms of numbers of species, numbers of individuals, and biomass (Sanders et al. 1965; Hessler and Jumars 1974; Boesch et al. 1977; Knox 1977; Fauchald and Jumars 1979). In Placentia Bay and the adjacent shelf, a total of 118 infaunal species were collected and 63 (53%) of these were polychaetes. In terms of abundance, polychaetes comprised 88% (by number) of total infauna. It has also been shown that polychaetes can be important indicators of pollution (Grassle and Grassle 1974; Pearson and Rosenberg 1978) and this, along with growing interest in conservation and biodiversity of the marine environment, make the proper identification of these organisms essential.

This was the first comprehensive study of sedimentary infauna in Placentia Bay. A complete list of infaunal species collected along with abundances for each site sampled are given in Appendix 3.1. This final chapter provides a taxonomic summary of species of Placentia Bay and adjacent shelf, including a list of polychaetes that were collected and identified to species, the key characteristics that were used to identify them, digital photographs of some of these key characters and, a glossary of taxonomic terms. It is organised as follows. Species descriptions are organised alphabetically by family and then by genus, within each family and species are described on a separate pages with illustrations of the key characters. The information provided is referenced from several identification keys (e.g. Hartman 1965; Banse and Hobson 1974; Fauchald 1977; Gosner 1978; Light 1978; Appy et al. 1980; Hobson and Banse 1981; Pocklington, 1984; Pocklington, unpublished), and the keys that were most helpful in identifying each species are listed at the end of each species description. A glossary of the terms used for these descriptions is presented at the end of the descriptions, followed by a short discussion of some of the challenges and limitations associated with identifying polychaetes from this region. Polychaetes that could not be identified to species are not included in this summary.

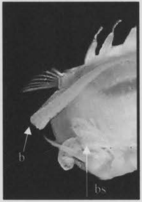
The main goal of this chapter is to provide documentation of species identifications as well as help others in the future who are working in this area. Digital photographs should also aid with taxonomic terminology by providing visual representation that is often lacking in identification keys.

3.2 Family: Ampharetidae

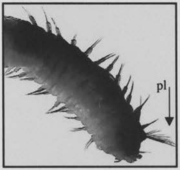
3.2.1 *Ampharete acutifrons* (Grube, 1860)

Key characteristics:

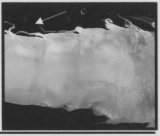
- more than two pairs of branchiae (b), (some missing but can see branchial scars (bs))
- branchiae in 2 groups separated by a space equal to 1-2 branchial bases
- prostomium not pointed (trilobed)
- no large dorsal hooks behind branchiae/gills



- peristomial or buccal tentacles pinnate (use compound scope to view) and approximately subequal
- paleae (pl) well developed (10-30 pairs), long and slender

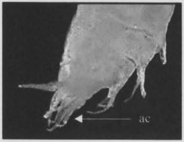


- neuropodia cirri (c) of abdominal neuropodia very long
- teeth of uncini in 2 rows



Key characteristics of (*A. acutifrons*) continued:

- numerous long and slender anal cirri (ac)



References:

Pocklington, unpublished. Pg. 163 (description) & Pg. 242 (Plate XXVI, Fig. d)

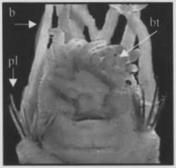
3.2.2 *Ampharete finmarchica* (Sars, 1866)

Key characteristics:

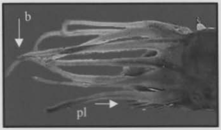
- more than two pairs of branchiae (b), prostomium not pointed

- no large dorsal hooks behind branchiae/gills

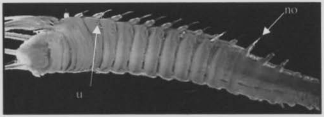
- peristomial or buccal tentacles (bt) pinnate (use compound scope) and approximately subequal



- paleae (pl) present and well developed, stout, curved with short offset tip

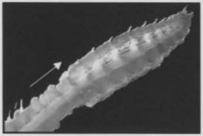


- capilliform notosetae (no) on 14 segments, uncini (u) begin on setiger 3

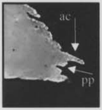


Key characteristics (*A. finmarchica*) continued:

- 13 abdominal setigers



- pygidium has 2 long anal cirri (ac) and a number of short papillae (pp)

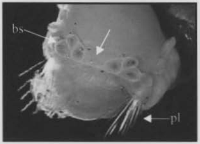


References:

Pocklington, unpublished. Pg. 164 (description) & Pg. 260 (Plate XXVI, Fig. f, g)

3.2.3 ***Ampharete goesi*** (Malmgren, 1866)

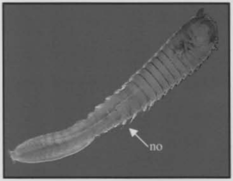
Key characteristics:



- more than two pairs of branchiae (broken off in this specimen but can see branchial scars (bs)), prostomium not pointed

- no large dorsal hooks behind branchiae/gills

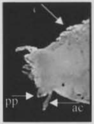
- branchial groups separated by a space approximately equal to one brachial base diameter



- paleae (pl) present and well developed, relatively short, stout, curved at tip and sharp

- peristomial or buccal tentacles pinnate (use compound scope), approximately subequal

- capilliform notosetae (no) on 14 or 15 segments, uncini begin on setiger 3



- 17 abdominal setigers

- cirri (c) on abdominal neuropodia small

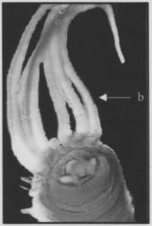
- 2 long anal cirri (ac) and papillae (pp) if present short

References:

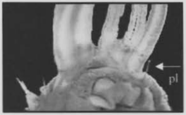
Pocklington, unpublished. Pg. 165 (description) & Pg. 260 (Plate XXVI, Fig. f, g)

3.2.4 ***Lysippe labiata*** (Malmgren, 1866)

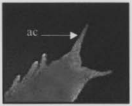
Key characteristics:



- more than two pairs of branchiae (b)
- no large dorsal hooks behind branchiae/gills
- peristomial or buccal tentacles smooth (use compound scope) approximately subequal



- paleae (pl) present but scarcely perceptible
- capilliform notosetae on 16 segments and begin at segment 3, uncinate setae begin on segment 4
- 14 abdominal segments



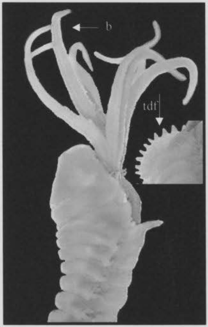
- 2 long anal cirri (ac)

References:

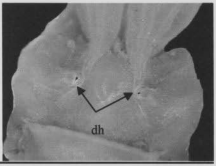
Pocklington, unpublished. Pg. 169 (description) & Pg. 261 (Plate XXVII, fig. b)
Hartman 1965. Pg. 218 (description)

3.2.5 *Melinna cristata* (Sars, 1851)

Key characteristics:



- prostomium not pointed
- more than 2 pairs of branchiae (b)
- transverse dorsal fold (tdf) posterior to hooks with 10-20 teeth



- 2 large dorsal hooks (dh) located behind gills/branchiae (retracted somewhat on this specimen)
- dorsal hooks long with slightly bent tips

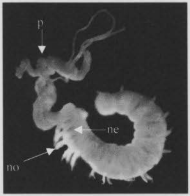
References:

Pocklington, unpublished. Pg.169 (description) & Pg. 261 (Plate XXVII, Fig. c)
Hobson and Banse 1981. Pg. 85 (Fig. 21o)

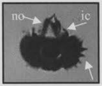
3.3 Family: Apistobranchidae

3.3.1 *Apistobranchus typicus* (Webster and Benedict, 1887)

Key characteristics:



- prostomium rounded with one pair of long palps (p)
- thorax is made up of 7 setigers with lanceloate notopodia (no), each with a aciculum but without notosetae
- neuropodia (ne) with several rows of fine setae
- below the notopodia are interramal cirri (ic)



- postsetal neuropodial lamellae of setigers 5-7 form a subpodal fimbriated flange almost meeting ventrally
- setigers 8-11 transitional, without interramal cirri
- posterior region with cylindrical noto- and neuropodia, paired anal appendages

References:

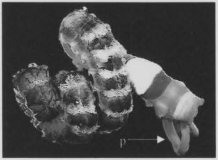
Hartman 1965. Pg. 145 (description) & Pg. 313 (Plate 27 a-h)
Appy et al. 1980. Pg. 22 (Fig. 39 a,b) as *A. tullbergi*
Pocklington, unpublished. Pg. 100 (description)

3.4 Family: Chaetopteridae

3.4.1 *Spiochaetopterus typicus* Sars 1856

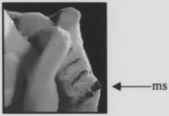
Key characteristics:

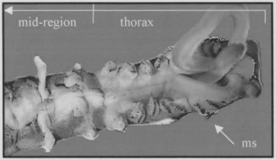
- 1 pair of long palps (p)



- body with 3 distinct regions including:
- thorax with 9 uniramous setigers
- mid-region of 2-10 elongate segments
- posterior region with numerous segments and biramous parapodia

- setiger 4 with large stout setae (ms)





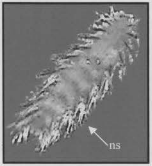
References:

Pocklington, unpublished. Pg. 115 (description) & Pg. 247 (Plate XIII, Fig. e,f)

3.5 Family: Chrysopedtalidae

3.5.1 *Dysponetus pygameus* Levinsen, 1879

Key characteristics:



- small oval shaped species with approximately 15 segments
- eyes absent
- dorsal and ventral cirri present
- parapodia biramous
- notosetae (ns) dark brown and arranged in fan shaped groups laterally and dorsally
- dorsal cirri large and subulate, equal to or larger than the notosetae
- prostomium with 3 short elliptical shaped antennae

References:

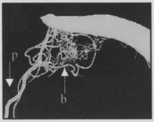
Pocklington, unpublished. Pg. 25 (description)
Appy et al. 1980. Pg. 26 (Fig. 47)

3.6 Family: Cirratulidae

3.6.1 *Chaetozone setosa* Malmgren 1867

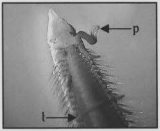
Key characteristics:

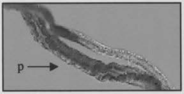
- body elongate, fusiform in outline
- prostomium conical and pointed



- branchiae (b) numerous (more than six pairs), found along entire surface

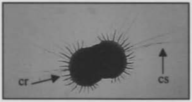
- large grooved tentacular palps (p)





Key characteristics (*C. setosa*) continued:

- acicular setae or crotchets (cr) present as well as capillary setae (cs)



- crotchets restricted to posterior segments and almost encircling body

- epitokous specimens contain long swimming setae (capillary) which begin at about setiger 18

References:

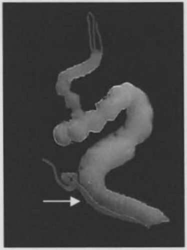
Appy et al. 1980. Pg. 28 (Fig. a,b)
Pocklington, unpublished. Pg. 117 (description) & Pg. 247 (Plate XIII, Fig. h, i)

3.7 Family: Cossuridae

3.7.1 *Cossura longocirrata* (Webster and Benedict 1887)

Key characteristics:

- prostomium without appendages
- single long cirrus (c) present dorsally on segment four
- without branchiae



References:

Appy et al. 1980. Pg. 29 (Fig. 52)
Hartman 1965. Pg. 170 (description) & Pg. 329 (Plate 35 a, b)
Note: most of Placentia Bay specimens were broken into two pieces

3.8 Family: Flabelligeridae

3.8.1 *Brada villosa* (Rathke, 1843)

Key characteristics:

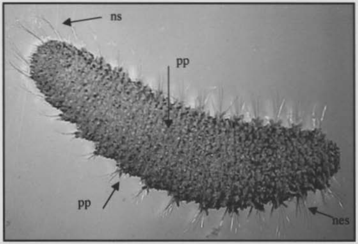
- cephalic cage absent

- body grub-like and mucous cover absent

- 2-5 well developed notosetae (ns) per segment

- neuropodia with "ring" of long papillae (pp) and with 3-6 neurosetae (nes), (amber colored)

- dermal papillae (pp) with filiform tip



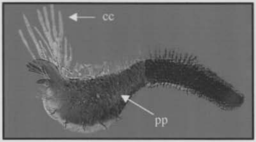
References:

Appy et al. 1980. Pg. 34 (Fig. 62)
Pocklington, unpublished. Pg. 123 (description) & Pg. 249 (Plate XV Fig. c,d)

3.8.2 ***Pherusa plumosa*** (Müller, 1776)

Key characteristics:

- body elongate (not grub like), with numerous papillae (pp) but without a mucous cover



- cephalic cage (cc) present
- notosetae capilliform
- neurosetae short, stout, uncinate and hooked (amber colored)

References:

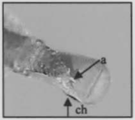
Pocklington, unpublished. Pg. 125 (description) & Pg. 242 (Plate XVI, Fig. b)

3.9 Family: Goniadidae

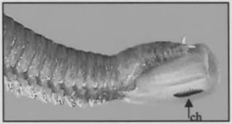
3.9.1 *Goniada maculata* Oersted 1843

Key characteristics:

- prostomium conical and transversely annulated, also with 4 minute antennae (a)



- chevrons (ch) on proboscis (7-11)



- anterior region with uniramous parapodia (38-40)

Key characteristics (*G. maculata*) continued:

- posterior region with biramous parapodia

- anal cirri (ac)

References:

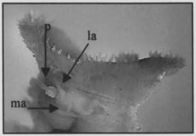
Appy et al. 1980. Pg. 38 (Fig. 69)
Banse and Hobson 1974. Pg. 81 (Fig. 22 f)

3.10 Family: Hesionidae

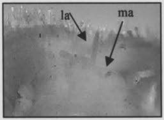
3.10.1 *Gyptis* sp.

Key characteristics:

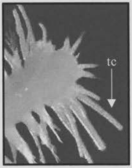
- biarticulate oral palps (p)



- prostomium with 1 median (ma) and two lateral (la) antennae

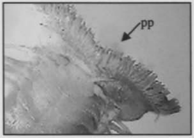


- 8 pairs of tentacular cirri (tc)

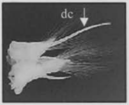


Key characteristics (*Gyptis* sp.) continued:

- eversible pharynx with circlet of papillae (pp) distally (>100)



- dorsal cirri long, monofiliform; ventral cirri shorter than neuropodia



References:

Note: these specimens from Placentia Bay are similar to both *G. vittata* and *Paragyptis margaretae*

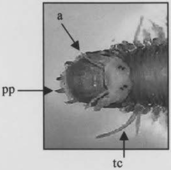
Pocklington 1984. Pg. 2334-2338. (comparison between *G. vittata* and *P. margaretae*)

3.10.2 *Nereimyra punctata* (Müller, 1788)

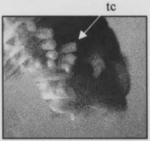
Key characteristics:

- 2 antennae (a), (no median antennae)

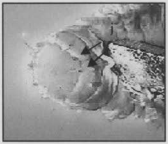
- eversible pharynx with circlet of papillae (pp) (<100) distally



- 6 pairs of cirri (tc) on each side



- jaws (j) present on pharynx (2 sets located ventrally)



Key characteristics (*N. punctata*) continued:

- neuropodia trilobed

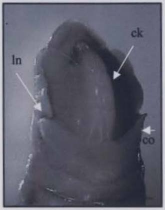
References:

Fauchald 1977. Pg. 76
Gosner 1971. Pg. 364 (Fig. 17.16 c)
Pocklington, unpublished. Pg. 42 (description)

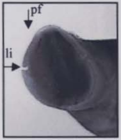
3.11 Family: Maldanidae

3.11.1 *Maldane glebifex* Grube 1860

Key characteristics:



- cephalic plate with large rim
- setiger 1 without anterior collar (co)
- cephalic keel (ck) long and high, shallow lateral notches (ln) on rim



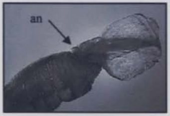
- with pygidial funnel (pf) or plate
- pygidial plate with narrow rim, with weak lateral incision (li)

- ventral rim of pygidial plate dentate (d)

Key characteristics (*M. glebifex*) continued:

- anus (a) dorsal to pygidial plate

- 19 setigers



References:

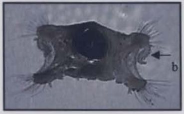
Fauchald 1977 Pg. 40
Hobson and Banse 1981. Pg. 74 (Fig. 16 p,q)

3.12 Family: Nephtyidae

3.12.1 *Nephtys ciliata* (Müller, 1776)

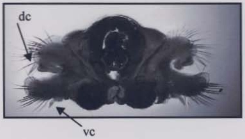
Key characteristics:

- branchiae (b) recurved with convex side toward laterial side of body



- branchiae (b) cirriform and begin on segment 4-8 and reduced in posterior segments

- with dorsal (dc) and ventral cirri (vc)



- anterior parapodial lamellae rudimentary

- posterior parapodial lamellae sub-equal to acicular lobe


anterior end


posterior end

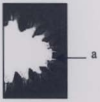
References:

Appy et al. 1980. Pg. 48 (Fig. 90)
Pocklington, unpublished. Pg. 65 (description)

3.12.2 *Nephtys neotena*

Key characteristics:

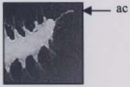
- prostomium with 4 minute antennae (a)



- eyes on setiger 3 (usually very difficult to see)

- branchiae (b) point inwardly toward lateral side of body, begin on setiger 5-6

- single anal cirrus (ac)



References:

Appy et al. 1980. Pg. 45 (Fig. 85 a,b) as *Aglaophamus neotenus*

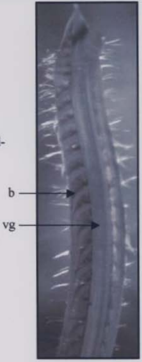
3.13 Family: Opheliidae

3.13.1 *Ophelina acuminata* Oersted, 1843

Key characteristics:

- body elongate (without distinct regions) with a ventral groove (vg) running the entire length of the body

- branchiae (b) begin at setiger 2 and are present in mid-region



- anal tube ventrally incised and with papillae (pp) around open edges

References:

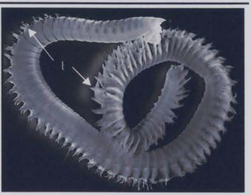
Appy et al. 1980. Pg. 52 (Fig. 99 a, b)
Pocklington, unpublished. Pg. 132 (description) & Pg. 251 (Plate XVII, Fig. g)

3.14 Family: Orbiniidae

3.14.1 *Scoloplos armiger* (Müller, 1776)

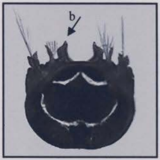
Key characteristics:

- prostomium conical
- branchiae (b) begin on segments 9-17
- thoracic setigers 12-20



anterior end

- thoracic neurosetae include hooks
- with 1-2 extra subpodial papillae on last few thoracic segments (not shown)
- parapodia without interramal cirri



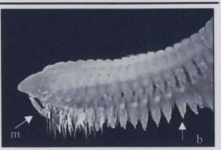
References:

Appy et al. 1980. Pg. 56 (Fig. 106 a,b)
Pocklington, unpublished. Pg. 93 (description) & Pg. 237 (Plate III, Fig. i, j)

3.15 Family: Paraonidae

3.15.1 *Aricidea nolani* Laubier, 1967

Key characteristics:



- prostomium with a non-articulated median antennae (ma)
- median antennae (ma) short, subulate to fusiform, reaching to setiger 2
- has up to 30 pairs of branchiae (b)
- modified setae in posterior neuropodia with long slender spine

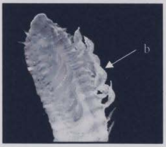
References:

Appy et al. 1980. Pg. 58 (Fig. 111) as *A. suecica*
Pocklington, unpublished. Pg. 95 (description) & Pg. 238 (Plate IV, Fig. c,d)

3.15.2 *Aricidea quadrilobata* Webster and Benedict, 1887

Key characteristics:

- prostomium with a non- articulated median antennae (ma)
- median antennae (ma) is long and filiform, reaching to setiger 4-6
- 9-10 pairs of pointed branchiae (b), beginning on setiger 4



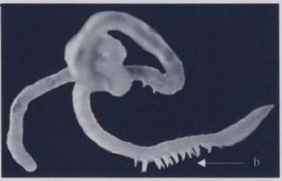
References:

Appy et al. 1980. Pg. 58 (Fig. 110 a-c)

3.15.3 *Tauberia gracilis* (Tauber 1879)

Key characteristics:

- median antennae absent
- 7- 17 pairs of strap-like branchiae (b)
- branchiae begin on setigers 6-7 and 9-14 pairs
- posterior neuropodial setae capillary and 3-6 hooked crotchets beginning on setiger 20



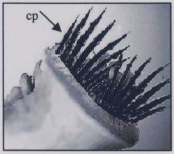
References:
Appy et al. 1980. Pg. 60 (Fig. 114 a, b)

3.16 Family: Pectinariidae

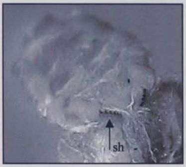
3.16.1 *Pectinaria granulata* (Linnaeus, 1767)

Key characteristics:

- cephalic paleae (cp) 7-10 pairs



- scaphal hooks (sh) 6-10 pair, curved or with distinct shoulder



Smaller specimen ⟶

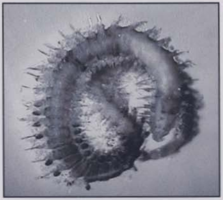
References:
Appy et al. 1980. Pg. 20 (Fig. 34 a-d) as *Cistena granulata*

3.18 Family: Phyllodocidae

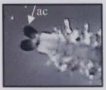
3.18.1 *Eteone longa* (Fabricius, 1780)

Key characteristics:

- 2 pair of tentacular cirri (subequal) on one segment (not shown)



- anal cirri (ac) short and thick almost spherical



- dorsal cirri (dc) longer than wide (not spherical), not much larger than parapodial lobe

References:

Appy et al. 1980. Pg. 62 (Fig. 117 a,b.c)
Banse and Hobson 1974. Pg. 40. (Fig. 8d)

3.18.2 *Phyllodoce maculata* (Linnaeus, 1767)

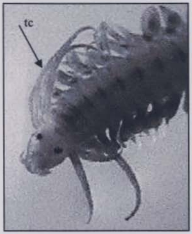
Key characteristics:

- 4 pairs of tentacular cirri (tc)

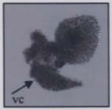
- no median antennae

- prostomium heart-shaped

- body with brownish spots mid-dorsally



- ventral cirrus (vc) oval not pointed



References:

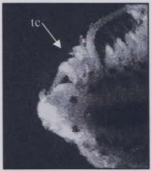
Hobson and Banse 1974. Pg. 47 (Fig. 10 c)
Pocklington, unpublished. Pg. 36 (description)
Do not use Appy 1980. Diagrams are not very good.

3.18.3 ***Phyllodoce groenlandica*** Oersted, 1842

Key characteristics:

-no median antennae

- prostomium heart-shaped



- tentacular cirri (tc) 4 pair

- parapodia dorsal cirrus (dc) with lobe below cirrophore

- ventral cirrus (vc) turned downward at tip

References:

Appy et al. 1980. Pg. 66 (Fig.127)
Banse and Hobson 1974. Pg. 45 (Fig. 10 b)

3.19 Family: Polynoidae

3.19.1 *Antinoella sarsi* (Kinberg in Malmgren 1866)

Key characteristics:

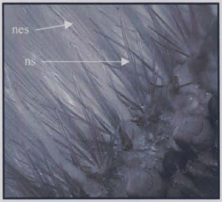
- lateral antennae (la) inserted ventral to median antennae (ma), (broken off in this specimen)

- notopodia with notosetae (ns) and acicula

- at least 15 pairs of elytra (e)

- notosetae (ns) stouter than neurosetae (nes)

- two types of neurosetae (not shown) (i.e., long capillary tips and stouter with a slight sub-distal expansion)



References:

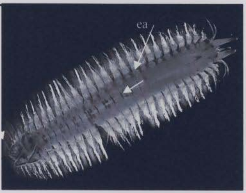
Pocklington, unpublished. Pg. 12 (description)

3.19.2 *Arcteobia anticostiensis* (McIntosh, 1874)

Key characteristics:

- fewer than 45 segments

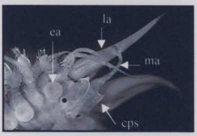
- irregularly banded mid-dorsally



- elytra (e) covers dorsum (this specimen is missing most of its elytra but can see elytral attachments (ea)

- elytra with pigmented areas

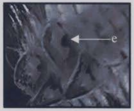
- prostomium with distinct cephalic peaks (cps)



- anterior pair of eyes anteroventral

- lateral antennae (la) inserted ventral to median antennae (ma)

- upper notosetae shorter, stouter, with blunt tips; rest of notosetae with capillary tips (not shown)



References:

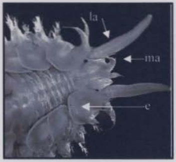
Appy et al. 1980. Pg. 49 (Fig. 134 a,b)
Pocklington, unpublished. Pg. 10 (description)

3.19.3 *Enipo canadensis* (McIntosh, 1874)

Key characteristics:

- lateral antennae (la) inserted ventral to median antennae (ma)

- prostomium rounded

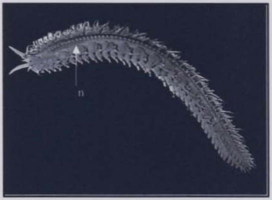


- more than 45 segments, elytra (e) on anterior segments only

- two mid-dorsal nodules (n) per segment

- elytra occupying lateral regions only

- at least some notosetae with slender capillary tips; or notosetae more slender than neurosetae

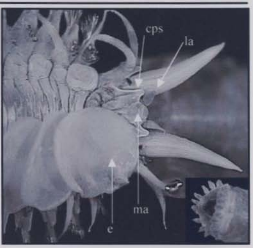


References:

Hobson and Banse 1974. Pg. 32 (Fig. 5 f) as *Polynoe*
Pocklington, unpublished. Pg. 13 (description)

3.19.4 *Nemidia torelli* (Malmgren, 1865)

Key characteristics:



- lateral antennae (la) inserted ventral to median antennae (is broken off in this specimen), (ma)
- prostomium with well developed, pointed cephalic peaks (cps) and 4 eyes
- at least 45 segments and elytra on anterior segments only (approximately 15 pairs)

- elytra (e) smooth and not completely covering dorsum
- notopodia with notosetae (ns) and acicula

- notosetae (ns) more slender than than neurosetae (nse), (difficult to see the difference in this photo)

References:

Pocklington, unpublished. Pg. 21 (description)

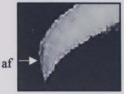
3.20 Family: Sabellidae

3.20.1 *Euchone incolor* Hartman, 1965

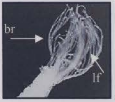
Key characteristics:

- uncini not completely encircling the abdominal segments (not shown)
- possessing long-handled, acicular thoracic uncini (not shown)
- collar oblique

- abdomen with more than three setigers
- posterior abdominal segments (last three setigers) modified into an anal funnel (af)



- 3-4 pairs of branchial rays (br), each bearing lateral filaments (lf) and terminating in a long free filiform tip, no branchial membrane



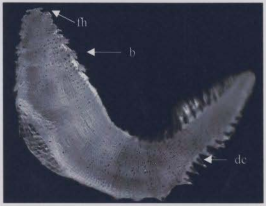
References:

Hartman 1965. Pg. 231 (description) & Pg. 361 (Plate 51 a-d)
Pocklington, unpublished. Pg. 192 (description) & Pg. 265 (Plate XXXI, Fig. p)

3.21 Family: Scalibregmatidae

3.21.1 *Scalibregma inflatum* Rathke, 1843

Key characteristics:



- body arenicoliform (not grub-like) and inflated anteriorly
- prostomium T-shaped due to frontal horns (fh)
- posterior parapodia with digitiform dorsal cirri (dc) and ventral cirri
- with branchiae (b) (appear bushy)
- without acicular spines

References:

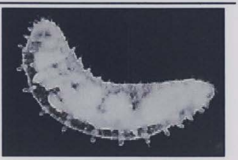
Appy et al. 1980. Pg. 78 (Fig. 152)
Pocklington, unpublished. Pg. 128 (description) & Pg. 251 (Plate XVII, Fig. a)

3.22 Family: Sphaerodoridae

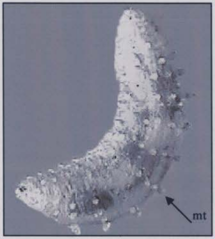
3.22.1 *Sphaerodoropsis minuta* (Webster and Benedict 1887)

Key characteristics:

- body short, cylindrical (grub-like)
- segmentation indistinct except marked by parapodia



- spherical glandular macrotubercles (mt) encircle dorsum in transverse rows
- 10-14 spherical and sessile macrotubercles (mt) per setiger
- setae compound



References:

Appy et al. 1980. Pg. 84 (Fig. 163 a,b)
Pocklington, unpublished. Pg. 69 (description)

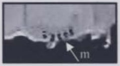
3.23 Family: Spionidae

3.23.1 ***Polydora caulleryi*** Mesnil, 1897

Key characteristics:

- palps (p) long

- setiger 5 (s5) larger than adjacent segments and contain modified setae (ms)



- modified spines of setiger 5 (s5) falcate with bushy tip

- cylindrical hooded hooks begin on setiger 7

- hooded hooks without constriction on shaft

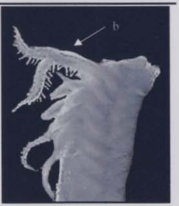
References:

Pocklington, unpublished. Pg. 104 (description) & Pg. 240 (Plate VI, Fig. a-d)

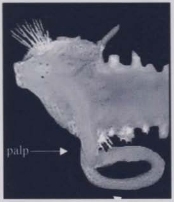
3.23.2 ***Prionospio steenstrupi*** Malmgren, 1867

Key characteristics:

- setiger 5 not modified
- 4 pair of branchiae (b) that begin on setiger 2 (only 2 pairs are present on this specimen)
- the 1st and 4th pair of branchiae are pinnate



- neuropodial hooded hooks begin at setiger 12-17



- anal cirri (ac)

References:

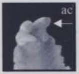
Light 1978. Pg. 88 (Fig. 89 a-d)
Pocklington, unpublished. Pg. 108 (description) & Pg. 242 (Plate VIII, fig. d,e,f)

3.23.3 *Spio filicornis* (Müller 1776)

Key characteristics:

- setiger 5 not modified (similar to adjacent segments)
- branchiae (b) present, begin on setiger 1 and present on most segments
- branchiae on setiger 1 approximately subequal to others

- 4 thick subulate anal cirri (ac) surrounding anus



- neuropodial uncini or crotchets (cr) hooded, bidentate, 6-10 beginning on setigers 10-24

References:

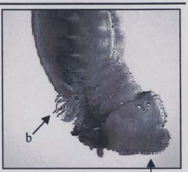
Light 1978. Pg. 45
Pocklington, unpublished. Pg. 110 (description) & Pg. 245 (Plate XI, Fig. f)
Hobson and Banse 1981. Pg. 44 (Fig. 6 j)

3.24 Family: Terebellidae

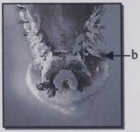
3.24.1 *Artacama proboscidea* Malmgren, 1865

Key characteristics:

- large conical proboscis covered with papillae (pp)

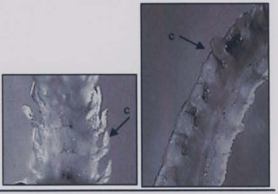


- groups of filiform branchiae/gills (b) on segments 2-4



- 17 thoracic setigers

- abdominal parapodia with rounded leaf- like cirri (c)



References:

Fauchald 1977 Pg. 130

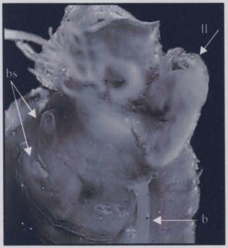
Pocklington, unpublished. Pg. 174 (description) & Pg. 262 (Plate XXVIII a,b)

3.24.2 ***Filibranchus roseus*** Malm 1874

Key characteristics:

- thoracic setae and uncini are first present from the 6th segment and continue posteriorily through 15 segments

- 1st segment has a pair of large lateral lobes (ll) extending ventrally which are completely separable medially



- 2 pair of cirriform branchiae (b) and each pair is inserted on each of the 2nd and 3rd segments (only one branchie is present on this specimen but branchial scars (bs) are present)

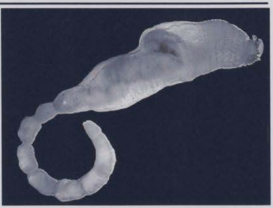
References:

Hartman 1965 pg. 227
Fauchald 1977 pg. 134

3.24.3 ***Lysilla loveni*** Malmgren, 1866

Key characteristics:

- branchiae absent
- segmentation indistinct
- uncinate neurosetae absent and abdominal segments achaetous



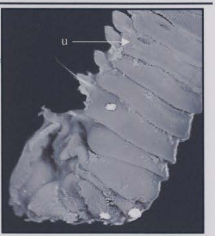
- approximately 6 thoracic notopodia (no)
- capilliform notosetae (cn) minute (barely visible)
- thorax with numerous, large epidermal papillae (pp)

References:

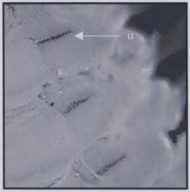
Pocklington, unpublished. Pg. 174 (Subfamily Key) & Pg. 185 (description)
Hobson and Banse 1981. Pg. 91

3.24.4 *Polycirrus eximius* group (Leidy, 1855)

Key characteristics:



- 16-31 thoracic segments bearing notosetae
- uncini (u) begin on segment 7-9
- branchiae absent



- posterior thoracic uncini (u) in 1 row

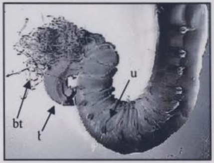
References:
Pocklington, unpublished. Pg. 174 (Subfamily Key) & Pg. 185 (description)

3.25 Family: Trichobranchidae

3.25.1 *Terebellides stroemi* Sars 1835

Key characteristics:

- buccal tentacles (bt) numerous
- 18 thoracic setigers
- uncini (u) begin at setiger 6 (in single rows)
- 1 median branchiae (b) with 4 pectinate lobes



median branchiae

References:
Appy et al. Pg. 98 (Fig. 194)
Hobson and Banse 1981. Pg. 97 (Fig. 24 c,d)

3.26 Glossary of polychaete terms. Definitions are based on Appy et al. (1980) and Fauchald (1979).

Abdomen – posterior portion of body, behind the thorax

Achaetous – without setae

Acicular seta – thick, projecting setae

Aciculum – stout supportive setae embedded in each parapodial lobe (ramus)

Anal cirrus/cirri – one or more elongate projections from the pygidium

Annulated – external division of segments, not true segmentation

Antennae – one or more elongate projections (sensory in function) located on the prostomium

Arenicoliform – body cylindrical and elongate, tapering toward posterior

Asetigerous - segments lacking setae, without setae

Biarticulated – with two points, used to describe antennae, palps, and tentacles

Bidentate – with two prongs or teeth

Biramous – with two branches, usually used to describe parapodia having both notopodia (upper division) and neuropodia (lower division)

Branchiae – an extension of the body wall which contains many capillary blood vessels (e.g. a gill)

Branchial rays – array of elongated appendages on the head of sabellids and serpulids used for feeding and respiration

Branchial scars – areas where branchiae attach to the body, scars left after branchiae have fallen off or been removed

Buccal cirri – cirri in or around the mouth, sensory rather than feeding

Capillary setae – slender usually long setae tapering to a fine tip

Capilliform - slender and cylindrical

Cephalic cage – numerous long setae enclosing and protecting the head region

Cephalic rim – flange encircling the head

Chevron – v – shaped chitinized jaw piece at the base of the eversible pharynx in some goniadids

Cirri – sensory projection, usually slender

Cirriform – slender and cylindrical

Clavate – club – shaped

Compound setae – setae having a terminal portion which articulates with a shaft, jointed setae

Crochet – small hook

Dentate – with notches or teeth

Digitiform – finger - shaped

Dorsal cirri – sensory projection, usually slender and cylindrical located on the notopodium

Elytra – dorsal scales like those found on scale worms

Epitoke – modified reproductive stage

Eversible proboscis/pharynx – part of pharynx being capable of being extended by turning the inner part outwards

Falcate setae – distally curved, usually blunt setae

Falciger – distally blunt and curved setae

Filiform – slender and threadlike

Frontal antennae – antennae situated at anterior end

Fusiform – spindal – shaped

Hooded hook – seta distally covered by a delicate chitinous enveloped or guard

Hook – used to describe stout – shafted, blunt, often distally curved and dentate setae

Lamellae – flattened feshy plates anterior and posterior to the setae

Ligule – finger – shaped major process on a parapodium

Lateral – side of body

Lobe – conical process of a parapodium

Long – handled – used to describe uncini, with a long basal rod supporting the uncinus

Moniliform – beaded or beadlike

Neuropodium – ventral lobe (ramus) of parapodium

Neurosetae – setae of neuropodium

Notopodium – dorsal lobe (ramus) of a parapodium

Notosetae – setae of notopodium

Paleae – strong or broad, usually flattened setae

Palps or tentacular palps – sensory or food gathering appendages on the prostomium or anterior segments (usually paired)

Papillae – conical dermal structures, nipple like

Parapodia – foot, paired, lateral appendages extending from the body segments. A parapodium can be biramous or uniramious, consisting of the upper division called the notopodium and a ventral division called a neuropodium.

Pectinate – a series of projections arranged like teeth of a comb

Peristomium – the presegmental region of the body surrounding the mouth

Pinnate – featherlike

Postsetal – posterior to the setae; used about parapodial lobes or ligules

Presetal – anterior to the setae

Prostomium – anteriormost, pre - segmental part of the body, sometimes bearing eyes and antennae; may not be externally recognizable

Pygidium – post – segmental part of the body surrounding the anus

Ramus – branch – like structure, used when describing notopodium (dorsal ramus) and neuropodium (ventral ramus)

Rudimentary – not present or extremely reduced, usually used in reference to parapodia

Scaphe – flattened caudal appendage of Pectinariids

Setae – chitinous hair protruding from the body

Setiger – refers to a segment bearing setae

Short – handled – used to describe uncini, without a long rod–shaped support

Simple setae – unjointed setae

Sub–biramous parapodia – parapodia with neuropodium well developed and notopodium reduced

Sub–equal – same size

Subulate – awl - shaped, tapering to a fine point

Tentacular cirri – dorsal and/or ventral cirri of parapodia of cephalised segments, often more elongate than those of more posterior parapodia

Thorax – anterior region of the body, posterior to the head

Trilobed – with three lobes

Uncini – deeply embedded setae with only its expanded multidentate head protruding from the body; usually hooked and arranged in rows

Unidentate – distally entire

Uniramous – with one branch, used to describe parapodia with one lobe, usually the notopodium is absent

Ventral cirri - sensory projection, usually slender and cylindrical located on the neuropodium

Ventral groove – groove located on ventral side of body

3.27 Discussion

This chapter is not intended to be used as a "stand alone" taxonomic key and referenced keys should be used for identification. Indeed, as a general rule it is best to consult more than one key while identifying. All keys have their strengths and weaknesses and using them in combination can make identification more efficient and accurate. In addition, keys are usually developed for a specific area, and care must therefore be taken in using them to identify fauna from other areas because the specimen in question may not be included in the key, resulting in misidentifications.

The need to incorporate several keys into the identification process was especially pertinent in this study. The polychaetes of Newfoundland are not well known and no published key specific to this area exists. Moreover, the influence of both the Gulf Stream and Labrador Current in Placentia Bay results in a unique mixture of arctic and boreal species, some of which are reported as being at their northern or southern limit. Members of this assemblage are therefore not usually found together in a single key.

This chapter references several keys. In terms of identifying to the family level, the family key provided in Appy et al. (1980) along with illustrations and summaries of some external diagnostic characters of each family provided by Hobson and Banse (1981) and Banse and Hobson (1974) were very helpful. The species keys developed by Appy et al. (1980) were also useful and contained numerous figures making character identification easy. The greatest limitation of the Appy et al. (1980) key is that it focuses on the Bay of

Fundy area, and therefore does not include many of the species found in Placentia Bay. This key is therefore especially poor for several families, including Ampharetidae, Terebellidae, Dorvilleidae, Sigalionidae, and Polynoidae.

Pocklington's unpublished key entitled "The Polychaetes of Eastern Canada including the Eastern Arctic" is the best representative key for species found in this area. The species descriptions are detailed and informative and include information on the distribution and ecology of each species, which is lacking in most other keys for the region. Although this reference contains some very useful figures, illustrations are completely lacking for several families including Polynoidae, Sigalionidae, Phyllodocidae, Hesionidae, Nephtyidae and Syllidae. An excellent key, was produced by Fauvel (1923; 1927). It has exceptionally detailed species descriptions and figures showing setae and jaws which are usually only described rather than diagramed in the other keys. Because of its level of detail, however, it is not recommended for anyone new to polychaete taxonomy, particularly if they are not fluent in French. Pettibone (1963) is also a very good reference.

Several obstacles were encountered in identifying the Placentia Bay polychaetes that are not uncommon to taxonomy. Specimens were often broken into two or more pieces and others were missing such diagnostic characters as antennae, palps, and scales. In these cases it is necessary to look for scars where these appendages may have been attached, and examples of which are shown in the digital photographs provided. Different characters are more readily visible at particular angles and lighting regimes. It is also good practice to try placing specimens against light and dark backgrounds. The family Maldanidae was particularly difficult because in order to identify it to the species level, the anterior and posterior regions must both be present and this was complicated by the fact that individuals were often broken into several pieces. Members of the family Dorvilleidae and Syllidae also posed much difficulty because they were very small and particularly fragile.

Placentia Bay specimens did not always conform precisely to species descriptions in keys developed for other areas. For example, several specimens from the family Hesionidae were similar to the species *Gyptis vittata* in that they had a median antennae, but unlike this species they also contained >100 papillae on their pharynx as seen in *Paragyptis margaretae* (see Pocklington 1984 for details on the description of these two species). Because these specimens could not be classified as either of these two species, they were only identified to the genus level (*Gyptis* sp.) It is unknown whether this discrepancy is a more general taxonomic problem or a feature specific to Newfoundland. A similar situation occurred in the family Paraonidae where a relatively common polychate found in the inner bay resembled both *Aricidea nolani* and *A. catherinae*. It was similar to *A catherinae* in that its anterior region was dorsal ventrally flattened giving it a fusiform shape, that is a distinctive character in other areas, however, it had setae with an arista or slender spine that is specific to *A. nolani* and is described as cylindrical in shape. Because setae are better characters than body shape, these specimens were identified as *A. nolani*.

This same trend in Newfoundland polychaetes, and the need for these and other differences to be described, has been acknowledged by P. Pocklington (pers. communication).

Another interesting outcome from this study was that it extended a number of species ranges. For example, *Polycirrus eximius* was previously distributed along the New England States. This range was extended northward when reported in the southwestern and lower Bay of Fundy in the 1980's by Appy et al. (1980) and Peer et al. (1980) respectively, however, the Placentia Bay record extends its range even further northward. *Aricidea quadrilobata* was previously distributed from Nova Scotia to Massachusetts as well as a record from Nain Bay, Labrador (Bousfield 1981), but this study further extends its range. *Pholoë longa* is considered to be an arctic species (Pocklington, unpublished) and this record, along with a record from the Gulf of St. Lawrence (Pocklington 1988), extends its range southward. *Lysilla loveni* is also considered to be an Arctic species, and until this study was only reported as far south as Ungava Bay (Grainger 1954).

3.28 References

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3.29 Summary and Conclusions

It was evident from analysis of spatial patterns of community composition and environmental variation that Placentia Bay contains distinct inshore and offshore regions. The inshore region compared to the offshore was characterized by greater mixed layer temperatures, higher surface production (chl *a*), and large amounts of relatively fresh organic carbon. The higher levels of organic carbon inshore reduced species richness and diversity and this area contained many species that are known to be abundant in organic rich areas elsewhere. Different variables appeared to operate at different scales. At smaller scales (e.g. head of the bay and within the offshore), grain size was particularly important, even though areas of high surface production (chl *a*) had correspondingly elevated amounts of organic carbon. Abundance patterns suggested a negative relationship between surface production and abundance, however, it was found that this relationship was confounded by low abundance patterns at three sites within the inshore and elevated densities at a single site offshore (Oderin Bank) that is known to be productive.

Analyses of patterns within the inshore region of the bay in Chapter 2 revealed spatial patterns that were not evident in the analyses of broad-scale patterns in Chapter 1. Moreover, the results of these two chapters indicated that different variables structured these communities at different scales. Water column productivity-related variables, which were important to the larger scale inshore/offshore comparisons in Chapter 1, were not of primary importance to benthic patterns within the inshore, where sediment-related factors (i.e., grain size and quality of organic material) and depth showed similar spatial patterns as species data. In terms of abundance patterns, evidence suggests the quality, rather than quantity, of organic material, was important in influencing macrofaunal densities among inshore sites. Further study is needed to be conclusive.

Polychaete taxonomy can be very challenging and time consuming, and Chapter 3 was designed to assist others in the future who are working on polychaetes from this area. The polychaetes of Newfoundland are not well known, and no published key specific to this area exists. The polychaetes of Placentia Bay contain a unique mixture of arctic and boreal species, some of which are reported as being at their northern or southern limit. Indeed, this study extended a number of species ranges. Placentia Bay specimens did not always conform precisely to species descriptions in keys developed for other areas and it is unknown whether this discrepancy is a more general taxonomic problem or a feature specific to Newfoundland. This same trend in Newfoundland polychaetes, and the need for these and other differences to be described, has been acknowledged by P. Pocklington (pers. communication).

3.10 Appendix (Raw species data)

Number	Site	ELO	CSE	PST	MGL	NNE	AQU	ANO	CLO	GMRI	NPU	PGR	SSP	DOR	ACT	TAN
1	H(1)	1	6	6	15	6	0	11	30	3	1	10	3	3	2	1
2	H(2)	6	6	27	3	5	0	18	151	7	3	145	2	10	0	0
3	H(3)	0	0	10	0	2	0	2	20	1	0	7	9	4	0	0
4	H(4)	1	6	4	2	6	0	7	57	1	1	38	5	2	0	0
5	H(5)	1	5	24	3	7	0	3	79	5	1	26	7	2	6	3
6	H(6)	1	4	15	1	1	0	6	1	4	3	18	7	4	0	0
7	C(1)	0	9	6	1	14	0	4	50	6	0	0	0	0	0	1
8	C(2)	0	6	9	0	5	0	1	55	8	0	0	0	2	0	0
9	C(3)	0	6	7	0	10	0	3	80	6	0	0	0	1	0	0
10	C(4)	0	0	1	0	6	0	0	26	7	0	0	0	1	0	0
11	C(5)	0	2	5	0	7	0	1	41	5	0	0	0	1	0	0
12	C(6)	0	4	7	0	8	0	0	171	4	0	0	0	6	0	0
13	E2(1)	0	4	10	0	4	0	0	283	4	0	1	0	12	0	0
14	E2(2)	0	0	4	0	2	0	0	32	6	0	0	0	6	0	0
15	E2(3)	2	4	8	0	9	0	1	392	5	0	2	0	15	0	0
16	E2(4)	0	2	4	0	0	0	2	262	5	0	1	0	11	0	0
17	E2(5)	2	3	7	0	10	0	0	234	8	0	1	0	1	0	0
18	E2(6)	5	7	9	0	7	0	0	409	10	0	1	0	11	0	0
19	W2(1)	2	9	35	0	10	0	8	655	10	0	0	1	74	1	0
20	W2(2)	5	14	30	0	4	0	4	417	11	0	3	1	51	0	0
21	W2(3)	0	5	42	0	8	0	8	159	8	0	1	0	19	0	0
22	W2(4)	2	4	16	0	2	0	1	95	8	0	0	0	13	0	0
23	W2(5)	3	14	39	0	8	0	3	507	9	0	0	0	44	0	0
24	W2(6)	2	4	15	0	4	0	1	217	10	0	0	0	24	0	0
25	E1(1)	1	4	1	0	5	0	0	277	8	0	1	0	14	0	0
26	E1(2)	1	1	0	0	8	0	0	238	3	1	1	0	15	0	0
27	E1(3)	1	4	0	0	8	0	0	468	5	0	1	1	36	0	0
28	E1(4)	0	6	8	0	4	0	5	367	13	0	0	0	33	0	0
29	E1(5)	0	2	0	0	11	0	0	177	10	23	0	0	5	0	0
30	E1(6)	2	1	8	0	8	0	2	153	13	114	1	0	12	0	0
31	W1(1)	3	3	5	0	7	0	0	49	9	0	1	0	5	0	0
32	W1(2)	0	3	8	0	7	0	2	70	4	0	0	0	19	0	0
33	W1(3)	1	2	10	0	9	0	1	54	1	0	0	0	0	0	0
34	W1(4)	0	5	10	0	3	0	0	127	0	0	0	0	4	0	0
35	W1(5)	1	3	4	0	6	0	2	21	7	0	0	0	3	0	0
36	W1(6)	0	1	5	0	0	0	1	3	1	0	0	0	0	0	0
37	S1(1)	0	1	44	0	11	0	1	78	0	0	0	0	1	0	0
38	S1(2)	2	1	112	0	11	0	6	82	1	0	0	0	10	0	0
39	S2(1)	0	15	115	0	28	0	7	173	0	0	0	0	1	0	0
40	S2(2)	1	1	144	0	34	0	9	129	1	0	0	0	1	0	1
41	S2(3)	4	10	136	1	52	0	4	107	0	0	0	0	2	0	0
42	S3(1)	0	17	16	0	0	17	3	33	0	0	0	1	1	1	1
43	S3(2)	0	34	25	0	0	36	0	31	0	0	0	3	0	2	0
44	S3(3)	0	26	29	0	1	39	11	35	0	0	0	8	0	2	2
45	O(1)	1	23	18	0	18	0	5	315	11	0	1	0	6	3	0
46	O(2)	1	19	29	0	27	0	11	494	21	0	0	0	11	4	0
47	O(3)	2	15	78	0	14	0	8	242	11	0	1	0	3	3	0

Number	Site	AAN	SFI	CUM	AGO	PPL	LUM	PLO	SMI	PFE	BAT	EIN	HY2	HY1	HY3	MON
1	H(1)	1	1	2	1	2	1	4	0	0	0	0	0	0	0	0
2	H(2)	0	0	2	0	0	0	1	2	1	1	0	0	0	0	0
3	H(3)	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0
4	H(4)	0	1	2	0	3	1	3	0	0	1	0	0	1	0	1
5	H(5)	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
6	H(6)	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1
7	C(1)	0	0	3	0	0	6	0	0	0	1	0	0	2	0	0
8	C(2)	0	0	2	0	0	3	0	0	0	0	0	0	2	0	0
9	C(3)	0	0	0	0	0	8	0	1	0	0	0	1	10	0	0
10	C(4)	0	0	2	0	0	3	0	0	0	0	0	0	1	1	0
11	C(5)	0	0	0	0	0	4	0	0	0	0	0	1	1	0	0
12	C(6)	0	0	0	0	0	0	0	1	2	0	0	1	1	0	0
13	E2(1)	0	0	13	0	0	2	0	0	0	0	0	1	10	1	0
14	E2(2)	0	0	1	0	0	11	0	0	0	0	0	1	0	0	0
15	E2(3)	0	0	0	0	0	10	0	0	0	0	0	8	6	0	0
16	E2(4)	0	0	0	0	0	1	1	0	0	1	0	0	5	0	0
17	E2(5)	0	0	0	0	0	8	0	0	0	1	0	0	6	0	0
18	E2(6)	0	0	1	0	0	10	0	0	0	0	0	0	11	0	0
19	W2(1)	0	0	3	0	0	20	0	4	0	0	1	0	1	0	0
20	W2(2)	0	0	1	0	0	3	1	7	1	2	0	3	18	1	0
21	W2(3)	0	0	2	0	0	44	1	5	0	1	0	0	0	1	0
22	W2(4)	0	0	1	0	0	3	0	1	0	0	1	0	0	0	0
23	W2(5)	0	0	3	0	1	16	0	5	0	1	1	0	0	1	0
24	W2(6)	0	0	0	0	0	4	0	1	0	0	0	0	1	1	0
25	E1(1)	0	0	1	0	0	4	0	0	0	0	0	0	0	0	0
26	E1(2)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
27	E1(3)	0	0	0	0	0	4	0	0	0	0	0	0	2	0	0
28	E1(4)	0	0	1	0	0	9	0	0	0	2	0	0	2	0	0
29	E1(5)	0	0	0	0	0	3	0	0	0	0	0	1	6	0	0
30	E1(6)	0	0	0	0	0	13	0	0	0	0	0	0	2	0	0
31	W1(1)	0	0	0	0	0	1	0	0	0	0	0	3	2	0	0
32	W1(2)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
33	W1(3)	0	0	0	0	0	3	0	0	0	0	0	1	1	0	0
34	W1(4)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
35	W1(5)	0	0	2	0	0	0	0	0	0	0	0	0	6	0	0
36	W1(6)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
37	S1(1)	0	0	2	0	0	0	0	0	1	4	0	0	3	0	0
38	S1(2)	0	0	2	0	0	1	0	0	0	0	0	6	9	0	0
39	S2(1)	0	0	22	0	0	7	0	3	0	9	5	2	1	0	0
40	S2(2)	0	0	10	0	0	9	0	0	0	6	9	2	0	0	0
41	S2(3)	1	0	14	0	0	4	0	0	0	2	6	1	3	0	0
42	S3(1)	0	0	4	0	0	6	0	1	0	0	1	3	17	0	0
43	S3(2)	0	1	2	0	1	3	0	0	0	1	0	4	3	0	0
44	S3(3)	0	1	3	0	1	10	0	1	0	0	0	1	0	0	0
45	O(1)	0	0	15	0	0	33	0	0	4	6	19	6	15	0	0
46	O(2)	0	0	12	0	1	46	0	0	7	1	12	0	10	0	0
47	O(3)	0	0	11	0	0	48	1	0	1	0	18	0	2	0	0

Number	Site	ANX	CHA	BGA	SAR	GMA	PGO	PMA	SIP	AEN	NCI	NEM	OVI	TST	CCR	AFI
1	H(1)	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
2	H(2)	0	0	0	0	1	0	0	4	0	0	3	0	0	0	0
3	H(3)	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
4	H(4)	1	1	0	0	0	0	0	2	0	0	4	0	0	0	0
5	H(5)	0	0	2	2	1	0	0	4	0	0	6	0	0	0	0
6	H(6)	0	0	0	0	2	1	1	1	0	0	3	0	0	0	0
7	C(1)	0	0	0	1	0	0	0	0	4	1	1	0	0	0	0
8	C(2)	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
9	C(3)	0	0	0	1	0	0	0	0	1	0	4	7	0	0	0
10	C(4)	0	1	0	0	0	0	0	3	1	0	3	0	1	0	0
11	C(5)	0	0	0	0	0	0	0	0	1	0	6	2	3	1	0
12	C(6)	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0
13	E2(1)	0	0	0	0	0	0	0	5	0	0	10	1	0	0	0
14	E2(2)	0	0	0	0	0	0	0	1	1	1	0	2	1	0	0
15	E2(3)	0	0	0	0	0	0	0	0	1	0	3	3	3	0	0
16	E2(4)	0	0	0	0	0	0	0	0	0	0	4	0	2	0	0
17	E2(5)	0	0	0	0	0	0	0	2	0	0	7	2	2	0	0
18	E2(6)	0	0	0	0	0	0	0	0	1	0	5	5	3	0	0
19	W2(1)	0	0	0	0	0	0	0	1	0	0	2	0	1	0	1
20	W2(2)	0	0	0	0	0	0	0	1	0	0	16	0	1	0	0
21	W2(3)	0	0	0	0	0	0	0	1	4	0	1	0	2	0	0
22	W2(4)	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
23	W2(5)	0	0	0	0	0	0	0	0	2	1	1	1	2	0	0
24	W2(6)	0	0	0	0	0	0	0	2	3	0	3	2	0	0	0
25	E1(1)	0	0	0	0	0	0	0	0	1	0	1	1	3	0	0
26	E1(2)	0	0	0	0	0	0	0	1	0	0	2	1	1	0	0
27	E1(3)	0	0	0	0	0	0	0	0	1	0	0	1	8	0	0
28	E1(4)	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0
29	E1(5)	0	0	0	0	0	0	0	0	1	0	3	2	1	0	0
30	E1(6)	0	0	0	0	0	0	0	1	0	0	1	0	3	0	0
31	W1(1)	0	0	0	0	0	0	0	0	9	0	0	2	0	0	0
32	W1(2)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
33	W1(3)	0	0	0	0	0	0	0	3	9	0	16	0	0	0	0
34	W1(4)	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
35	W1(5)	0	0	0	0	0	0	0	0	4	0	0	0	1	0	0
36	W1(6)	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
37	S1(1)	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
38	S1(2)	0	0	0	0	0	0	0	0	0	0	12	2	1	1	0
39	S2(1)	0	0	30	14	1	0	0	0	0	0	10	1	2	1	0
40	S2(2)	0	0	51	7	2	0	0	4	1	1	4	1	1	0	0
41	S2(3)	0	0	24	9	1	0	0	2	1	0	6	1	0	0	1
42	S3(1)	0	0	0	9	0	0	1	1	4	0	21	0	14	0	0
43	S3(2)	0	0	0	18	0	0	0	3	6	0	21	3	21	0	0
44	S3(3)	0	0	0	7	2	0	0	0	5	1	8	3	14	0	0
45	O(1)	0	0	6	14	0	0	0	1	0	1	14	3	1	1	1
46	O(2)	1	0	1	3	0	0	0	5	0	0	9	3	5	0	2
47	O(3)	0	0	2	8	0	0	0	0	0	0	14	3	5	0	0

Number	Site	STR	ASA	ATY	PLT	HAR	MEA	MFO	ALA	SCR	BVI	HEM	AAC	DSP	FRO	MYS
1	H(1)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
2	H(2)	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
3	H(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	H(4)	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
5	H(5)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
6	H(6)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
7	C(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	C(2)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
9	C(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	C(4)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
11	C(5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	C(6)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
13	E2(1)	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0
14	E2(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	E2(3)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
16	E2(4)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
17	E2(5)	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0
18	E2(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	W2(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	W2(2)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
21	W2(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	W2(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	W2(5)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
24	W2(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	E1(1)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
26	E1(2)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
27	E1(3)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	E1(4)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
29	E1(5)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
30	E1(6)	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
31	W1(1)	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0
32	W1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	W1(3)	2	0	3	12	0	0	0	0	0	0	0	0	0	0	0
34	W1(4)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
35	W1(5)	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
36	W1(6)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
37	S1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	S1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	S2(1)	0	0	3	0	0	0	0	0	0	7	1	1	0	0	1
40	S2(2)	0	0	0	1	0	0	0	0	0	4	1	0	0	0	0
41	S2(3)	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0
42	S3(1)	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0
43	S3(2)	0	0	1	0	0	0	0	0	0	5	0	0	0	5	0
44	S3(3)	1	0	5	0	0	0	0	0	0	0	1	0	0	3	1
45	O(1)	1	0	0	0	1	3	3	0	0	11	0	0	0	0	0
46	O(2)	0	0	1	0	0	4	2	1	1	5	2	0	0	0	0
47	O(3)	2	0	0	0	0	0	0	0	0	3	0	1	0	0	0

Number	Site	HSP	LLA	STY	PSP	SIN	SYN	SOL	ASC	BSD	ISO	EUP	LLO	CAP	UNB	SPA
1	H(1)	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0
2	H(2)	0	0	0	0	0	0	0	0	0	2	0	0	10	0	0
3	H(3)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
4	H(4)	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
5	H(5)	0	0	0	0	0	0	0	0	0	0	0	0	11	2	0
6	H(6)	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
7	C(1)	0	0	1	0	0	0	0	0	0	0	0	1	6	0	0
8	C(2)	0	0	1	0	0	0	0	0	0	0	0	3	4	0	0
9	C(3)	0	0	0	0	0	0	0	0	0	0	0	2	5	0	1
10	C(4)	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0
11	C(5)	0	0	0	0	0	0	0	0	0	1	0	4	2	0	1
12	C(6)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
13	E2(1)	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
14	E2(2)	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0
15	E2(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	E2(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	E2(5)	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
18	E2(6)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
19	W2(1)	0	0	0	0	0	0	1	0	0	0	0	0	8	0	0
20	W2(2)	0	0	0	0	2	0	0	0	0	0	0	1	3	0	0
21	W2(3)	0	0	0	0	0	0	0	0	0	0	0	1	10	0	0
22	W2(4)	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
23	W2(5)	0	0	0	0	0	0	0	0	0	0	0	3	6	0	0
24	W2(6)	0	0	0	0	1	0	0	0	0	0	0	1	7	0	0
25	E1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	E1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	E1(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
28	E1(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	E1(5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	E1(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	W1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	W1(2)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
33	W1(3)	0	0	0	0	0	0	0	0	0	0	0	1	5	0	0
34	W1(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	W1(5)	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
36	W1(6)	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
37	S1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	S1(2)	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0
39	S2(1)	1	2	1	0	0	0	0	0	0	0	0	0	21	0	1
40	S2(2)	0	0	0	1	2	0	0	0	0	0	0	0	13	0	1
41	S2(3)	0	0	0	0	0	0	1	0	0	0	0	0	27	0	0
42	S3(1)	0	0	0	0	2	2	0	1	0	0	0	0	15	0	0
43	S3(2)	0	0	0	0	1	1	0	1	0	0	0	0	24	0	0
44	S3(3)	1	0	0	0	0	0	0	0	0	0	0	0	25	0	0
45	O(1)	0	0	0	0	0	0	0	0	0	0	0	0	23	6	0
46	O(2)	0	0	0	12	0	0	0	0	0	0	0	0	27	2	0
47	O(3)	0	0	0	0	1	0	0	0	0	0	0	0	31	2	0

Number	Site	MSA	AMA	TSA	TSB	TSC	TSD	UNC	UND	UNF	TSE	PDA	DPY	ETE	YSP	MCA
1	H(1)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6
2	H(2)	0	0	0	0	0	0	0	0	0	0	0	0	2	1	22
3	H(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
4	H(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
5	H(5)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	13
6	H(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
7	C(1)	1	0	0	1	0	0	0	1	0	0	0	0	0	0	2
8	C(2)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
9	C(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	C(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	C(5)	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0
12	C(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
13	E2(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	3	5
14	E2(2)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
15	E2(3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
16	E2(4)	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
17	E2(5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
18	E2(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
19	W2(1)	0	0	0	1	0	0	0	0	0	0	0	1	0	0	3
20	W2(2)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
21	W2(3)	0	0	0	0	0	0	0	1	0	0	0	1	0	0	4
22	W2(4)	0	1	0	0	0	0	0	0	0	0	0	1	0	3	4
23	W2(5)	0	0	0	0	0	0	0	1	0	0	0	0	2	2	5
24	W2(6)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
25	E1(1)	0	0	0	0	0	0	0	0	0	0	0	0	1	4	4
26	E1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	10
27	E1(3)	0	0	0	0	0	0	0	1	0	0	0	0	2	5	17
28	E1(4)	0	0	0	0	0	0	0	0	0	0	0	0	2	3	7
29	E1(5)	0	0	0	0	0	0	0	0	0	0	0	1	5	3	0
30	E1(6)	0	0	0	0	0	0	0	1	0	0	0	0	0	5	4
31	W1(1)	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2
32	W1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	W1(3)	0	0	0	0	0	0	0	1	0	0	0	2	4	1	1
34	W1(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	W1(5)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
36	W1(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	S1(1)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
38	S1(2)	0	0	0	1	0	0	0	0	0	0	0	0	0	1	2
39	S2(1)	1	0	0	2	0	0	0	0	0	10	1	0	0	0	6
40	S2(2)	0	1	0	1	0	0	0	0	0	8	3	0	0	0	1
41	S2(3)	0	0	0	0	0	0	0	0	0	12	2	0	0	0	4
42	S3(1)	5	0	0	1	0	0	0	1	1	1	0	0	0	6	0
43	S3(2)	4	0	0	0	1	0	1	1	0	2	0	0	1	2	2
44	S3(3)	15	0	0	1	0	1	0	0	0	2	0	0	0	2	2
45	O(1)	0	1	0	1	0	0	0	0	0	0	8	1	0	0	26
46	O(2)	3	10	1	5	0	0	0	0	0	0	0	2	0	1	14
47	O(3)	1	3	0	4	0	0	0	0	0	1	0	1	0	0	10

Number	Site	NPE	THY	CCI	YHP	ROB	PRU	CSP	TUR	FPE	GSF	NAT	GSD	GSE	PSA	QCA
1	H(1)	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
2	H(2)	0	3	0	0	5	0	0	0	0	0	0	0	0	0	0
3	H(3)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
4	H(4)	0	0	0	0	3	0	0	0	0	0	0	1	0	6	0
5	H(5)	0	2	0	0	1	0	0	1	1	0	0	0	2	0	0
6	H(6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	C(1)	1	23	0	0	0	0	0	0	0	0	0	0	0	0	0
8	C(2)	1	8	0	0	0	0	0	0	0	0	0	1	0	0	0
9	C(3)	2	7	0	0	1	0	0	0	0	0	0	0	0	0	0
10	C(4)	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0
11	C(5)	4	16	0	1	0	0	0	1	0	0	0	0	0	0	0
12	C(6)	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
13	E2(1)	5	1	0	0	3	0	0	0	0	0	0	0	0	0	0
14	E2(2)	3	4	0	0	1	0	0	0	0	0	0	0	0	0	0
15	E2(3)	4	3	0	1	2	0	0	0	0	0	0	0	0	0	0
16	E2(4)	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
17	E2(5)	3	0	0	0	4	0	0	1	0	0	0	0	0	0	0
18	E2(6)	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0
19	W2(1)	2	6	0	0	0	0	0	0	0	1	0	0	0	0	0
20	W2(2)	4	8	0	0	0	0	0	0	0	0	0	0	0	0	0
21	W2(3)	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0
22	W2(4)	2	4	0	0	0	0	0	3	0	0	0	0	0	0	0
23	W2(5)	3	12	0	0	0	0	0	1	0	0	0	0	0	0	0
24	W2(6)	2	5	0	0	0	0	0	2	0	0	0	0	0	0	0
25	E1(1)	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0
26	E1(2)	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
27	E1(3)	4	1	0	0	1	0	0	1	0	0	0	0	0	0	0
28	E1(4)	2	1	1	2	1	0	0	0	0	0	0	0	0	0	1
29	E1(5)	2	1	0	1	5	0	0	0	0	0	0	0	0	0	0
30	E1(6)	0	3	0	0	2	0	0	0	0	0	0	0	0	0	0
31	W1(1)	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0
32	W1(2)	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0
33	W1(3)	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0
34	W1(4)	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	W1(5)	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0
36	W1(6)	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0
37	S1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	S1(2)	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
39	S2(1)	0	2	0	0	2	1	0	0	2	0	0	0	0	1	0
40	S2(2)	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0
41	S2(3)	0	5	0	0	0	1	0	0	0	0	0	0	0	0	0
42	S3(1)	0	1	0	0	15	0	0	0	1	0	1	0	2	11	0
43	S3(2)	0	2	0	0	9	0	0	1	11	0	0	0	0	31	0
44	S3(3)	0	0	0	0	8	0	1	0	6	0	0	0	0	21	0
45	O(1)	0	14	0	0	0	0	0	1	0	0	0	0	0	0	0
46	O(2)	0	17	0	0	5	0	0	4	1	0	0	0	0	0	0
47	O(3)	0	10	0	0	3	0	0	0	0	0	0	0	0	0	0

Number	Site	NTO	PEX	APR	HIP	ECA	PPA	OAC	MEL	AMP	BFR	TGR	PSB	UNV
1	H(1)	0	0	0	0	0	0	0	0	0	0	0	0	1
2	H(2)	0	0	0	2	0	0	0	0	0	0	0	0	0
3	H(3)	0	0	0	0	0	0	0	0	0	0	0	0	0
4	H(4)	0	0	0	0	0	0	0	0	0	0	0	0	0
5	H(5)	0	0	0	0	0	0	0	0	0	0	0	0	0
6	H(6)	0	0	0	0	0	0	0	0	0	0	0	0	0
7	C(1)	0	0	0	0	0	0	0	0	0	0	0	0	0
8	C(2)	0	0	0	0	0	0	0	0	0	0	0	0	0
9	C(3)	0	0	0	0	0	0	0	1	0	0	0	0	0
10	C(4)	0	0	0	0	0	0	0	0	0	0	0	0	0
11	C(5)	0	0	0	0	0	0	0	0	0	0	0	0	0
12	C(6)	0	0	0	1	0	0	0	0	0	0	0	0	0
13	E2(1)	0	0	0	0	0	0	0	0	0	0	0	0	0
14	E2(2)	0	0	1	0	0	0	0	0	0	0	0	0	0
15	E2(3)	0	0	1	0	0	0	0	0	0	0	0	0	0
16	E2(4)	0	1	0	0	0	0	0	0	0	0	0	0	0
17	E2(5)	0	0	1	0	2	0	0	0	0	0	0	0	0
18	E2(6)	0	0	1	0	0	0	0	0	0	0	0	0	0
19	W2(1)	0	0	0	0	0	0	0	0	0	0	0	0	0
20	W2(2)	0	0	0	0	0	0	0	0	0	0	0	0	0
21	W2(3)	0	0	1	0	0	0	0	0	0	0	0	0	0
22	W2(4)	0	0	0	0	0	0	0	0	0	0	0	0	0
23	W2(5)	0	0	3	0	0	0	0	0	0	0	0	0	0
24	W2(6)	0	0	0	0	0	0	0	0	0	0	0	0	0
25	E1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0
26	E1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0
27	E1(3)	0	0	0	0	0	0	0	0	0	0	0	0	0
28	E1(4)	0	0	0	0	0	0	0	0	0	0	0	0	0
29	E1(5)	0	0	2	0	1	0	0	0	0	0	0	0	0
30	E1(6)	0	0	0	0	0	0	0	0	0	0	0	0	0
31	W1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0
32	W1(2)	0	0	0	0	0	0	0	0	0	0	0	0	0
33	W1(3)	0	0	0	0	0	0	0	0	0	0	0	0	0
34	W1(4)	0	0	0	0	0	0	0	0	0	0	0	0	0
35	W1(5)	0	0	0	0	0	0	0	0	0	0	0	0	0
36	W1(6)	0	0	0	0	0	0	0	0	0	0	0	0	0
37	S1(1)	0	0	0	0	0	0	0	0	0	0	0	0	0
38	S1(2)	0	0	1	1	0	0	0	0	0	0	0	0	0
39	S2(1)	0	0	1	16	0	0	1	0	0	0	1	0	0
40	S2(2)	0	0	2	4	0	0	0	0	0	0	0	0	1
41	S2(3)	1	0	1	1	0	2	0	0	0	0	0	0	1
42	S3(1)	0	0	0	3	0	0	0	0	2	0	0	1	0
43	S3(2)	0	0	0	0	0	0	0	0	0	0	0	0	0
44	S3(3)	0	0	0	0	0	0	0	0	0	1	0	1	0
45	O(1)	0	0	1	9	0	0	0	0	0	0	0	0	0
46	O(2)	0	0	4	14	0	0	0	0	0	0	0	0	0
47	O(3)	0	0	13	5	0	0	0	0	0	0	0	0	0

Number	Code	Taxa
1	ELO	*Eteone longa*
2	CSE	*Chaetozone setosa*
3	PST	*Prionospio steenstrupi*
4	MGL	*Maldane glebifex*
5	NNE	*Nephtys neotena*
6	AQU	*Aricidea quadrilobata*
7	ANO	*Aricidea nolani*
8	CLO	*Cossura longocirrata*
9	GMA	*Gyptis* sp.
10	NPU	*Nereimyra punctata*
11	PGR	*Pectinaria granulata*
12	SSP	*Syllides longocirrata*
13	DOR	Dorvilleidae spp. (i.e. *Dorvillea rudolphi* and *Parougia eliasoni*)
14	ACT	Order:Actiniaria
15	TAN	Tanaidacea
16	UKV	unidentified sp. V
17	SFI	*Spio filicornis*
18	CUM	Cumacean
19	AGO	*Ampharete goesi*
20	PPL	*Pherusa plumosa*
21	LUM	Lumbrineris spp. (i.e. *L. impateins*)
22	PLO	*Pholoë longa*
23	SMI	*Sphaerodoropsis minuta*
24	PFE	*Pontoporeidae femorata*
25	BAT	*Bathymedon* sp.
26	EIN	*Euchone incolor*
27	HY2	Hydrozoa (hydranth)
28	HY1	Hydrozoa (polyp)
29	HY3	Hydrozoa (medusa)
30	MON	*Monoculodes* sp.
31	ANX	*Anonyx* sp.
32	CHA	Chaetognatha
33	BGR	*Byblis gaimardi*
34	SAR	*Scoloplos armiger*
35	GMA	*Goniada maculata*
36	SIP	Sipunculoidea
37	AEN	*Antalis entale*
38	NCI	*Nephtys ciliata*
39	NEM	Nemertea spp.
40	OVI	*Ophiotjalfa vivipera*
41	TST	*Terebellides stroemi*
42	CCR	*Ctenodiscus crispatus*
43	AFI	*Ampharete finmarchica*
44	STR	*Strongylocentrotus* sp.
45	PGO	*Phyllodoce groenlandica*
46	PMA	*Phyllodoce maculata*
47	ASA	*Antinoella sarsi*
48	ATY	*Apistobranchus typicus*
49	PLT	Platyhelminthesis
50	HAR	*Hyas araneus*
51	MEA	*Melita* sp.
52	MFO	*Melita formosa*
53	ALA	*Aceroides laptipes*
54	SCR	*Syrrhoe crenulata*
55	BVI	*Brada villosa*
56	HEM	Hemichordata
57	AAC	*Ampharete acutifrons*
58	DSP	*Diplocirrus* sp.
59	FRO	*Filibranchus roseus*
60	MYS	Mysid
61	HSP	*Harpina* sp.
62	LLA	*Lysippe labiata*
63	STY	*Spiochaetopterus typicus*
64	PSP	*Protomedeia* sp.
65	SIN	*Scalibregma inflatum*
66	SOL	Solenogaster
67	ASC	Ascidiacea (tunicates)
68	BSD	Bivalve sp. D
69	ISO	Isopoda
70	EUP	Euphausid
71	LLO	*Lysilla loveni*
72	CAP	Capitellidae spp. (i.e. *Mediomastus* sp. and *Barantolla* sp.),
73	UNB	unidentified sp. B
74	SPA	Paraonidae sp. A
75	MSA	Maldane sp. A
76	AMA	Ampharetidae sp
77	TSA	Terebellidae sp. A
78	TSB	Terebellidae sp. B
79	SYN	Synaptidae
80	TSC	Terebellidae sp. C
81	TSD	Terebellidae sp. D
82	UNC	Unidentified sp. C

Number	Code	Taxa
83	UND	Unidentified sp. D
84	UNF	Unidentified sp. F
85	TSE	*Tharyx* sp. A
86	PDA	*Polydora* sp. A ? *Caulleryi*
87	DPY	*Dysponetus pygmaeus*
88	ETE	*Ennucula tenuis*
89	YSP	*Yoldia* sp.
90	MCA	*Macoma calcarea*
91	NPE	*Nuculana pernula*
92	THY	*Thyasira* sp.
93	CCI	*Clinocardium ciliatum*
94	YHP	*Yoldia hyperborea*
95	ROB	*Retusa obtusa*
96	PRU	*Propebela rugulata*
97	CSP	*Curitotoma* sp.
98	TUR	Turridae sp.
99	FPE	*Frigidoalvania pelagica*
100	GSF	Gastropod sp. F
101	NAT	Naticidae
102	GSD	Gastropod sp. D
103	GSE	Gastropod sp. E
104	PSB	Paraonidae sp. B
105	QCA	*Questa caudicirra*
106	NTO	*Nemidia torelli*
107	PEX	*Polycirrus eximius* group
108	APR	*Artacama proboscidea*
109	HIP	*Hippomedon* sp.
110	ECA	*Enipo canadensis*
111	PPA	*Poliaices pallida*
112	OCA	*Ophelina acuminata*
113	MEL	*Melinna cristata*
114	AMP	Amphuridae
115	BFR	*Brisaster fragilis*
116	TGR	*Tauberia gracilis*
117	PSA	Paraonidae sp. A
118	AAN	*Arcteobia anticostiensis*