Ecology of the Hexactinellid Sponge Reefs on the Western Canadian Continental Shelf

by

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ABSTRACT

Hexactinosidan sponges have built seven reef complexes in the Queen Charlotte and Georgia Basins on the Western Canadian continental shelf. These reefs are composed of a matrix of sediment mixed with dead sponge fragments, which remain remarkably intact after the death of the sponge, with live reef-building sponges growing on the tops of the reef mounds. The reef complexes discontinuously cover over 1000 km^2 of the continental shelf and are found at depths between 150 and 230 metres. The objectives of this thesis are to describe quantitatively the megafaunal community of the reefs using video transects and the macrofaunal polychaete community from grab samples, to compare the reef community to the off-reef communities, and to describe how organisms are utilizing the reef substrate.

The video used to compare the megafaunal community of live reef, dead reef and off-reef habitat was collected on two reef complexes during cruise PGC9901. The video was analyzed by taking 'snapshots' at every ten seconds along the transect or at each GPS fix and at each snapshot habitat type was recorded and each megafaunal organism was identified and counted. A qualitative complexity value (high, medium or low) was also recorded when it became clear that topographical and biological heterogeneity also influenced the communities identified on the video. Univariate measures of richness, abundance and diversity were used in conjunction with the multivariate analyses ANOSIM and SIMPER to compare habitats and complexity values.

The major conclusions drawn from this study are: live reef habitat has increased richness when all fauna are combined and increased abundance of individuals when boot sponges and demosponges are removed from the analysis; live reefs are nursery habitats for juvenile rockfish; live reef and off-reef habitats have significantly different community structures; trends in abundance between habitats for specific taxonomic groups depend on which group is being explored; high complexity areas have increased richness and abundance of individuals and a significantly different community structure compared to the other complexity values; and off-reef, high complexity areas have the highest richness and abundance of individuals of all the shelf communities.

The video used to study how the organisms found on the reefs utilize the substrate was collected on reef complexes A, D and the Fraser Ridge during cruise PGC02004. The video was analyzed by identifying each organism on the video to family and recording the substrate it was utilizing. The five substrate categories are: fallen dead sponge, standing dead sponge, live *Aphrocallistes vastus* and *Heterochone calyx*, live *Farrea occa* and rossellid sponges. All counts were standardized by the length of each transect into individuals per 100 meters. The main conclusions of this study are that dead sponge supports a larger population of megafauna in terms of abundance, richness and diversity than live sponge and that there are substrate preferences within families.

On-reef and off-reef grab samples were collected at and near two reef complexes during cruise PGC02004 to determine if there were differences in the macrofaunal polychaete community between the two habitats, both at the species and family level. A total of 643 individual polychaetes were identified to family; of those, 430 could be identified to 105 different species. All counts were standardized by surface area of the grab sample. Univariate measures of richness, abundance and diversity were used in addition to multivariate techniques to examine the communities. The major conclusions are that polychaete richness and diversity are significantly higher in on-reef habitat at the family level, but not at the species level; on-reef and off-reef habitats are different in terms of overall polychaete community structure; and tubiculous deposit feeders are the dominant taxa at both on-reef and off-reef sites.

There are some implications that can be drawn from the conclusions presented in this thesis. The major implication has to do with fisheries management on and around the sponge reefs. The reef community is unique and is a nursery habitat for juvenile rockfish, some of which are commercially important species. Although the reefs have already been protected from bottom trawling, the implications of these conclusions indicate that a greater degree of protection is warranted, perhaps in the form of a marine protected area. Another major implication is that a study more directed to specific questions of importance to fisheries management is required.

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CHAPTER 1:
Introduction to the Sponge Reefs

THE SPONGE REEFS

During a geophysical survey of the north coast of British Columbia, Canada carried out in 1986, several acoustic anomalies were noted by K. W. Conway, J. V. Barrie and J.L. Luternaur while mapping the seafloor using sidescan sonar (Conway et al. 1989, Conway et al. 1991). After photographs and cores taken on cruises during 1987 and 1988 were analyzed by W.C. Austin, the anomalies were identified as sponge mounds, also called reefs. These mounds were classified as reefs using the definition of a reef as a self-perpetuating, three-dimensional structure that is resistant to erosion. From these and subsequent expeditions, four separate sponge reef complexes in the Queen Charlotte Basin (QCB) were discovered (DFO 2000, Conway et al. 2001, Krautter et al. 2001). More recently, three additional reef complexes have been found in the Georgia Basin (GB), one on the Fraser Ridge and and two at McCall Bank (Conway et al. 2004, Conway et al. In Press) (see Figure 1.1 for locations).

The reefs are formed by hexactinosidan sponges, order Hexactinosida of the class Hexactinellida, more informally known as glass sponges, the largest of four orders of sponges which form a hard skeleton composed of fused silica spicules (Reiswig 2002). When the sponges die and the living tissue is macerated the fused skeletons remain remarkably intact. Since these sponges require hard substrate for initial attachment, the macerated skeleton acts as substrate for settlement of new larvae which form a tendril-like mesh of spicules around the old skeleton (Krautter et al. 2002). The sponges are extremely plastic in their morphology and can stabilize themselves by creating supporting outgrowths, which can even overgrow a neighboring sponge or incorporate the

neighbours' skeleton for further support (Krautter et al. 2002, Conway et al. 2005). By these processes a three dimensional framework of sponges is formed. This framework baffles sediment out of the water column, which is trapped by and eventually buries the dead sponge. This matrix of dead sponge (either broken down or standing intact), sediment and living sponges creates the sponge reefs (Krautter et al. 2001, Conway et al. 2002, Conway et al. 2005). The continual addition of sediment causes the reefs to grow over time. Eventually they coalesce to form larger reef complexes, which discontinuously cover more than 1000 km^2 of the Western Canadian continental shelf (Krautter et al. 2001). The reefs are found at depths between 150 and 230 metres.

The three hexactinosidan reef-building species are *Aphrocallistes vastus*, *Heterochone calyx* and *Farrea occa* (see Figure 1.2) (Conway et al. 1991, Conway et al. 2001), although *Farrea occa* is absent in the GB reefs (Conway et al. 2004, Conway et al. In Press). All of these species can be found singly or in groups where there is hard substrate such as the rock walls of outer coasts and fjords of B.C. and around the Pacific Rim (Leys et al. 2004). These species, however, are known to form reefs only on the Western Canadian continental shelf, and no other siliceous sponge species is known to build reefs anywhere.

The known reef complexes show considerable variability in both initial settlement and growth patterns and can be made of biohermal mounds (those which are larger, up to 21m in height, with more steeply sloping sides) and sheet-like reefs referred to as biostromes (which rarely grow higher than 2 to 10m) (Krautter et al. 2001). The complexes in the QCB are much larger than those in the GB and were found to be more variable in structure (Conway et al. In Press). The QCB reefs were also found to have

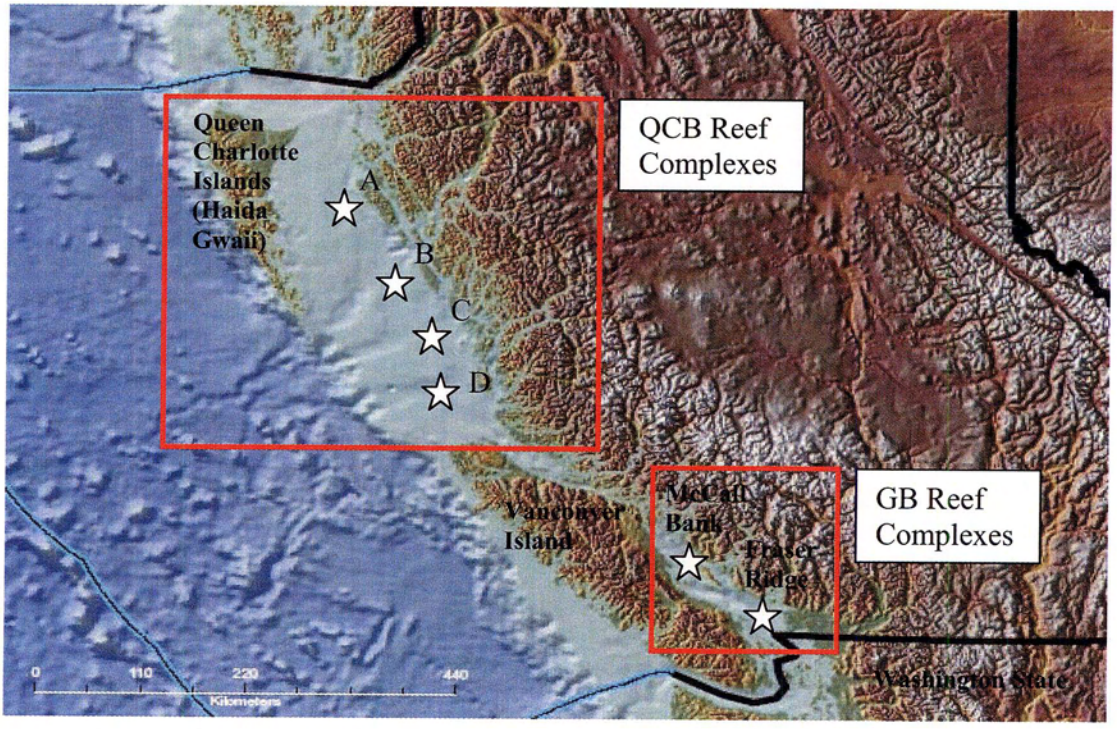

Figure 1.1: Location of sponge reef complexes on the Western Canadian Continental Shelf (British Columbia). Letter designations for the QCB reef complexes follows (Jamieson and Chew 2002).

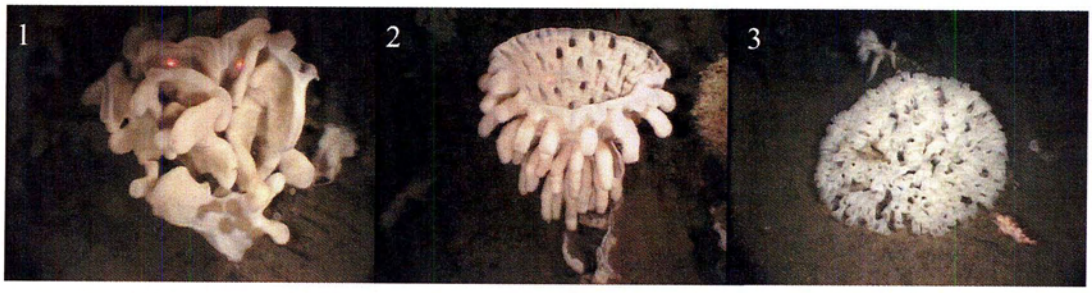

Figure 1.2: The three reef-building species of hexactinosidan sponges: 1) *Aphrocallistes vastus*, 2) *Heterochone calyx* and 3) *Farrea occa*. Photographs and permission for their use was provided by K. W. Conway.

predominantly settled in iceberg scour, a phenomenon also known from deep-sea coral reefs in Norwegian waters (Freiwald et al. 1999), while the GB reefs settled on bank surfaces that were devoid of sedimentation, usually ascribable to the predominant current regime (Conway et al. 2004, Conway et al. In Press).

Variation in growth and shape of individual mounds is almost certainly the result of competition of the sponges for space in the local water current field. Many mounds in lower current areas are circular, likely due to the expansion of the new sponges away from each other in competition for resources (space and access to unfiltered water). In higher current areas the sidescan sonar maps and measurements of the prevailing currents indicate that mounds will elongate in the direction of the predominant current as the sponges presumably grow more rapidly at higher current margins (Krautter et al. 2001). The current regime may also influence the morphology of individual sponges; in areas with higher suspended sediment loads (such as the Fraser Ridge complex) the sponges tend to be more tube shaped whereas in the QCB reefs, where suspended sediment load is lower, funnel, cup and plate-like sponges are common (Conway et al. 2004). Tube-shaped morphology has been identified as a possible adaptation of hexactinosidan sponges to higher sedimentation rates in fossil reefs (Krautter 1995).

Global oceanographic properties might explain the unique presence of the siliceous sponge reefs on the Western Continental Shelf of Canada (bearing in mind that reefs may exist in other locations which have not yet been well surveyed). The shelf waters of B.C have been observed to have a very high relative concentration of dissolved silica (Austin 1999), a fact confirmed by global measurements taken by the World Ocean Circulation Experiment (WOCE) which clearly shows that two regions, the North Pacific and the

Southern Ocean near Antarctica, have extremely high silica concentrations at 200m depth compared to the rest of the world's oceans (Conway et al. 2005). It is unlikely to be coincidence that areas which are known to have very large populations of siliceous sponges (Dayton et al. 1974, Barthel 1992, Barthel and Gutt 1992, Austin et al. 2002) correlate with the location of the only known siliceous sponge reefs.

Sponge reefs were very common during the Late Jurassic Period (approximately 160 mya) and formed the largest bioconstruction ever created, a discontinuous deep water sponge reef belt that extended more than 7000 km across what was then the northern shelf of the Tethys Ocean (Ghiold 1991, Krautter et al. 2001). The reefs began to decline as the Jurassic came to a close and disappeared during the Cretaceous Period. The known fossil sponge reef belt now extends through Romania, Poland, Germany, Switzerland, France Spain and Portugal, among other countries. The modern sponge reefs on the British Columbia shelf provide an unprecedented glimpse into an extinct ecosystem. Already some differences in how the ancient reefs and the modern reefs were built have been noted, with microbial carbonate encrustations, which caused early lithification of the mounds being very important in building the ancient reefs, but which are completely lacking in our modern reefs (Conway et al. 2004). These types of observations can be invaluable in drawing conclusions about the oceanographic conditions and the ecological function of the ancient reefs.

Most of the work regarding the modern reefs has been determination of how and when they formed and, more recently, how the oceanographic conditions of the areas they occupy shape and influence their placement and growth (Krautter et al. 2001, Krautter et al. 2002, Conway et al. 2005, Whitney et al. 2005, Conway et al. In Press).

Work on the invertebrate and fish community associated with the reefs has been extremely limited. Austin (2002) noted that the sponges of B.C. (and here he includes the rossellid spicule mats that also occur in certain areas) act as habitat amplifiers, playing an important role in structuring species occurrences and associations in the areas in which they are found; however, no specific examples were provided. The presence of at least five other hexactinellid sponges of the Order Lyssacinosida (such as *Rhabdocalyptus dawsoni*), demosponges of all kinds, crabs, shrimp, prawns, squat lobsters, euphausids, annelid worms, bryozoans, limited bivalves and gastropods, all types of echinoderms, abundant foraminifera, rockfish, ratfish and many types of flatfish have been reported on the reefs (Conway et al. 2001, Krautter et al. 2001, Conway et al. 2004, Conway et al. 2005). It has been suggested that the reefs act as a nursery habitat for juvenile rockfish as the size of the rockfish on the reefs appears to be quite small (Krautter et al. 2001). There has also been some suggestion that the on-reef fauna differs from that of the surrounding habitat which is mostly glacial till and sediment (Krautter et al. 2001). Some species have been identified but no attempt to quantify abundances has yet been made.

Jamieson and Chew (2002) compiled a comprehensive list of mega- and macrofaunal species brought up by trawlers from the QCB reef complexes who had fished the sponge reefs before their closure to bottom trawling in 2002. This data came from the onboard observer program conducted by the Department of Fisheries and Oceans. Their data indicates a very rich fish and invertebrate fauna both on the reefs and immediately adjacent to the reefs, including many commercially important fish species. It also indicates differences in the relative abundances of targeted fish species around the different reef complexes. This work was done as part of a research document to develop a

series of recommendations to assign Marine Protected Area Status to the sponge reefs. One of these recommendations was to initiate more research to determine the general importance of the reef ecosystems and the associated species dynamics.

OBJECTIVES OF THE STUDY

The objective of this study is to start the process of quantitatively describing the reef mega- and macrofauna, including some comparison with the fauna from the surrounding habitats, to determine the relative importance of the reefs to the shelf community and the role of the sponges as foundation species. A second objective is to describe how the reef habitat is used by the species found there. These are carried out by analysis of both video recordings and grab samples.

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CHAPTER 2:
Megafaunal Community: Habitat and Complexity Comparisons

ABSTRACT

The sponge reefs on British Columbia's Western Continental Shelf are unique but are comparable to other ecosystems that are also based on 'foundation species', meaning organisms that create habitat for other organisms, and thereby exert a disproportionately large influence on community structure. These complex habitats ameliorate stress of different kinds to provide refuges with increased taxonomic richness and diversity. The objective of this study is to compare the communities living on the live sponge reefs with dead reef and off-reef habitats and to explore the richness, abundance of individuals and diversity in each habitat. The study was also expanded to include a comparison of different values of complexity (described qualitatively) seen in each habitat.

All video for this study was collected on reef complexes A and B during cruise PGC9901 in July 1999. The video was analyzed by taking a 'snapshot' every ten seconds (equivalent to quadrats along a transect) and at each GPS fix. At each snapshot habitat type (live reef, dead reef or off-reef) and a qualitative complexity value (low, medium or high) was assigned. In addition all megafaunal organisms within the snapshot were identified and counted. Abundances were standardized in each transect by linear length of the snapshot (individuals per meter) and this standardized data set was used for all analyses. Both univariate measures of richness, abundance and diversity, and multivariate measures of community structure (including ANOSIM and SIMPER) were calculated.

The major results and conclusions drawn from this study are: 1) live reef habitat has increased richness compared to the other habitats, 2) trends in abundance between habitats for specific taxonomic groups depends on which group is being explored, 3) live reef areas are nursery habitats for juvenile rockfish, 4) live reef community structure is significantly different from off-reef community structure, 5) high complexity, off-reef areas have the highest richness and abundance of individuals of any areas and 6) some evidence suggests that dead reef areas are the result of bottom trawling and are therefore impacted habitats.

INTRODUCTION

The sponge reefs on the continental shelf of B.C. are globally unique; therefore, there is no ecosystem from any other part of the world that is directly comparable. However, there are several ecosystems that are very similar in terms of depth (below the photic zone) and that are dominated by habitat forming invertebrates. An example is the deep-sea coral reefs of the Atlantic (both those built by *Lophelia pertusa* and *Oculina* sp.) (Fossa et al. 2002, Husebo et al. 2002, Reed 2002) and even the coral 'gardens' of the Atlantic and the Pacific (which are not reefs in that they do not build three-dimensional mounds but provide important complex habitat with many associated species) (Buhl-Mortensen and Mortensen 2003, Heifetz 2002, Krieger and Wing 2002). Another obvious comparison is with the hexactinellid sponge spicule mat communities found in the Antarctic (Barthel 1992, Barthel and Gutt 1992) and even in patchy locations in the NE Atlantic (Bett and Rice 1992, Barthel and Tendal 1993). Dayton (1975) termed the organisms at the base of these communities 'foundation species' – those species that exert a disproportionately large influence on the structure of a community by the physical modification, maintenance or creation of habitat (Jones et al. 1997, Dayton 1975). Many other terms have been used for these types of species, such as 'habitat modifiers' (Bruno and Kennedy 2000), 'anchor species' (Dayton 1984) and the newest, 'ecosystem engineers' (Crooks 2002, Jones et al. 1997, Jones et al. 1994). Here the term 'foundation species' is used because, as noted by Stachowicz (2001), this term has fewer anthropomorphic connotations (the term engineering appears to imply conscious intent).

There are many ways in which foundation species, by the modification or creation of habitat, influence community structure and facilitate species interactions. The main way

in which this occurs is the amelioration of stress, which can be broken into several categories: physiological, physical and biological (Bruno and Bertness 2001). Physiological stresses are parameters such as temperature and salinity, which can affect internal biochemical processes when outside a species' optimal range (Bruno and Kennedy 2000, Bruno and Bertness 2001, Stachowicz 2001). Physical stresses, such as high currents, can exert direct mechanical force on an organism causing tissue damage, the removal of tissue or burial of tissue (Bruno and Bertness 2001). Biological stresses include competition, predation and limitation of resources such as food and living space (Dayton 1975, Dayton 1984, Jones et al. 1994, Jones et al. 1997, Bruno and Kennedy 2000, Bruno and Bertness 2001, Stachowicz 2001). In other words, foundation species create habitats that act as refuges from stress (Woodin 1978). The amelioration of these types of stress is associated with increases in species diversity and richness (Stachowicz 2001).

In all the literature on habitat modification and facilitation by foundation species, no author discusses in depth why the creation of habitat by a foundation species ameliorates stress, except in a few passing references to the creation of heterogeneity (Woodin 1978, Bruno and Kennedy 2000, Bruno and Bertness 2001, Stachowicz 2001). The important point is that foundation species create more complex habitats and it is this complexity that acts to ameliorate stress. A large body of literature links increased habitat complexity with increased niche space, species richness and species diversity.

There is no doubt that the sponge reefs are formed by foundation species that create complex habitat. The original objective of this study was to compare the megafaunal communities of three habitats: live sponge reef, dead sponge reef and off-reef, and to

explore the richness, abundance of individuals and diversity of the megafaunal groups in each habitat. Once the video was reviewed, however, this objective was expanded to include a comparison of areas of differing complexity as it became clear that differences in complexity in each habitat could affect any the conclusions drawn by a comparison of those habitats.

METHODS

The sites for this study were reef complexes A and B in the Queen Charlotte Basin (see Figure 2.1 for locations). All video for this study was collected in July 1999 during the research cruise PGC9901 aboard CCGS *John P. Tully* using the two-person scientific submersible *Delta*. The submersible was equipped with an external hi8 mm video camera mounted at a fixed angle (approx. 45° to the bottom). Fifteen video transects which encompassed areas of each habitat type were collected, amounting to over 35 hours of video. Geographic Positioning System (GPS) fixes were recorded for all transects except the last three, although the fixes were sometimes sporadic, being either several seconds or several minutes apart. The video was analyzed by taking a 'snapshot' every ten seconds and/or at each geographic fix unless the bottom could not be seen. A snapshot of video is equivalent to a quadrat along a transect line. At each snapshot all megafaunal organisms were identified and enumerated. In this study, megafauna was defined as any organism that could be clearly seen on video (approx. >5 cm). Habitat type (live reef, dead reef or off-reef) and a qualitative estimate of the complexity of the bottom topography (high, medium or low) was also recorded (see Figure 2.2 for examples of the different habitat and complexity types). Complexity is defined in this study as a combination of the rugosity of the physical substratum and the abundance of

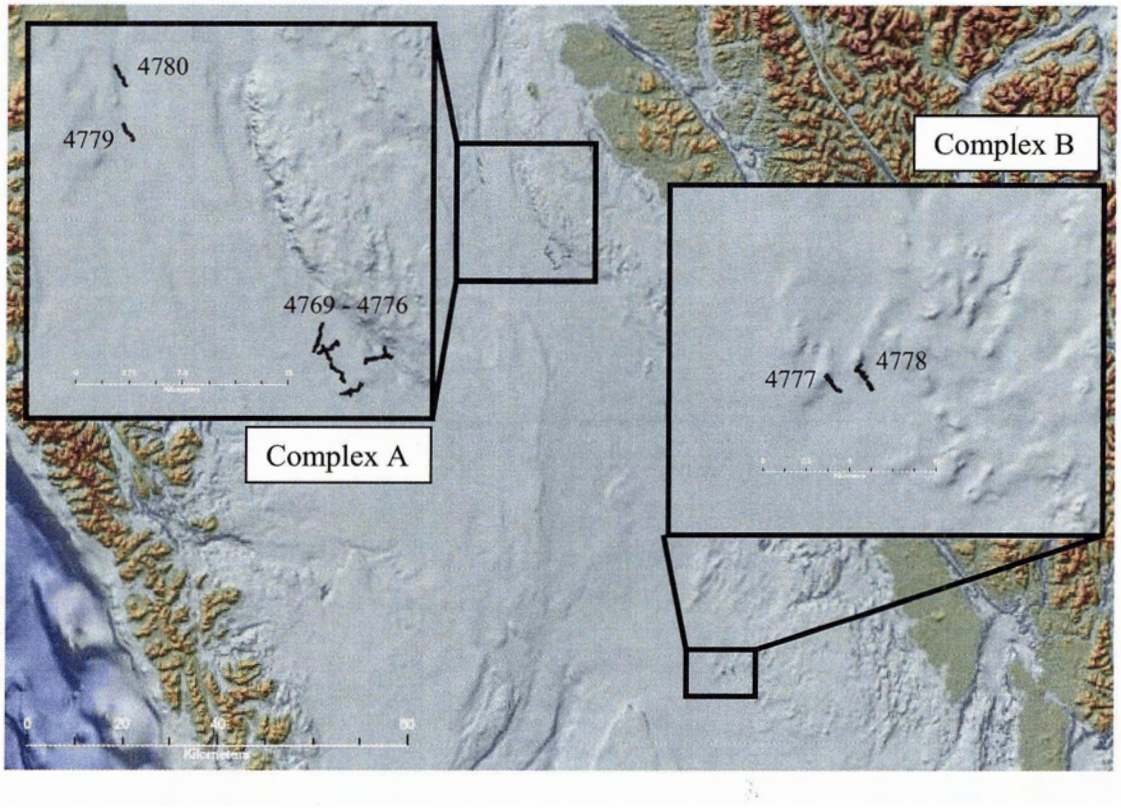

Figure 2.1: Locations of video transects taken from complexes A and B in 1999 except 4781 through 4783 because continuous DGPS information was not recorded for those transects.

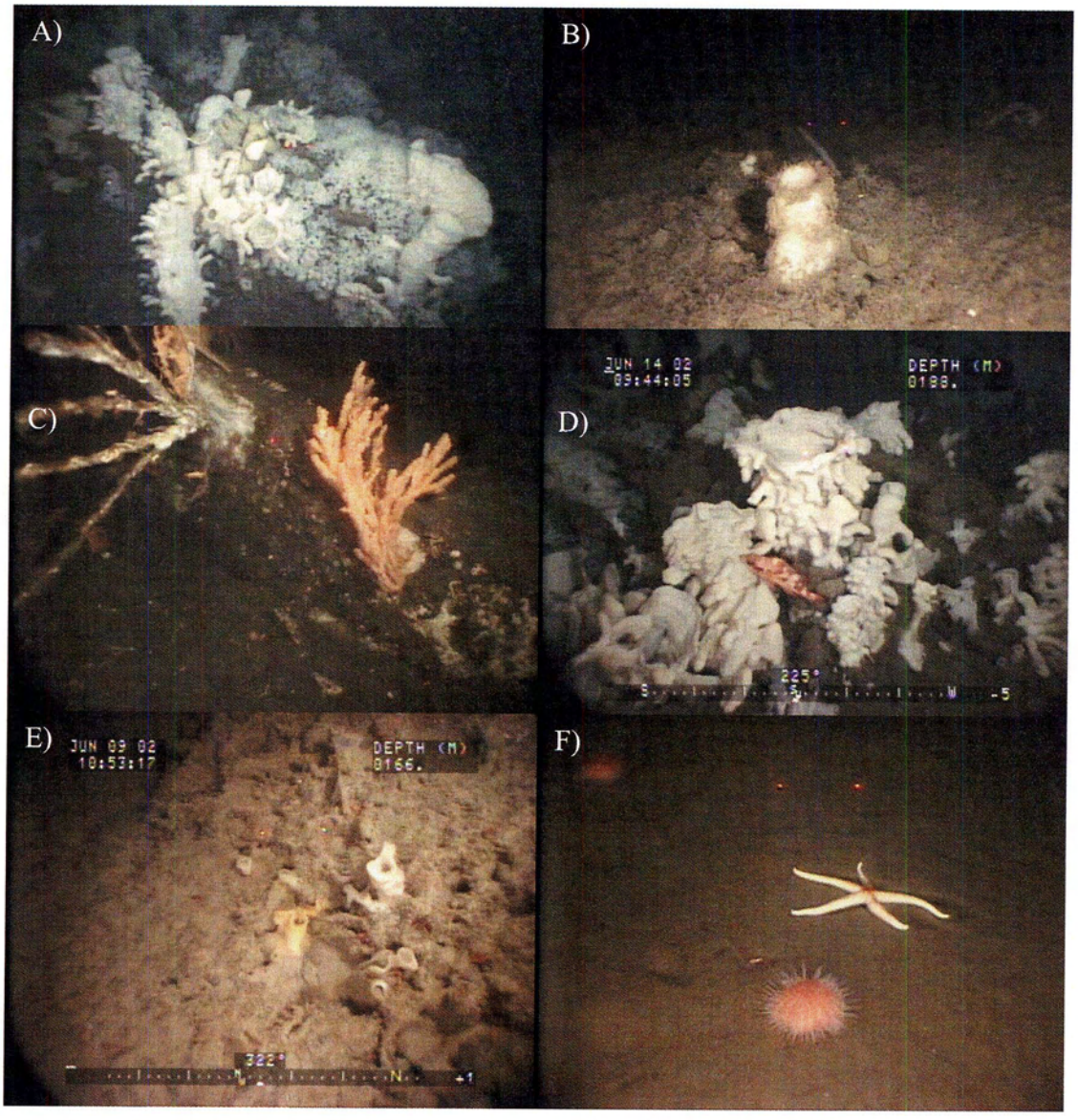

Figure 2.2: Examples of habitat and complexity types. Live reef (A), dead reef (B) and off-reef habitat (C); high (D - although C is a good example of off-reef high complexity), medium (E) and low (F) complexity. Photos used with permission of K.W. Conway.

habitat forming biotic components, such as corals or sponges, or any other group that would provide habitat to megafaunal groups. Off-reef is defined as an area in which the substratum is glacial till or sediment and live reef habitat is defined as a three dimensional structure, usually rising at least two meters off the seafloor, composed of a matrix of dead sponge fragments and sediment with live sponge growing on that matrix. In this case, the reef-building sponges are treated as structural elements and not as animals. Live reef habitat can include large areas of dead sponge in both fallen and standing form. The boundary between live reef and off-reef is usually quite distinct, and often starts with an area of dead sponge on a distinct incline. Dead reef is distinct from live reef in that it is a flat area of broken, dead sponge fragments covered in sediment and organic 'fuzz', with no reef-building sponges growing on it and little, if any, standing dead sponge. This habitat type could be the result of natural reef disintegration or destruction of reefs by bottom trawling, but this cannot be determined from the video.

The linear (horizontal) distance of each snapshot was also recorded in meters using the formula:

$$\mathbf{X = [(N_a \times N_s) / N_p] / 100}$$

where $\mathbf{X}$ = linear distance (in meters)
$\mathbf{N_a}$ = actual distance between the laser pointers (which was fixed at 20 cm)
$\mathbf{N_s}$ = actual horizontal width of the TV screen (in cm)
$\mathbf{N_p}$ = distance between the laser pointers on the TV screen (in cm)

This allowed for the standardization of abundances of organisms into number of individuals per linear meter of video for each snapshot. All analyses used these standardized abundances. Dive locations, depth range of the transects, number of snapshots and total linear distance of snapshots per dive are listed in Table 2.1.

Table 2.1: Dive analysis information for cruise PGC9901.

Dive	Location (Reef Complex)	First GPS Fix	Last GPS Fix	Depth Range (m)	# of snapshots	Total linear length (m)
4769	A2	53.142 N 130.415 W	53.160 N 130.441 W	175 to 230	142	452.20
4770	A2	53.165 N 130.447 W	53.176 N 130.464 W	167 to 183	469	773.58
4771	A2	53.180 N 130.428 W	53.187 N 130.405 W	170 to 213	418	975.91
4772	A2	53.166 N 130.428 W	53.157 N 130.447 W	158 to 188	353	820.25
4773	A2	53.186 N 130.401 W	53.190 N 130.410 W	188 to 218	275	556.15
4774	A2	53.178 N 130.465 W	53.185 N 130.476 W	169 to 180	278	588.25
4775	A2	53.188 N 130.460 W	53.181 N 130.479 W	160 to 174	375	895.30
4776	A2	53.181 N 130.485 W	53.200 N 130.480 W	143 to 176	429	1010.79
4777	B	52.439 N 129.700 W	52.445 N 129.714 W	168 to 208	255	619.28
4778	B	52.454 N 129.686 W	52.442 N 129.673 W	150 to 210	417	986.30
4779	A1	53.297 N 130.715 W	53.306 N 130.729 W	171 to 182	299	729.56
4780	A1	53.331 N 130.732 W	53.342 N 130.748 W	157 to 178	328	740.70
4781	A1	53.341 N 130.748 W	53.339 N 130.743 W	158 to 169	102	224.34
4782	A1	53.254 N 130.654 W	53.250 N 130.643 W	169 to 174	200	424.84
4783	A1	53.250 N 130.646 W	53.247 N 130.636 W	165 to 175	92	181.51
Total				150 to 230	4432	9978.95

The megafaunal organisms observed in these video snapshots were not generally identifiable to species (with a few exceptions) and thus were sorted into taxonomic groups that could be consistently identified with a reasonable degree of certainty given the quality of the video. Taxonomic groupings used in the analysis of the 1999 video

data are provided in Table 2.2. Note that the range of taxonomic groups is quite high (class to species) and that the common names are used in the analysis results to avoid confusion. The rockfish were divided into two categories, <20 cm in length and >20 cm in length, and the lengths were estimated using the laser pointers from the camera, which were 20 cm apart.

Error bar plots with means and 95% Confidence Intervals were created for taxonomic richness (S), number of individuals (N) and the Shannon-Wiener Diversity Index (H') for each habitat type and each complexity value as well as for each taxonomic group for habitat type. In this study $H' = -\Sigma(p_i)(\log_e p_i)$, where p_i is the proportion of the total sample belonging to the *i*th species (Krebs 1989, Clarke and Warwick 2001) for both habitat and complexity. All snapshots were used to calculate taxonomic richness and number of individuals but this methodology would have violated the assumption of equal standard deviations per sample for H', so to calculate this index the snapshots were grouped by reef complex, giving a sample size of 3 for each habitat type. Even this methodology may not be sufficient to satisfy the assumptions underlying H' so any conclusions drawn from this index should be made with caution. All error bar plots were created using the statistical software SPSS, version 11.0.

Each pair of error bars represents a t-test comparison, meaning that error bars that do not overlap the mean of another error bar represent a significant comparison. Only those plots with significant comparisons were included in the results section, so snails, nudibranchs, ratfish, dogfish and codfish were not plotted. Note that non-significant comparisons between two groups are indicated in the accompanying text description of the results section by a slash between the two group names.

Table 2.2: Taxonomic groupings used for the video analysis.

Phylum	Taxonomic Group	Common Name
Chordata	Family: Scorpaenidae	Rockfish <20 cm
Chordata	Family: Scorpaenidae	Rockfish >20 cm
Chordata	Family: Rajidae	Skates
Chordata	Family: Pleuronectidae	Flatfish
Chordata	Family: Squalidae	Dogfish
Chordata	Family: Chimaeridae	Ratfish
Chordata	Family: Gadidae	Codfish
Echinodermata	Class: Asteroidea	Sea Stars
Echinodermata	Class: Ophiuroidea	Brittle Stars
Echinodermata	Class: Holothuroidea	Sea Cucumbers
Echinodermata	Class: Echinoidea	Sea Urchins
Echinodermata	Class: Crinoidea	Feather Stars
Porifera	Family: Rossellidae	Boot Sponges
Porifera	Class: Demospongiae	Demosponges
Arthropoda	Species: *Pandalus platyceros*	Prawns
Arthropoda	Species: *Munida quadrispina*	Squat Lobsters
Arthropoda	Order: Pleocyemata	Crabs
Mollusca	Class: Gastropoda	Snails
Mollusca	Order: Nudibranchia	Nudibranchs
Cnidaria	Species: *Balticina septentrionalis*	Sea Whips
Cnidaria	Order: Actiniaria	Sea Anemones
Cnidaria	Subclass: Alcyonaria	Corals

The error bar plots are divided into two categories: all taxonomic groups combined and all taxonomic groups except boot sponges and demosponges. This was done because none of the three reef-building sponge species on the live reef were counted as individuals on the basis that they were creating habitat; this omission biased the total count of individuals and taxa. Since boot sponges and demosponges could also potentially be seen as habitat creating groups (Boyd 1981, Villamizar and Laughlin 1991, Barthel 1992, Bett and Rice 1992, Beaulieu 2001, Bill Austin, pers. comm.), it was decided that a more equitable comparison might be attained by removing all sponge groups.

A data matrix was created for analysis with the PRIMER-E statistics package. This data matrix was not formed from raw data but from grouping the snapshots into 'samples' made of a unique combination of reef complex, habitat and complexity (called factors in PRIMER) (Table 2.3). Only those combinations with more than 50 linear metres sampled were included in this matrix because less than 50 metres was considered insufficient sampling effort and could potentially bias the results. Not every combination of reef complex, complexity and habitat was encountered in the video transects, so there are more of some types of factors than others (for example, there are 6 samples each of off-reef and live reef but only 5 samples of dead reef). Fortunately, ANOSIMs are relatively robust to this kind of unbalanced sample design (Clarke and Warwick 2001).

Similarity percentages (SIMPER) were calculated using this data matrix to determine how dissimilar each habitat type is to each of the others and to indicate which taxonomic groups contributed most to that dissimilarity and the percentages of that contribution (Clarke and Warwick 2001). A similarity matrix was then calculated using Bray-Curtis similarity with a fourth-root transformation. Such a large transformation was used to clarify the differences between samples due to the small numbers involved. An Analysis of Similarity (ANOSIM) was performed to determine if the community structure, which can be defined as the number of taxonomic groups present, the identity of those groups and the number of individuals, differed between habitat types and complexity values (Clarke and Warwick 2001). This was a two-way crossed ANOSIM using habitat as factor A and complexity as factor B because they are interrelated. Dendrograms, which are a type of cluster analysis, were calculated to determine if taxonomic groups tend to occur in a parallel manner across various sites (Clarke and Warwick 2001) and therefore

groups the sites by their relative similarity. These were calculated using the sample matrix in PRIMER-E for all taxonomic groups and also for all taxonomic groups excluding the boot sponges and demosponges.

Table 2.3: PRIMER-E sample matrix with the three factors and linear distances per sample.

Sample	Reef Complex	Complexity	Habitat	Linear Distance (m)
1	A1	Low	Dead reef	761.19
2	A2	Low	Dead reef	2078.39
3	B	Low	Dead reef	777.32
4	A1	Medium	Dead reef	145.62
5	A2	Medium	Dead reef	416.71
6	A1	High	Live reef	397.48
7	A2	High	Live reef	1319.36
8	B	High	Live reef	54.88
9	A2	Low	Live reef	93.52
10	A1	Medium	Live reef	167.41
11	A2	Medium	Live reef	363.75
12	B	High	Off-reef	85.39
13	A1	Low	Off-reef	743.15
14	A2	Low	Off-reef	1333.42
15	B	Low	Off-reef	504.76
16	A2	Medium	Off-reef	418.36
17	B	Medium	Off-reef	141.54

Table 2.3 indicates that, despite the exclusion of those samples with less than 50 metres sampled, there is still a bias in sampling effort. For some samples as little as 54.88 meters were analyzed (sample 8) while as much as 2078.39 meters were analyzed for others (sample 2). The samples were grouped in this manner from a much larger data set, as stated earlier, because the whole data set of 4432 snapshots is much too large for ANOSIM analysis; the calculation of a similarity matrix is not possible with so many samples. To determine if this bias was affecting the ANOSIM results a new data matrix was created where 50 snapshots from the 17 unique factor sample groups were chosen at random from the larger set of snapshots and added together to get abundances for each

taxonomic group. This randomization test was repeated 20 times and the average of all tests was used to create a sample matrix (referred to as the randomized sample matrix). The randomized sample matrix, which included all taxonomic groups, ranged in sampling effort from 54.88 meters to 137.10 meters. If this less biased data set gives similar ANOSIM results to the complete data matrix then the bias in sampling effort could be considered of minor importance for determination of meaningful ANOSIM values.

Rank abundance plots for invertebrate and fish taxonomic groups were created using Sigma Plot 8.0 for both habitat and complexity. These plots combine information about average abundance and about how abundant each taxonomic group is in relation to the others. They give variance around the average by including error bars calculated from the standard deviation. Each plot is ranked according to one group (live reef for habitat type and high for complexity) so that the X-axis represents the most abundant to least abundant taxonomic group for that habitat or complexity.

RESULTS

The video analyzed for this study was of generally good quality. The amount of suspended sediment and plankton in the water column was usually quite low, making for good clarity, although if the submersible stopped for too long in one spot, the lights attracted large quantities of zooplankton, especially chaetognaths, and it sometimes took this 'cloud' a few moments to dissipate once the submersible started to move again. The field of view was fairly consistent, as the submersible stayed a relatively constant height off the seafloor; the only exception to this was in the live sponge reef habitat, when the field of view could be cut down rather dramatically by the presence of the large sponges, which often obscured large portions of the bottom from view. This may have biased the

counts of certain organisms on the live reefs, such as the crustaceans and rockfish, which tended hide either behind or inside the sponges when the submersible approached. This was also true, although to a lesser extent, on some of the boulder fields in the off-reef areas. The smaller organisms were also more difficult to see in the more complex habitats, as were the more cryptic organisms, such as the sea stars most of which were either white or beige, and therefore tended to stand out less in the structurally complex areas; therefore, these groups may have been underestimated in the live reef areas.

One general observation that is not reflected in the data analysis relates to the spatial distribution of organisms on the live reefs. It appeared that rockfish tended to be more abundant at the edges of the reef mounds, where they seemed to congregate in small schools, which sometimes scattered into the reefs when the submersible approached. Another general observation is that anywhere between 30 and 70% of any living reef mound is composed of expanses of dead sponge in either flattened or standing form. It can be assumed this is a natural phenomena, since trawling would have flattened the standing dead sponges. The cause of these areas of dead sponge among the living sponges is not yet known, but it can be speculated that hydrodynamics plays a large role in the distributions of any filter feeders, so perhaps these areas were deprived of nutrients by sponges that built 'upstream' of them in terms of the dominant current flow.

Habitat

Number of taxa per metre, or taxonomic richness (hereafter referred to as richness), number of individuals per metre (or abundance) and the Shannon-Wiener Diversity Index (hereafter referred to as diversity) for each habitat type are summarized in Figure 2.3. With all taxonomic groups combined, richness increases significantly from dead reef to

off-reef to live reef habitat. Abundance of individuals increases from dead reef to live reef to off-reef, with off-reef being slightly more variable than either of the other habitat types. Diversity is not significantly different between any of the three habitats; however, the variability between habitats increases from live reef to dead reef to off-reef. The trends do not change for richness and diversity when the rossellid and reef-building sponges are removed from the counts, only lowers the averages, and decreases the variability in the diversity measures, although the overall trends of higher variability of diversity in the dead reef and off-reef habitats remain unchanged. For number of individuals, however, the trend shifts so that there is no significant difference between live reef and off-reef habitats due to a major reduction in off-reef abundance, which is likely driven by the demosponge group.

Individual taxonomic groups vary widely in trends of abundance for each habitat type. Figure 2.4 shows abundance error bar plots for the major groups of fish and echinoderms observed on the transects. Small rockfish (which are likely juvenile rockfish) are more abundant in live reef habitat than in dead reef/off-reef; the mean number in live reef habitat is 0.097 per meter as opposed to 0.021 per meter averaged over dead reef and off-reef. Large rockfish (those greater than 20 cm in length) are less

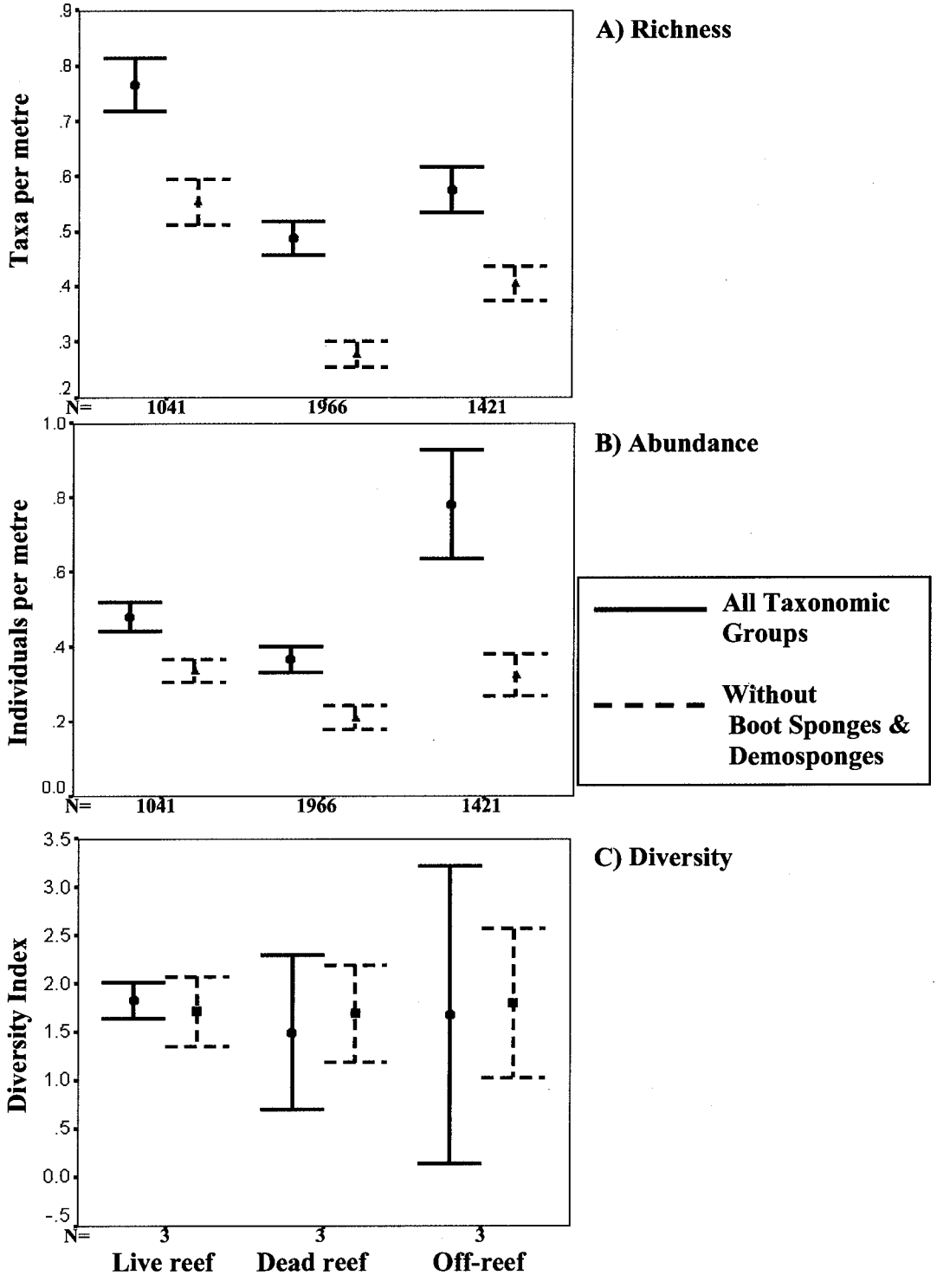

Figure 2.3: Taxonomic richness (A), number of individuals (B) and Shannon-Wiener Diversity Index (C) summarized for habitat types in error bar plots with means and 95% Confidence Intervals (N = number of snapshots analyzed).

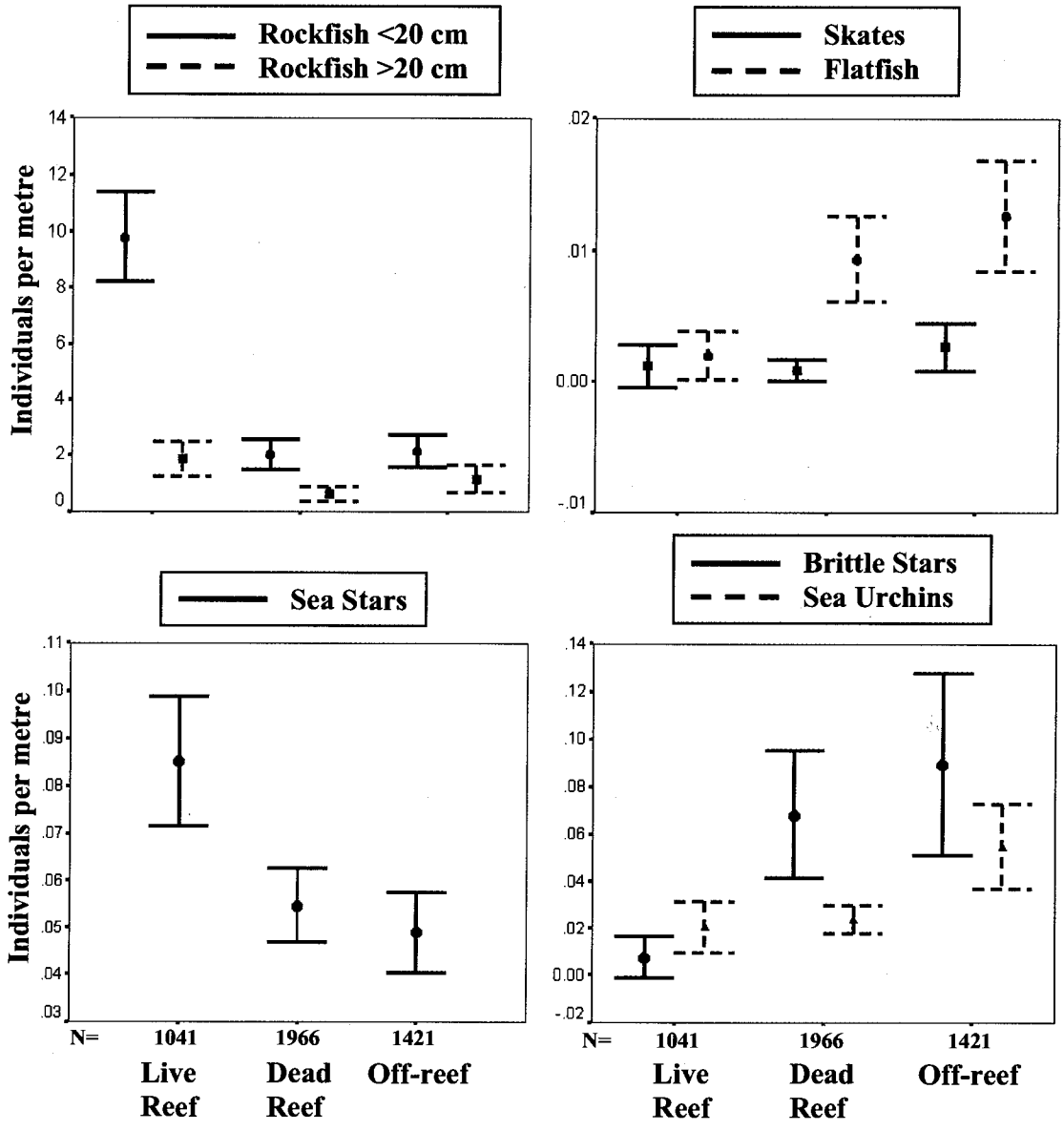

Figure 2.4: Fish and echinoderm abundances summarized for habitat types in error bar plots with means and 95% Confidence Intervals (N = number of snapshots analyzed).

abundant in each habitat, although abundance is significantly different in each habitat, increasing from dead reef to off-reef to live reef.

Flatfish increase from live reef to dead reef/off-reef habitat. Skates also show an increase from live reef/dead reef to off-reef, although this trend is not significant, but that may be due to the low overall abundance of skates observed (averaging less than 0.004 individuals per meter in any habitat).

Sea stars are significantly more abundant on the live reef habitat than the dead reef/off-reef habitat, although the opposite trend is true for brittle stars, which increase from live reef to dead reef/off-reef, and sea urchins, which increase from live reef/dead reef to off-reef habitat.

Abundances of sponges and crustaceans are summarized in Figure 2.5. Boot sponges show a general decrease in abundance from live reef/dead reef to off-reef although off-reef abundance does not differ significantly from that of live reef. The weak trend is towards higher abundances on dead reef habitat. The trend for demosponges is a significant increase in abundance from live reef/dead reef to off-reef (with less than 0.006 individuals per meter on live reef/dead reef but 0.345 individuals per meter off-reef).

Squat lobsters decrease in abundance by several orders of magnitude from live reef to dead reef to off-reef, with more than 0.04 per meter on live reef and less than 0.0004 per meter off-reef. Prawns and crabs show the same trend, although abundances on dead reef and off-reef are not significantly different from each other for either group. As a group, crustaceans are more abundant on live reef habitat than on the other shelf habitats.

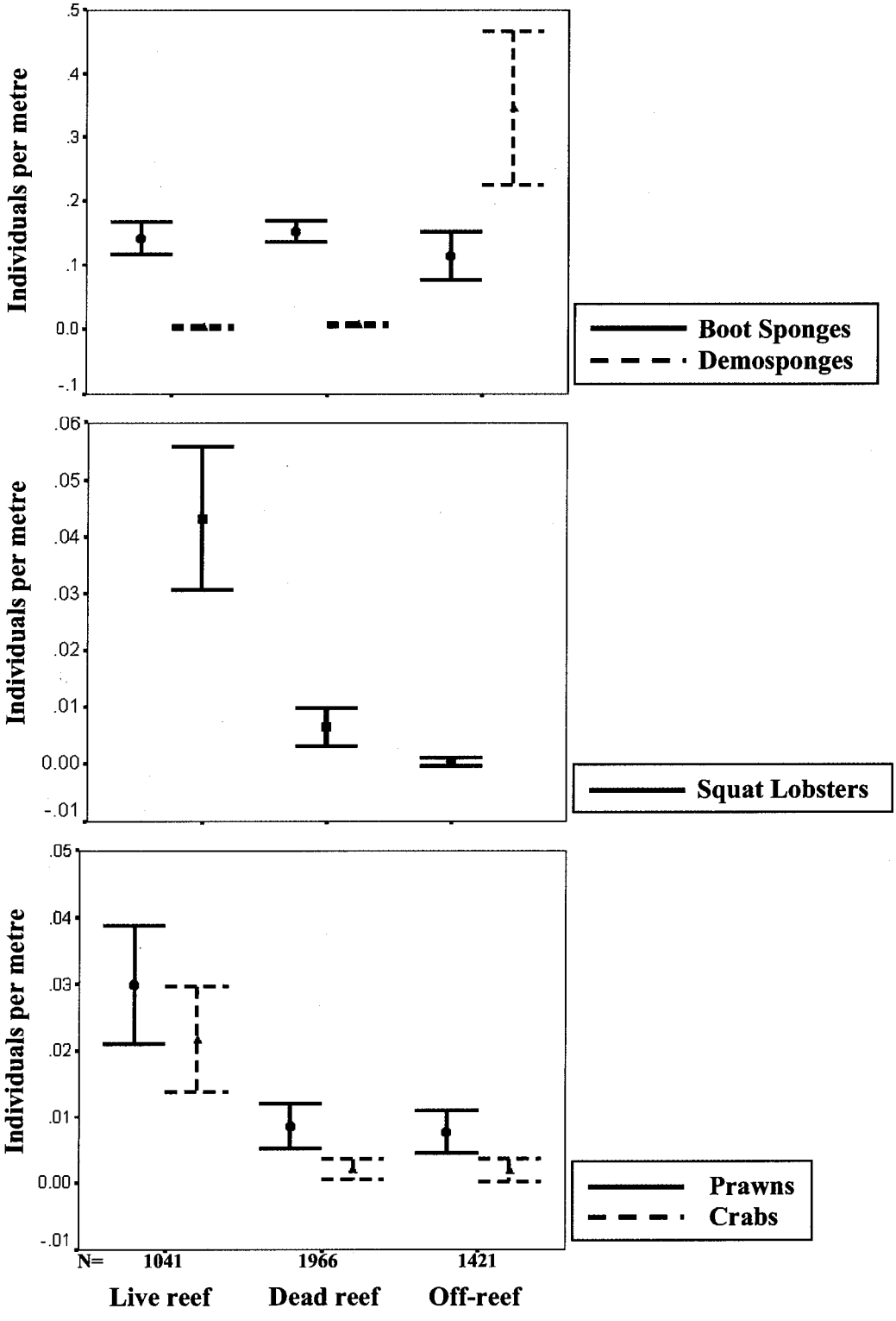

Figure 2.5: Sponge and crustacean abundances summarized for habitat types in error bar plots with means and 95% Confidence Intervals (N = number of snapshots analyzed).

Abundance of cnidarians is summarized in Figure 2.6. Sea anemones increase in abundance from live reef/dead reef to off-reef, although the extreme variability of the off-reef samples is worth noting (mean of 0.037 individuals per meter with an upper CI of 0.071 and a lower CI of 0.003). Sea whips and corals show exactly the same trend as sea anemones even though they require different substrata (seawhips require soft substrate and corals and anemones require hard substrate) but without the extreme variability in the off-reef habitat. As a group, cnidarians have higher abundances in off-reef habitat.

Univariate measures such as richness, abundance and diversity each describe one part of a community and provide a great deal of information about the different habitat types in this study, but multivariate measures can add an additional analysis of the community as a whole. An ANOSIM was calculated for the different habitats and, as in the univariate tests, was calculated for two groups: all taxonomic groups combined and all taxonomic groups except boot sponges and demosponges (Table 2.4). The ANOSIM with all taxonomic groups shows a global significance between habitats meaning that there are significant differences overall; however, only the comparison between live reef and off-reef habitat was significant. The ANOSIM with sponges removed showed identical results with only the live reef and off-reef comparison significant. The ANOSIM test with the randomized data matrix to check for sampling bias (as explained in the methods section) produced results almost identical to the complete data matrix results. The complete data matrix ANOSIM results can therefore be considered unbiased and are the only results discussed further.

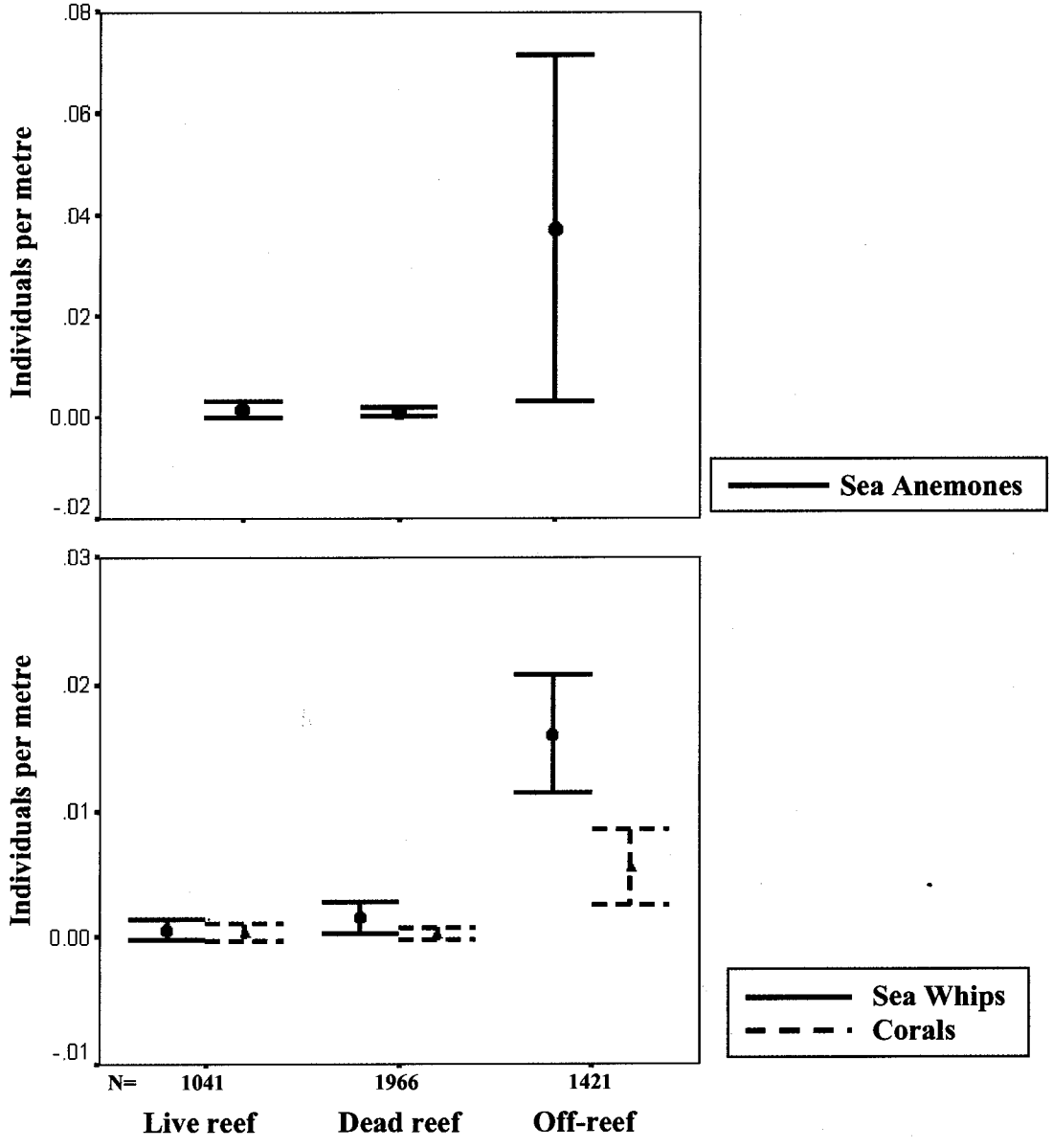

Figure 2.6: Cnidarian abundances summarized for habitat types in error bar plots with means and 95% Confidence Intervals (N = number of snapshots analyzed).

Table 2.4: ANOSIM results for analysis of different habitat types crossed with complexity values. Bold indicates significant comparisons.

Comparison	R Statistic	Significance Level
Global Test	0.408	**0.027**
live reef/off-reef	0.886	**0.021**
live reef/dead reef	0.256	0.333
off-reef/dead reef	0.086	0.400
Global Test (no sponges)	0.460	**0.014**
live reef/off-reef (no sponges)	0.800	**0.021**
live reef/dead reef (no sponges)	0.488	0.250
off-reef/dead reef (no sponges)	0.200	0.333
Global Test (randomized)	0.420	**0.025**
live reef/off-reef (randomized)	0.886	**0.021**
live reef/dead reef (randomized)	0.209	0.333
off-reef/dead reef (randomized)	0.086	0.367
Global Test (randomized, no sponges)	0.418	**0.022**
live reef/off-reef (randomized, no sponges)	0.743	**0.042**
live reef/dead reef (randomized, no sponges)	0.349	0.333
off-reef/dead reef (randomized, no sponges)	0.143	0.333

The other multivariate test done for this data set was SIMPER (Table 2.5), which indicates how dissimilar the habitat types are from each other and which species are contributing to that dissimilarity. Again, this test was run with all taxonomic groups included and also with the sponge groups removed. With all taxonomic groups included, the average dissimilarity between each habitat type ranges from 31 to 39%, with the live reef/off-reef comparison being the most dissimilar, a result which is consistent with the ANOSIM results. Demosponges and sea anemones feature prominently in any comparison involving off-reef, due to their high abundance in that habitat (an average of 1.92 individuals per metre per sample for demosponges and 0.26 individuals per metre per sample for sea anemones). Brittle stars contribute to dissimilarity in all comparisons, although their average abundance is not high in any one habitat, with a highest abundance of 0.06 individuals per metre per sample in dead reef habitat. In terms of percent

contribution to dissimilarity, the demosponges are apparently driving any off-reef comparison with values of over 17% in each comparison.

Table 2.5: SIMPER results for comparisons between habitat types. This shows the dissimilarity between the habitat types and the top three species that contribute to this dissimilarity (contribution to % dissimilarity includes all 22 taxonomic groups and is therefore out of 100).

Comparison	% Ave. Dissimilarity	Species	Ave. Species Abundance	Contribution to % dissimilarity
live reef/ off-reef	39.24	Demosponges Brittle Stars Sea Anemones	0.00 / 1.92 0.03 / 0.04 0.00 / 0.26	17.49 6.94 6.63
live reef/ dead reef	31.08	Brittle Stars Squat Lobsters Crabs	0.03 / 0.06 0.01 / 0.01 0.01 / 0.01	9.52 7.84 7.80
off-reef/ dead reef	35.35	Demosponges Brittle Stars Sea Anemones	1.92 / 0.01 0.04 / 0.06 0.26 / 0.00	17.12 7.90 7.38
live reef/ off-reef (no sponges)	38.40	Sea Anemones Brittle Stars Sea Whips	0.00 / 0.26 0.03 / 0.04 0.00 / 0.01	9.03 8.85 7.54
live reef/ dead reef (no sponges)	33.79	Brittle Stars Squat Lobsters Crabs	0.03 / 0.06 0.01 / 0.01 0.01 / 0.01	10.69 8.84 8.81
off-reef/ dead reef (no sponges)	35.11	Brittle Stars Sea Anemones Squat Lobsters	0.04 / 0.06 0.26 / 0.00 0.00 / 0.01	10.11 10.06 8.84

Once the sponge groups are removed, the range of average dissimilarities between pairs of habitat types is even tighter (between 34 and 38%), with the live reef/off-reef comparison still having the highest dissimilarity. Sea anemones still contribute to dissimilarity in any comparison involving off-reef habitat. Brittle stars also still contribute in all comparisons and squat lobsters contribute to any comparison involving dead reef. The only real change is the removal of the demosponge group. It is interesting to note that the groups in the live reef/dead reef comparison do not change once the sponge groups are removed because demosponges are not abundant in either habitat.

Rank abundance plots, showing the percent average relative abundance of each taxonomic group, were calculated for each habitat. The invertebrate groups are shown in Figure 2.7. The shapes of the curves are similar between the live reef and dead reef habitats, indicating a similar ranking in the abundance of taxonomic groups. The major difference between these two curves is not the shape but the abundances of the first five groups along the X-axis. The boot sponges have an average mean relative abundance (hereafter referred to as relative abundance) of 53% in the dead reef habitat compared to 39% in the live reef habitat, the sea stars have a relative abundance of 22% on dead reefs and 29% on live reefs and the crustaceans (which account for the next three groups along the axis) have a cumulative relative abundance of 5.5% on dead reef and 24% on live reefs. It could be said that boot sponges are dominant in dead reef habitat, while live reef habitat has a more even distribution of relative abundances, with no one group dominant. The off-reef curve is distinctly different from the other two curves, with four groups at about 20% relative abundance (sea stars, sea urchins, demosponges and brittle stars) while only two taxa (boot sponges and sea stars) make up 70% or more of the relative abundances on dead reef and live reef. Sea stars are similar in relative abundance to the other two habitats at 20% but that is the only similarity. One other similarity between all the curves is that the groups with the highest relative abundances also have the highest variabilities.

The rank abundance plots for the fish groups (Figure 2.8) also show a similarity in the shape of the curves for live reef and dead reef, at least compared to the off-reef curve which has a much flatter profile. Small rockfish are the dominant group on live reefs with a relative abundance of 75%. Together the rockfish groups make up a relative

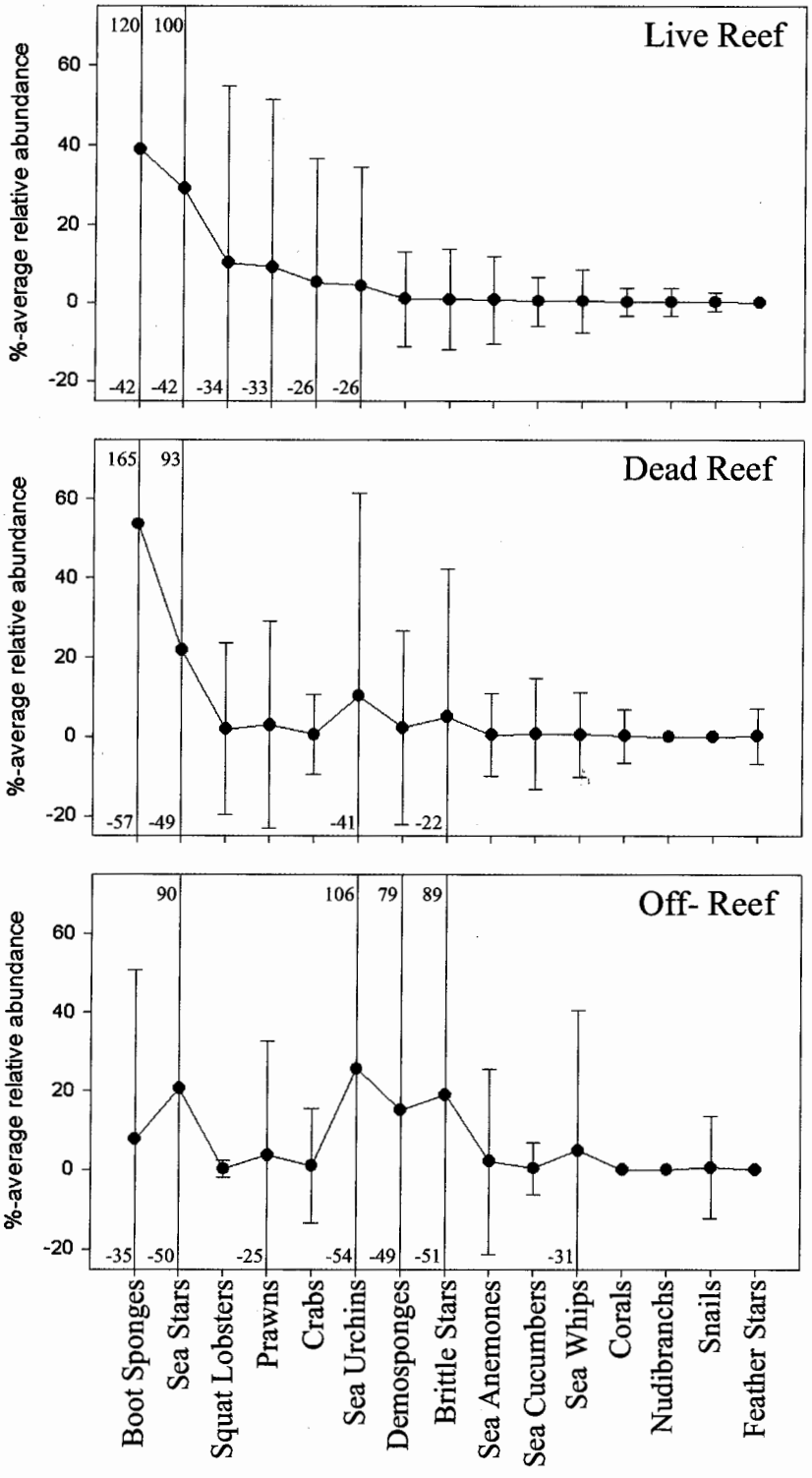

Figure 2.7: Rank abundance plots for each habitat. These plots show percent average relative abundance of each invertebrate taxonomic group, with standard deviation. Taxonomic groups are ordered by decreasing abundance on live reef. The error bars that are cut off have their values indicated beside the bars on the graph.

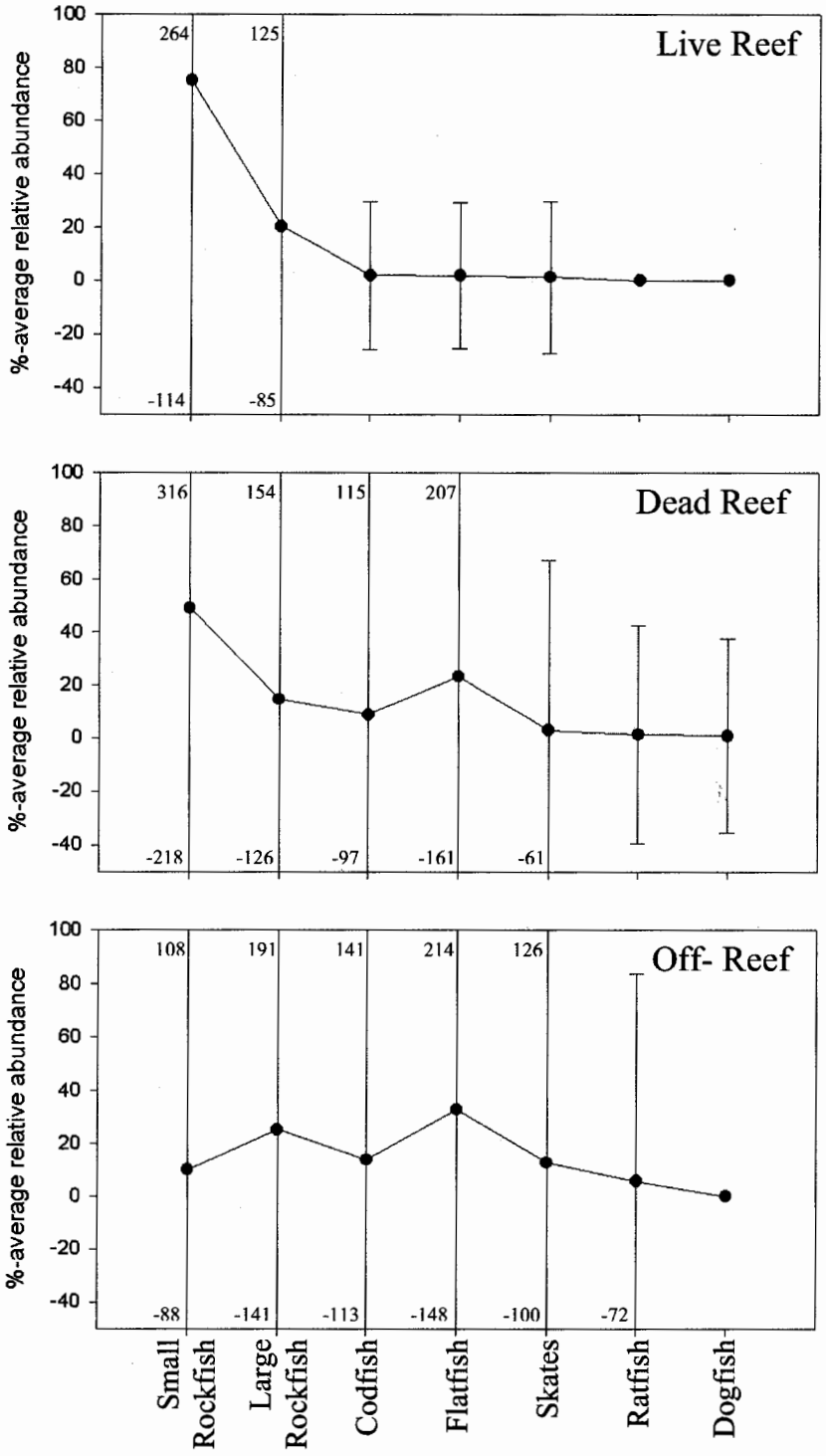

Figure 2.8: Rank abundance plots for each habitat. These plots show percent average relative abundance of each fish taxonomic group, with standard deviation. Taxonomic groups are ordered by decreasing abundance on live reef. The error bars that are cut off have their values indicated beside the bars on the graph.

abundance of 95% on live reef, 63% on dead reefs and 35% off-reef, but also have high variability in all habitats. Flatfish have the highest relative abundance in off-reef habitats at 33%. Another difference between the off-reef curve and the other two curves is the reversed trend in the relative abundances of the small rockfish and large rockfish; small rockfish have higher relative abundances in both live reef and dead reef, but the opposite is true on off-reef.

Complexity

The univariate measures of taxonomic richness, abundance and diversity compared between each complexity value is shown in Figure 2.9. For all taxonomic groups combined, high and medium complexity are not significantly different for any measure; however, both are significantly different from low complexity for richness and abundance, with a decreasing trend in values from high/medium to low. No complexity value is significantly different in terms of diversity although low complexity is more variable.

These trends change slightly when the sponge groups are removed. Richness becomes significantly different for each complexity value, decreasing from high to low. Abundance of individuals decreases from high to medium/low and diversity still is not significant for any complexity value, although low complexity variability is reduced, suggesting the sponge groups are more patchy in low complexity areas than in higher complexity areas.

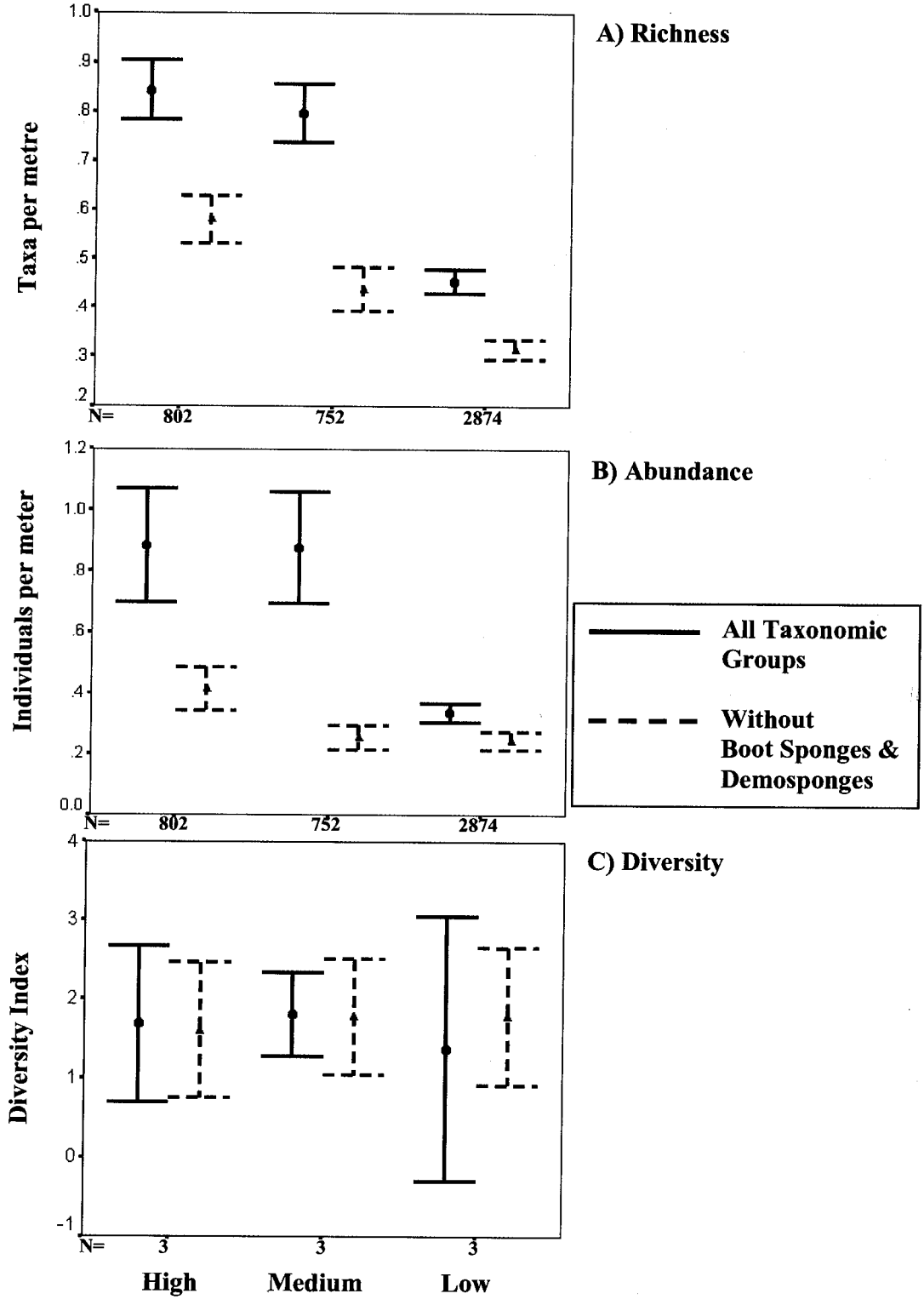

Figure 2.9: Taxonomic richness (A), number of individuals (B) and Shannon-Wiener Diversity Index (C) summarized for complexity values in error bar plots with means and 95% Confidence Intervals (N = number of snapshots analyzed).

The ANOSIM for complexity crossed with habitat type showed no significant comparisons between complexity types when all taxonomic groups are included (Table 2.6). With the exclusion of the rossellid sponges and demosponge groups the comparison between medium and low complexity areas becomes significantly different, although it is right at the threshold of significance.

The randomized data matrix ANOSIM gave almost identical results to the complete data matrix (as with habitat type), so it can again be assumed that the complete data matrix is an unbiased representation of the community structure and only the results from the complete data matrix will be discussed further.

Table 2.6: ANOSIM results for analysis of different complexity values crossed with habitat types. Bold indicates the significant comparisons.

Comparison	R Statistic	Significance Level
Global Test	0.284	0.089
high/low	0.333	0.313
high/medium	0.328	0.200
medium/low	0.186	0.220
Global Test (no sponges)	0.379	**0.031**
high/low (no sponges)	0.556	0.188
high/medium (no sponges)	0.328	0.167
medium/low (no sponges)	0.405	**0.050**
Global Test	0.184	0.165
high/low (randomized)	0.333	0.313
high/medium (randomized)	0.328	0.200
medium/low (randomized)	0.000	0.487
Global Test (randomized, no sponges)	0.362	**0.036**
high/low (randomized, no sponges)	0.444	0.188
high/medium (randomized, no sponges)	0.328	0.200
medium/low (randomized, no sponges)	0.405	**0.047**

The SIMPER results show the average dissimilarity between each complexity comparison and those taxonomic groups contributing to that dissimilarity (Table 2.7). With the sponge groups included, demosponges, brittle stars and sea anemones appear to

be contributing the most to dissimilarity between all the comparisons, except in the medium/low comparison where squat lobsters take the place of the sea anemones.

Without the sponge groups, however, the only real change is the removal of the demosponges; brittle stars and sea anemones still play the major role contributing to dissimilarity in all comparisons, with squat lobsters still taking the place of sea anemones in the medium/low comparison.

Table 2.7: SIMPER results for comparisons between complexity values. This shows the dissimilarity between the complexity values and the top three species that contribute to this dissimilarity (contribution to % dissimilarity includes all 22 taxonomic groups and is therefore out of 100).

Comparison	% Ave. Dissimilarity	Species	Ave. Species Abundance	Contribution to % dissimilarity
high/ low	40.00	Demosponges Brittle Stars Sea Anemones	1.58 / 0.03 0.06 / 0.07 0.38 / 0.00	11.46 8.21 7.47
high/ medium	37.32	Demosponges Brittle Stars Sea Anemones	1.58 / 0.84 0.06 / 0.00 0.38 / 0.00	14.90 10.96 8.38
medium/ low	31.92	Demosponges Brittle Stars Squat Lobsters	0.84 / 0.03 0.00 / 0.07 0.01 / 0.00	13.84 8.74 6.67
high/ low (no sponges)	41.39	Brittle Stars Sea Anemones Sea Urchins	0.06 / 0.07 0.38 / 0.00 0.01 / 0.04	9.79 9.76 7.84
high/ medium (no sponges)	38.96	Brittle Stars Sea Anemones Crabs	0.06 / 0.00 0.00 / 0.38 0.02 / 0.01	13.10 11.26 7.94
medium/ low (no sponges)	32.36	Brittle Stars Squat Lobsters Sea Whips	0.00 / 0.07 0.01 / 0.00 0.01 / 0.01	10.75 8.26 8.06

Rank abundance plots, showing the percent average relative abundance of each taxonomic group, were calculated for each complexity value. The invertebrate groups are shown in Figure 2.10. The shape of the curves for high and medium complexity are similar, although the abundances of the first four taxonomic groups differ somewhat.

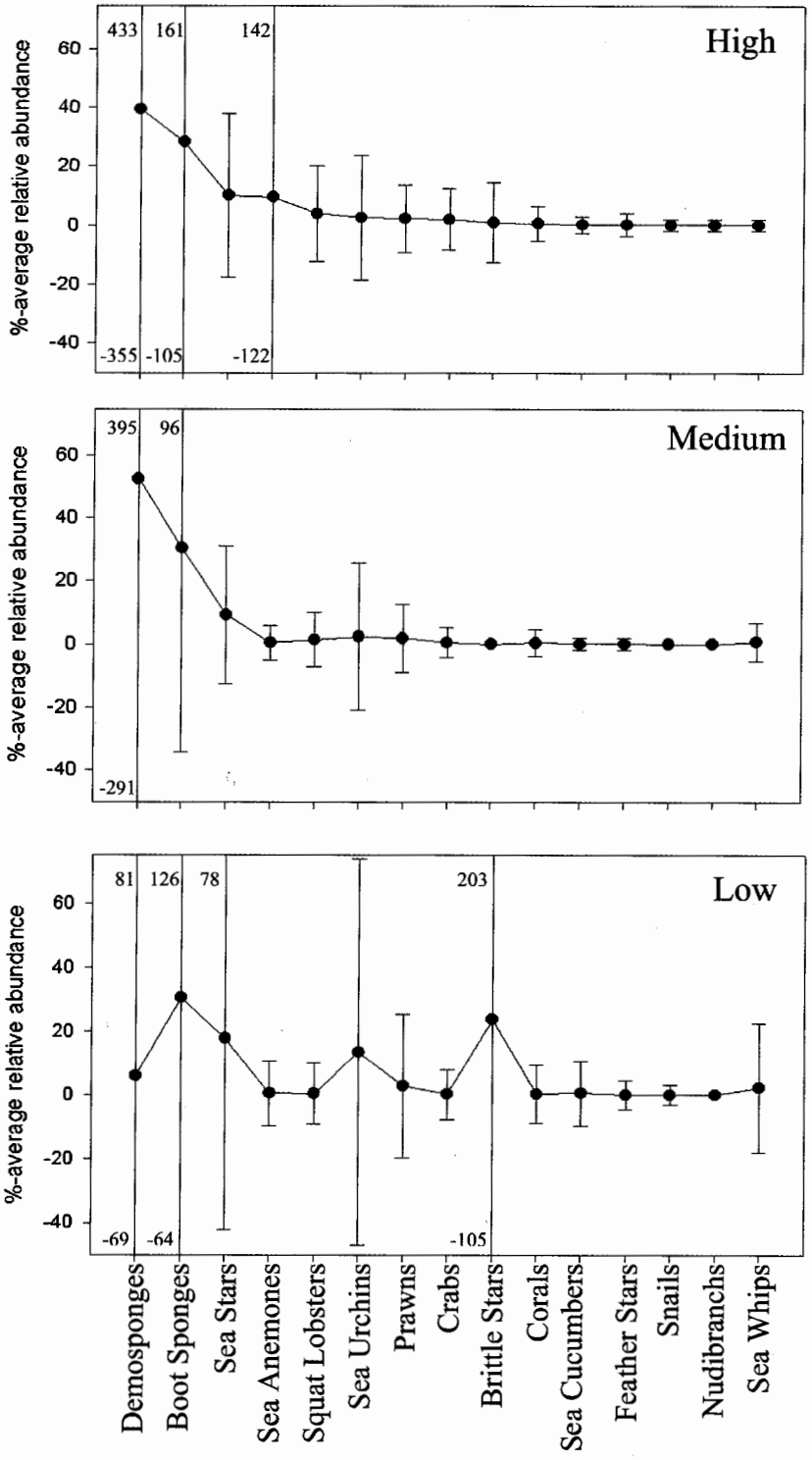

Figure 2.10: Rank abundance plots for each complexity. These plots show percent average relative abundance of each invertebrate taxonomic group, with standard deviations. Taxonomic groups are ordered by decreasing abundance in high complexity. The error bars that are cut off have their values indicated beside the bars on the graph.

It is the two sponge groups that are the most abundant in those two habitats and make up over 60% of the relative abundance in each. The demosponges have a relative abundance of 40% at high complexity and 52% at medium, and the boot sponges have a similar relative abundance at those two complexities at 28% in high and 30% in medium. Both sponge groups have high variability as well as high relative abundances. Sea anemones are more abundant at high complexity (9.5% at high and only 0.5% at medium) and much more variable. The shape of the low complexity curve is quite different from either of the others, especially the demosponges with a relative abundance of 6%, but the group with the highest relative abundance at low complexity are the boot sponges at 31%, which is almost the same as the relative abundance at high and medium complexity. The second most abundant group at low complexity are the brittle stars at 24% but also have high variability.

The fish groups are shown in Figure 2.11. Again, the high and medium complexity curves have a similar shape although the curve is much steeper at the beginning of high complexity due to the high relative abundance of small rockfish, which are dominant at 82%, although with very high variability. The small rockfish are relatively more abundant in all habitats although the values decrease with decreasing complexity (54% at medium complexity and 37% at low complexity). The shape of the low complexity curve is quite flat in comparison to the other two, and while the large rockfish are the second most abundant group at high and medium complexity, it is the flatfish at 24% relative abundance which are the second most abundant group at low complexity.

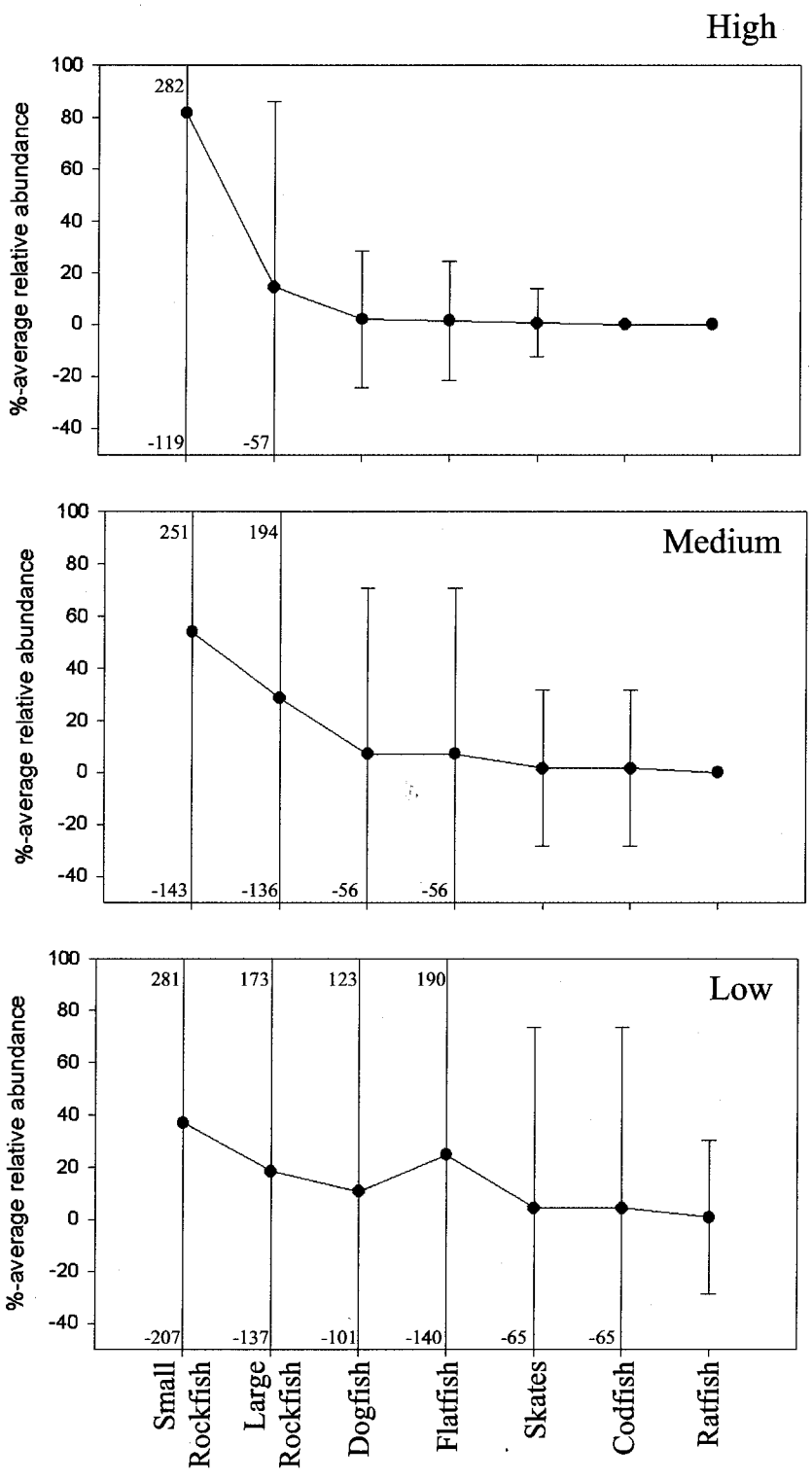

Figure 2.11: Rank abundance plots for each complexity. These plots show percent average relative abundance of each fish taxonomic group, with standard deviations. Taxonomic groups are ordered by decreasing abundance in high complexity. The error bars that are cut off have their values indicated beside the bars on the graph.

Habitat and Complexity

Habitat and complexity are interrelated but have been considered separately to this point. Taxonomic richness, abundance and diversity among habitat types and within each complexity value are in Figure 2.12. The sponge groups were not included because the complexity value is driven by these groups.

Richness and abundance of individuals are significantly higher in the high complexity off-reef areas compared to high complexity live reef and dead reef areas, although these areas also have higher variability. Those off-reef, high complexity areas are heterogeneous habitats in terms of physical rugosity, being boulder fields and bedrock walls, but they are also areas with high abundances of foundation species, such as rossellid sponges, demosponges, large corals, and even individual reef-building sponges. At medium complexity it is the live reef habitats that have the highest values of richness and abundance of individuals, followed by off-reef and then dead reef, although the difference between the two is not significant for abundance of individuals. At low complexity, live reef has such high variability that this habitat is not significantly different from either other habitat, although dead reef is significantly lower than off-reef at low complexity. Overall, dead reef has the lowest values of richness and abundance of individuals at any complexity (except at high, because there are no high complexity dead reef areas).

Diversity is not significantly different for any habitat at any complexity which is not surprising since there were no significant differences in diversity in either habitat or complexity alone. The extreme variability in diversity of high complexity off-reef areas is worth noting.

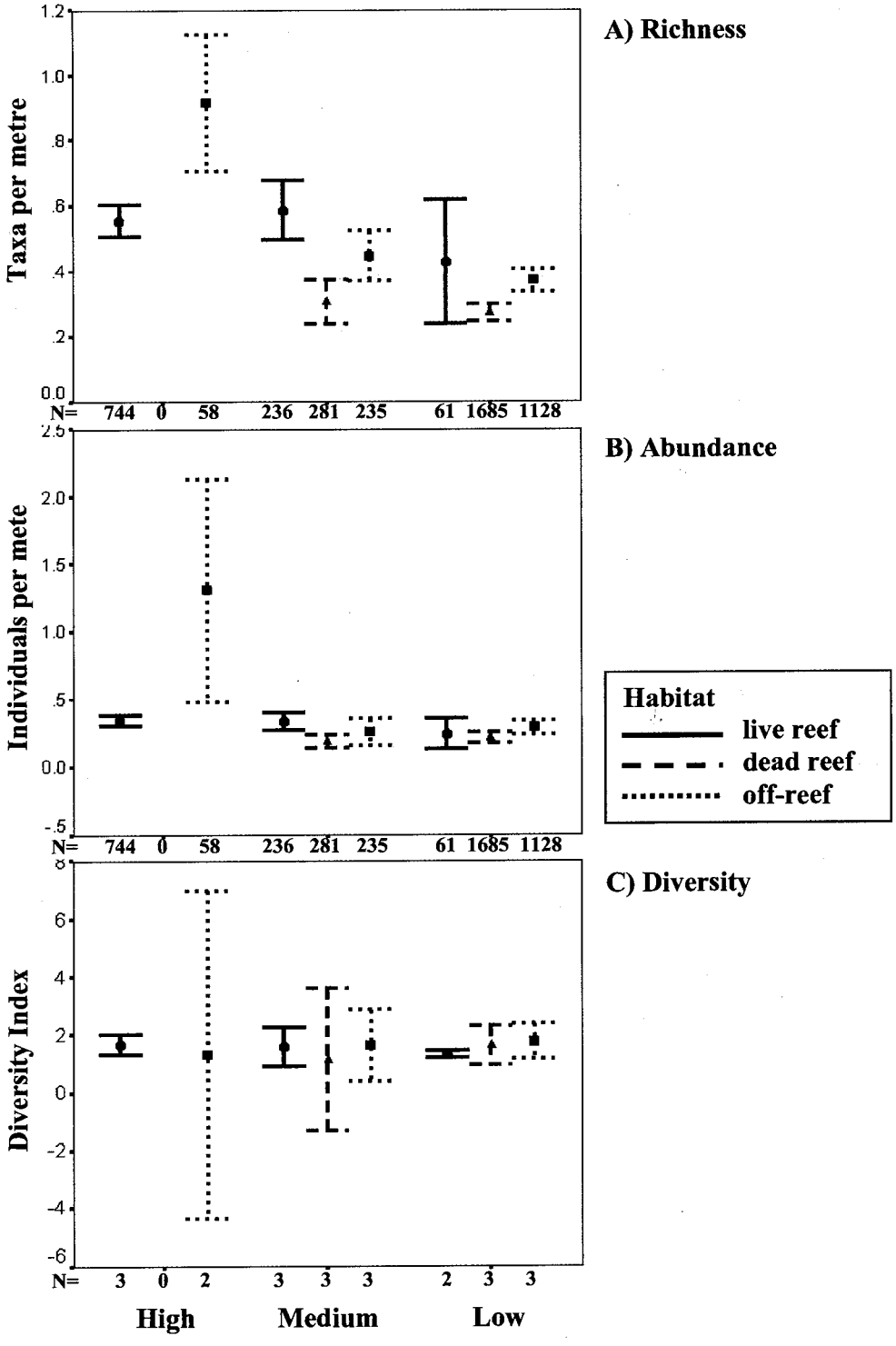

Figure 2.12: Taxonomic richness (A), number of individuals (B) and Shannon-Wiener Diversity Index (C) for habitat types and complexity values in error bar plots with means and 95% Confidence Intervals (N = number of snapshots analyzed). All calculations were done without the sponge groups.

The dendrograms which show the groupings of the samples from the PRIMER matrix are shown in Figure 2.13. The dendrogram with all taxonomic groups, shows several clusters, although none of the clusters appear to be related to any one factor or even any group of factors. The dendrogram with the sponge groups excluded also shows several clusters but only the one group which falls out at approximately 60% similarity. Those two samples are both from reef complex B and are at high complexity, although they are from different habitats. None of the other clusters show any groupings among the factors.

DISCUSSION

Habitat

The three species of hexactinosidan sponges that build reefs on B.C.'s continental shelf are acting as foundation species and are the base of a complex ecosystem, both in terms of heterogeneity of substrate and community structure. The live sponge reefs show increased abundance of individuals when other habitat forming sponges are removed from the analysis and increased taxonomic richness both with and without the other sponges included. This result is consistent with studies of other benthic habitats created by foundation species such as canopy kelps (Dayton 1975, Bruno and Bertness 2001), seagrasses (Woodin 1978, Jones et al. 1994), coral reefs (Bruno and Bertness 2001, Stachowicz 2001) and even polychaete worms (Woodin 1978). There are also numerous examples from terrestrial ecosystems (see Jones et al. 1994, Bruno and Kennedy 2000, Stachowicz 2001 and Crooks 2002 for lists of species). The implication is that the live sponge reefs are creating a refuge from some or all of the physiological, physical or biological stresses acting within the other habitats compared in this study.

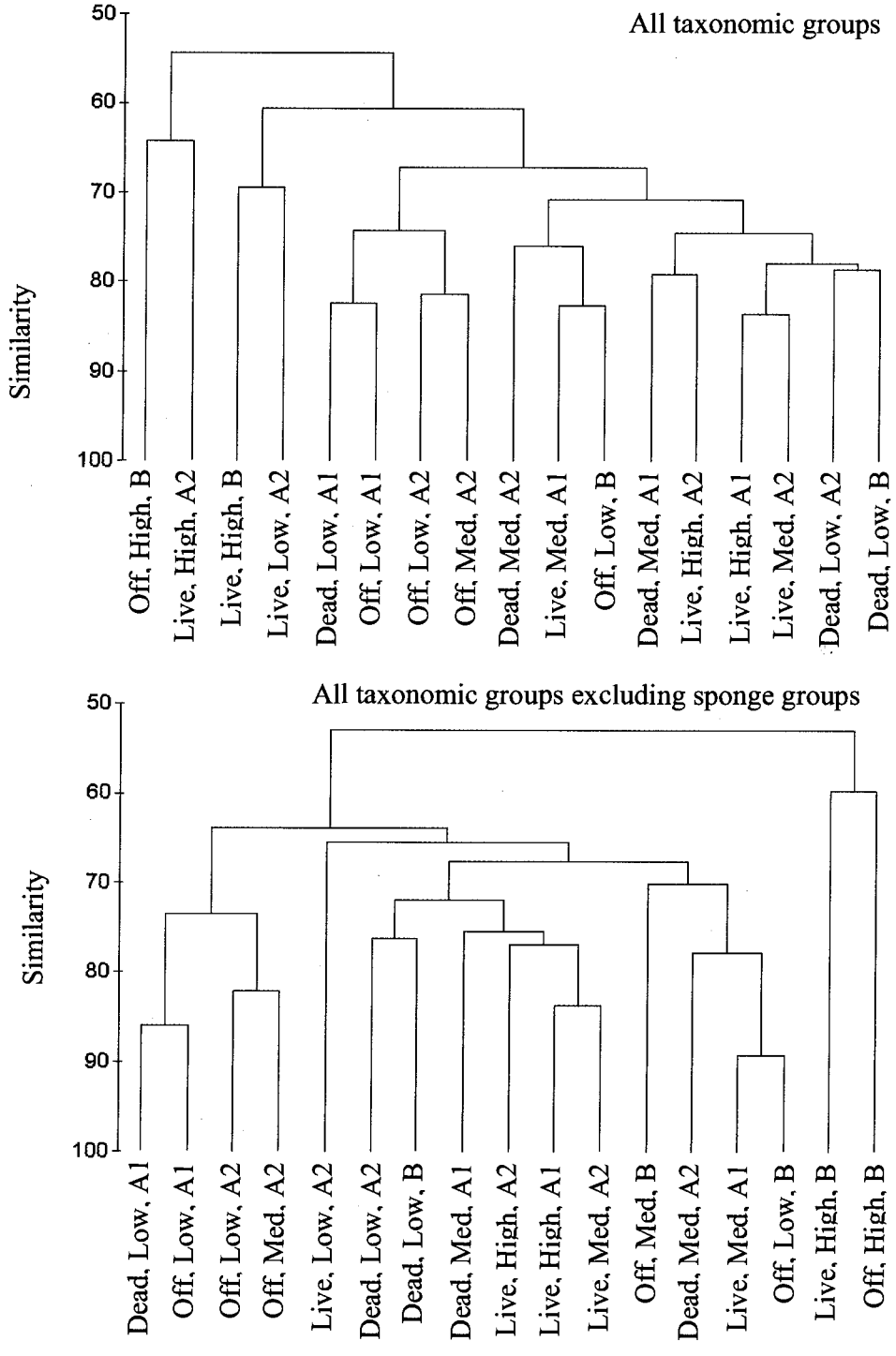

Figure 2.13: Dendrograms of samples used in PRIMER matrix, showing all three factors in each sample.

None of the literature reviewed for this study emphasizes that whether a habitat is a refuge from stress depends on the taxonomic group being looked at, an important point when interpreting results using a broad range of taxa. Live reefs are providing a refuge for rockfish, sea stars, boot sponges, squat lobsters, prawns and crabs, which all increase in abundance on live reefs. However, sea anemones, sea whips, corals, demosponges, flatfish, skates, brittle stars and sea urchins all decrease in abundance on the live reefs, implying that, for these groups, stress increases on live reefs and is decreased in off-reef areas. For some cryptic groups, such as brittle stars, this may also indicate a sampling bias.

The reason for these differences is likely linked to the physiological characteristics of each group. Squat lobsters are known to be more abundant in areas of structural complexity (McDaniel et al. 1976, Burd 1983, Burd and Brinkhurst 1984, Burd 1986) likely due to decreased predation pressure due to increased complexity in these areas. Rockfish (especially juveniles) also occupy heterogeneous habitat (Richards 1986, O'Connell and Carlile 1993, O'Connell and Carlile 1994, Diaz et al. 2003), again likely due to the decrease in predation pressure. The high abundance of small rockfish on live reefs, including some commercially important species, is very good evidence that these areas are nursery habitats for juveniles, a point that could be important to fisheries management in northern B.C. The sponge reefs also provide a refuge for large rockfish, although this may be due to decreased predation pressure or increased foraging efficiency. Sea stars, which, as noted earlier, can be quite cryptic on live reefs due to their coloration may find a refuge from predation on live reefs. An example of a group which decreases in abundance on live reefs is flatfish, which would not be able to

camouflage themselves in structurally complex habitats, increasing predation pressure. Another example is the cnidarians (sea anemones, sea whips and corals) which are suspension feeders, and would therefore be competing with the reef-building sponges for space and areas of high current velocity even if they don't directly compete for food resources. Demosponges are significantly lower in abundance on live reefs; however, this may be due to sampling bias, as small demosponges are more visible on boulders than among reef-building sponges, or it may be that megafaunal demosponges do not find dead sponge fragments suitable sites for attachment. It should be noted that no group had its highest abundance on dead reefs, suggesting that these areas do not provide as good a refuge from stress as off-reef or live reef areas or that this habitat type is the result of bottom trawling and the communities found there are impacted by the destruction bottom trawling can cause (Freese et al. 1999).

The ANOSIM results indicate that live reefs are significantly different from off-reef areas in terms of community structure, which includes taxonomic composition and abundance as well as abundance of individuals. This result agrees well with the univariate results and the comparisons of abundance of individuals within the major taxonomic groups. The ANOSIM also indicates that dead reef areas are not significantly different from either live reef or off-reef areas, suggesting there is significant overlap in the taxa and abundance of individuals found on dead reef with both other habitat types. This result does not agree well with the univariate results, where dead reef is significantly lower in richness and abundance of individuals than either other habitat, although abundances within the individual taxonomic groups were often not significantly different between dead reef and at least one of the other two habitat types, indicating some kind of

overlap. This may support the idea that dead reefs are naturally occurring areas that are transitional between live reef and dead reef, although no process has yet been suggested for natural reef death and subsequent leveling; however, none of the evidence presented in this study conclusively supports either of the two different origins suggested for dead reefs thus far.

The SIMPER analysis indicates that the greatest dissimilarity is between live reef and off-reef habitat, with all taxonomic groups included and with the boot sponges and demosponges excluded, which is consistent with the ANOSIM results, although the average dissimilarity between these two habitats is only 4 to 8% greater than between the other habitat comparisons. Demosponges are driving the dissimilarity between any comparison including off-reef due to their high average abundance in that habitat compared to the other habitats, until that group is removed from the analysis. Brittle stars appear to an important taxonomic group driving the dissimilarity between all three habitats, even though their average abundance is not high in any one habitat. Crustaceans and cnidarians are also important taxonomic groups in the dissimilarity between the habitats. This agrees well with the rank abundance curves calculated for the invertebrate groups. The sponge groups, the crustacean and the cnidarian groups as well as the brittle stars have relative abundances that vary widely among the three habitats. The only point where the SIMPER analysis and the rank abundance curves for invertebrate groups appear to deviate is in the case of the boot sponges which appear to also vary widely between the three habitats, being dominant on dead reefs, lower in relative abundance on live reefs and much lower in relative abundance off-reef. This apparent discrepancy is likely due to the difference in the data sets used to create the SIMPER and the rank

abundance curves. The SIMPER analysis uses the PRIMER data matrix, which, as explained in the methods section, does not include the full set of snapshots, while the rank abundance curves were calculated using the full data set. Putting the information from these two analyses together suggests that both sponge groups play a major role in discriminating between the three habitats. Once those groups are removed, the crustaceans, cnidarians and brittle stars are driving any dissimilarity.

The rank abundance plot for fish groups indicates that small rockfish are the dominant group on live reefs and possibly dominant on dead reefs as well although the variability in the relative abundance is extremely high. Off-reef areas do not appear to have a dominant fish group, although flatfish are the most relatively abundant group followed by large rockfish. These results reinforce the conclusion that live reefs are nursery habitats for juvenile rockfish.

Complexity

The univariate comparisons of the different complexity values show different results when demosponges and boot sponges, the non-reef building, habitat producing sponges, are included in the analysis. This could indicate a bias is introduced when these foundation species are included in the analysis when the reef-building sponges are not. Without the demosponges and boot sponges, high complexity areas have higher taxonomic richness and abundance of individuals. These results correspond with those of Heck and Wetstone, 1977, Crowder and Cooper, 1982 and Diehl, 1992, who found that invertebrate abundance increased with increased complexity in seagrass meadows due to decreased effectiveness of predation on the invertebrates. The affinity of fish for higher complexity habitats is well documented including Atlantic cod (Fraser et al. 1996, Cote et

al. 2003), juvenile fishes on the continental shelf (Diaz et al. 2003) and tropical reef fishes (Levin and Hay 1996, Ferreira et al. 2001); Wyda et al. (2002) found that fish richness increased with complexity in an eelgrass meadow. The effect of complexity on richness or abundance of individuals for whole communities (i.e. fish and invertebrates together) does not appear to have been studied.

The ANOSIM analysis comparing the community structure of the different complexity values showed no significant comparisons when all taxonomic groups were included; however, since complexity is partially determined by the presence of habitat creating sponges (boot sponges and demosponges), a better comparison of complexity values is when those groups are removed. The ANOSIM without the sponge groups included shows that there is a significant difference between medium and low complexity areas. This result is not consistent with the SIMPER results, however, since the medium and low comparison had the lowest average dissimilarity both with and without the sponge groups included. These groups are therefore considered to be the most similar to each other. It is the comparison between the high and low complexity groups that has the highest average dissimilarity. This result is the most consistent with the results from the univariate analyses and the rank abundance curves for invertebrate groups. The curves for high and medium complexity are very similar in shape but are very different from the curve for low complexity. The rank abundance curves also agree with the SIMPER analysis in terms of the species driving the dissimilarity between the complexity values because demosponges, brittle stars and sea anemones are the groups driving the dissimilarity with the sponge groups included and the rank abundance curves show very different relative abundances for those three groups between the three complexity values.

Boot sponges show similar relative abundances between the three complexity types, so it is not surprising they are not driving the dissimilarity between the complexity types in the SIMPER analysis. Since the ANOSIM is a two-way analysis of habitat crossed with complexity, the relationship of complexity with habitat may be why the SIMPER analysis and the rank abundance curves of sessile groups do not appear to agree with the ANOSIM results.

The rank abundance curves for the fish groups show that small rockfish are dominant in high and medium complexity habitats and have the highest relative abundance of all fish groups even in low complexity areas. This result agrees with Diaz et al. (2003) who found that juvenile fishes have increased abundances in higher complexity habitats. There does not appear to be a dominant fish group in low complexity areas, and this is the only complexity value where flatfish have a higher relative abundance than large rockfish.

Habitat and Complexity

The separate comparisons of habitat types and complexity values indicate there is a connection and an interaction between the two, since habitat type partially determines complexity value and complexity is assessed partially by the habitat being looked at, as explained in the methods section. For the univariate measures it is the high complexity, off-reef habitat which has significantly higher richness and abundance of individuals than any other comparison even with an extremely high variability, which could be due to the low number of snapshots taken at these areas (58 compared to 744 on the live reef). As mentioned in the results section these areas have high numbers of foundation species such as sponges and corals. These groups are likely found in areas of high physical

rugosity because the boulders and bedrock walls elevate them off the seafloor, providing hydrodynamic turbulence and therefore a better food source for suspension-feeding organisms. This non-biological physical rugosity is lacking on the live reefs, so perhaps it is the combination of the physical and biological complexity which makes the off-reef, high complexity areas so high in taxonomic richness and abundance of individuals. This is a phenomenon worth further study since such areas would area of high productivity on the continental shelf, especially for commercially important species such as rockfish and would also be very sensitive to destruction, as are the sponge reefs themselves.

At medium complexity, live reef has higher richness, followed by off-reef and then dead reef, although abundance of individuals is significantly higher on live reefs than off-reef areas, it is not significantly different between dead reef and off-reef areas. The number of snapshots at medium complexity for each habitat is almost identical making this a less biased comparison, so it can be concluded that at medium complexity, the live reef community is richer and has higher abundance of benthic megafaunal organisms than the other habitats looked at in this study and are therefore potentially areas of higher productivity.

Only 61 snapshots were taken in low complexity, live reef habitats and over 1000 in each of the other habitats. This likely explains the wide variability of the live reef measures at low complexity, especially since those low complexity, live reef areas are likely adjacent to higher complexity live reef areas. Although mean taxonomic richness is higher in low complexity, live reef habitat, it is not significant due to the high variability and could be due to sampling bias since megafaunal organisms are easier to see in lower complexity areas. Low complexity, off-reef areas are significantly higher in

richness and abundance of individuals than low complexity, dead reef areas and these areas have similar numbers of snapshots. This suggests one of two things: that the sponge fragments provide less desirable habitat than the gravel and sediment low complexity, off-reef areas or it provides further evidence that the dead reef areas have been trawled. It is known that some reef areas have been heavily trawled in the past (Jamieson and Chew 2002) and that trawling is very damaging to benthic sponges (Freese et al. 1999) and can lead to decreased productivity, although results of the few studies done have been inconclusive overall (Messieh et al. 1991, Watling and Norse 1998, Freese et al. 1999, Kaiser et al. 2000).

The dendrograms, which include both habitat and complexity, as well as reef complex, do not show any groupings between samples, so no additional conclusions can be drawn from these results.

CONCLUSIONS

- Live reef habitat has significantly higher taxonomic richness than dead reef or off-reef habitat and higher abundance of individuals without the boot sponges or demosponges included.
- Trends noted in comparisons of abundance of individuals between habitats within a taxonomic group depend on the group and its particular physiological characteristics.
- Live reefs are nursery habitats for juvenile rockfish.
- The community structure of live reef and of off-reef habitats are significantly different and demosponges, brittle stars, crustaceans and cnidarians are important groups driving dissimilarities between the habitats.

- High complexity areas have significantly higher richness and abundance of individuals when boot sponges and demosponges are removed from the analyses.
- No clear trends in terms of community structure emerge when comparing the different complexity values, and the ANOSIM results appear to contradict the SIMPER and rank abundance curves.
- High complexity, off-reef areas have the highest richness and abundance of individuals of any shelf habitats possibly due to the combination of physical rugosity and biological complexity in those areas
- Medium complexity, live reef areas have higher richness and abundance of individuals than dead reef and off-reef areas at the same complexity.
- Some evidence points to the conclusion that dead reef areas are caused by bottom trawling and are therefore impacted habitats.

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CHAPTER 3:
Megafaunal Substrate Use on Reef

ABSTRACT

Video transects from five sites on three reef complexes at depths between 150 and 200 metres were analyzed to study how the megafaunal organisms that inhabit the glass sponge reefs utilize the substrate the sponges provide and whether there were measurable associations with different substrates within each megafaunal group. Five distinct substrates were categorized: fallen dead sponge, standing dead sponge, live *Aphrocallistes vastus* and *Heterochone calyx*, live *Farrea occa* and rossellid sponges. All organisms were identified to family (those that could not be identified to family were excluded) and the substrate they were occupying was recorded. Abundances were standardized per 100 linear meters of transect. Statistical comparisons between sites was not possible because differences in abundance of organisms could be due to differences in abundance of substrate at that site, a factor not measured in this study. Qualitative comparisons between sites are discussed. Multidimensional scaling plots (MDS) were made for each site to determine if communities on the different substrates are consistent within a site.

The main conclusions of this study are: 1) dead sponge supports a larger population of megafauna in terms of numbers of individuals, taxonomic richness and diversity than live sponge and 2) there are definite substrate associations within families but this varies greatly between sites and between families at each site. The cause of this variability could only be speculated upon and further research on this aspect is suggested. Some possible explanations for variation in substrate associations are differences between sites in substrate availability, as well as predation pressures, competition, currents, life-histories and physical and chemical factors such as temperature and salinity.

INTRODUCTION

Understanding how organisms use the habitat created by a foundation species is important if we are to understand the ecology of that habitat and gain some clear understanding as to the relative importance of that habitat in a larger ecological context. One of the most important habitat resources in any ecological system is the substrate. It can provide places to forage for food (Shirvell and Dungey 1983, DeMartini 1996), shelter from predation (Shirvell and Dungey 1983, Garcia-Rubies and Macpherson 1995, DeMartini 1996, Cote et al. 2003), an arena for competition (Hlohowskyj and Wissing 1986, Fraser et al. 1996, Grillet and Barrera 1997, Turra and Denadai 2002, Cote et al. 2003) and reproduction sites (Shirvell and Dungey 1983, Cordoba-Aguilar 1994, Ormond et al. 1996). An individual may or may not use the same substrate for each activity and variations in substrate use may occur temporally, both daily and during changes in life-history stages (Fraser et al. 1996, Grillet and Barrera 1997, Cote et al. 2003).

The term 'microhabitat' has been used to describe the subset of environmental characteristics that satisfy the needs of any organism at any given time; in other words, it is the location and conditions where an individual spends its time (Shirvell and Dungey 1983). This differs only slightly from the concept of 'niche breadth', which is basically defined as the resource states used by any given organism where a resource state can include food, habitat or sampling units (such as leaves or other substrates) (Krebs 1989). The distinction between these is unimportant for the present study since neither microhabitat or niche breadth is directly measured here.

Substrate is only one part of the defined microhabitat for any given organism. Other factors, especially the physical characteristics of the surrounding environment, are also

important. For example, for any organism living in an aquatic setting current velocity, temperature, salinity and depth likely play roles in differentiating microhabitats and therefore the substrate usage of the organism (Shirvell and Dungey 1983, Grillet and Barrera 1997).

The objective of this study is to examine the association of reef organisms for different reef substrates. This is a first step towards understanding the microhabitats (or niches) of the organisms that use the sponge reefs. Although only substrate association is truly examined in this study, the results obtained here can point toward other characteristics that might be important to measure to provide a better understanding of the microhabitats (or niches) occupied by reef organisms.

METHODS

The sites for this study are the Fraser Ridge reef complex and complexes A and B of the Queen Charlotte Basin reefs (see Figure 3.1 for locations). All sites were between 150 and 200 metres. All video tapes for this analysis were collected using a Deep-Ocean Engineering HD2+2 Phantom Remote Operated Vehicle (ROV) during cruise PGC02004 in June 2002 from the Coast Guard vessel CCGS *John P. Tully*. The ROV was linked to the ship's Global Positioning System (GPS) by telemetry, allowing accurate plotting of the transects. Four dives were recorded at the Fraser Ridge site, three dives at complex A and one dive at complex B. The four dives at the Fraser Ridge overlapped each other because it is such a small complex, and were therefore treated as one continuous dive (Site 1) during data analysis. All other dives were at least 1 km apart and were treated as separate sites, leaving 5 sites total (Table 3.1).

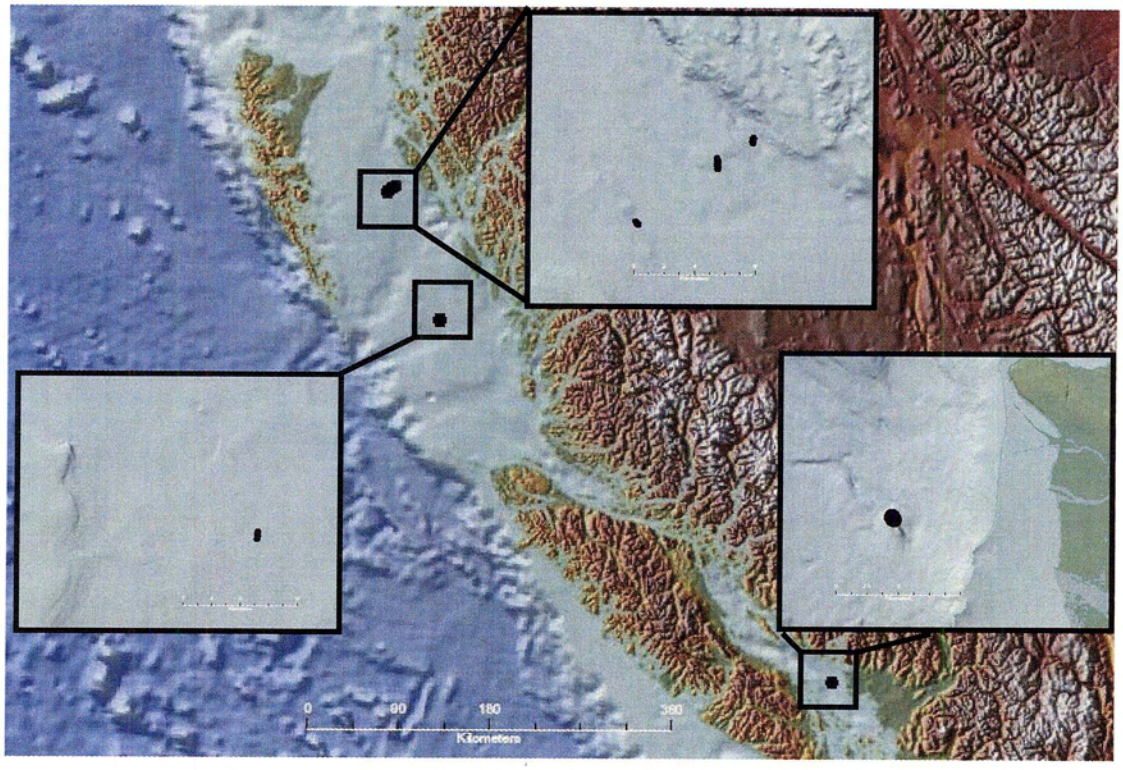

Figure 3.1: Locations of video transects taken from complexes A, B and Fraser Ridge in July 1999.

Table 3.1: Video transect information for cruise PGC02004.

Dive/Site	Location	Start Point	End Point	Length of Transect (m)
Dive 1/ Site 1	Fraser Ridge	49.156 °N 123.381 °W	49.156 °N 123.382 °W	2139
Dive 2/ Site 1	Fraser Ridge	49.157 °N 123.383 °W	49.159 °N 123.385 °W	2531
Dive 3/ Site 1	Fraser Ridge	49.158 °N 123.387 °W	49.158 °N 123.387 °W	1729
Dive 4/ Site 1	Fraser Ridge	49.157 °N 123.383 °W	49.158 °N 123.386 °W	2031
Dive 5/ Site 2	QCB Complex A	53.113 °N 130.499 °W	53.114 °N 130.503 °W	3323
Dive 6/ Site 3	QCB Complex A	53.156 °N 130.431 °W	53.164 °N 130.435 °W	8479
Dive 7/ Site 4	QCB Complex A	53.177 °N 130.402 °W	53.180 °N 130.402 °W	4160
Dive 8/ Site 5	QCB Complex B	52.038 °N 129.424 °W	52.045 °N 129.423 °W	3977

Analysis of the transect video consisted of counting every megafaunal organism (except reef-building sponges), identifying it to the lowest possible taxonomic level and recording the type of substrate it was first encountered on. Megafauna is defined as anything large enough to be seen on video (greater than approximately 5 cm). Some organisms moved as the ROV approached, but only the first substrate the organism utilized was recorded. See Table 3.2 for the number of individuals counted per substrate per site. For definitions of the different substrate types see Table 3.3 and for photographic examples see Figure 3.2. Note that the standing dead sponge is easily distinguished from the living sponge by its colour. Occasionally, however, a skeleton is inhabited by a demosponge of similar colour to living hexactinellid sponge tissue, making distinguishing live reef-building sponges from dead ones more difficult.

Table 3.2: Number of megafaunal individuals that could be identified to family per site per substrate.

Site	Location	Substrate Type	Number of Individuals Counted
1	Fraser Ridge	Fallen Dead	119
		Standing Dead	187
		Live A/H	159
		Rossellidae	2
2	QCB Complex A	Fallen Dead	118
		Standing Dead	227
		Live A/H	26
		Live Farrea	12
		Rossellidae	1
3	QCB Complex A	Fallen Dead	362
		Standing Dead	53
		Live A/H	50
		Live Farrea	45
		Rossellidae	2
4	QCB Complex A	Fallen Dead	180
		Standing Dead	132
		Live A/H	23
		Live Farrea	8
		Rossellidae	1
5	QCB Complex B	Fallen Dead	665
		Standing Dead	231
		Live A/H	22
		Live Farrea	8
		Rossellidae	18
Total			2651

Table 3.3: Definitions of substrate categories in video descriptions of the sponge reefs.

Category	Description
Fallen Dead	On fallen dead sponge fragments and sediment
Standing Dead	In/On/Among standing dead sponge
Live A/H	In/On/Among live *Aphrocallistes vastus* and *Heterochone calyx* (It is not possible to consistently differentiate these species on video)
Live *Farrea*	In/On/Among live *Farrea occa*
Rossellidae	In/On/Among live rossellid sponges (non-reef-building sponges)

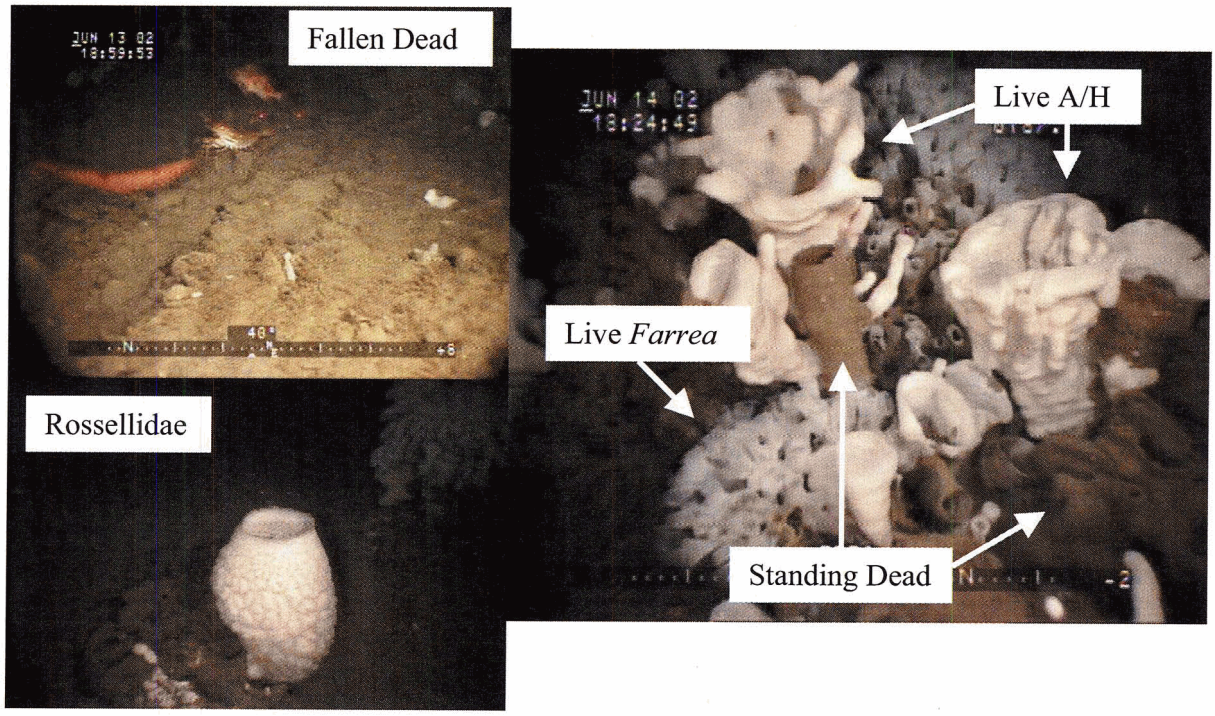

Figure 3.2: Examples of substrate categories used in analysis of video. On the fallen dead sponge is *Pandalus platyceros* (Pandalidae), *Parastichopus leukothele* (Stichopodidae) and *Sebastes* sp. (Scorpaenidae). Note the dead sponge fragments projecting from or lying on top of the sediment, as well as the organic 'fuzz' that covers the fragments. The laser pointers in the images are 10 cm apart.

The range of taxonomic classification level to which organisms could be assigned is quite broad (class to species) since the ROV did not remain a consistent distance from the bottom. The data set was therefore standardized to family level before statistical analysis. 149 individuals that could not be identified to family were excluded from the analysis. See Appendix I for a list of species identified within each family.

All counts of organisms were standardized per 100 linear meters of transect length. Transect length was calculated by using trigonometry to calculate the linear distance between each GPS fix in meters, once the fixes had been converted to the Universal Transverse Mercator system (UTM). This standardization does not permit true quantitative, statistical comparison between sites because any differences noted could be due to differences in the amount of the five substrate types available between sites. For example, Site 1 (Fraser Ridge) does not have any *Farrea occa*. The availability of the five substrates at each site was not measured; therefore, comparisons between sites must be considered qualitative only.

Statistical analysis within sites was possible. The family matrix for each site considered each substrate as a sample, so there were only five samples per site. The total number of individuals per 100 meters for each substrate per site was plotted using Microsoft Excel. The statistical package PRIMER-E was used to calculate family richness (S), number of individuals (N) and the Shannon-Wiener Diversity Index (H') which was plotted per substrate type per site using Excel. $H' = -\Sigma(p_i)(\log_e p_i)$, where p_i is the proportion of the total sample belonging to the *i*th species (Krebs 1989, Clarke and Warwick 2001).

The relative abundance of the 14 most abundant families was plotted by substrate type for each site using Microsoft Excel. Note that the Ophiuroidea were only identified to class level because they could not be seen clearly enough on the video to be identified to family level; however, they were too numerous to leave out of the analysis and so are considered at the same level as family for the purposes of this analysis.

Each of the 14 most abundant families was also placed into a Functional Feeding Group (FFG) as defined in MacNeil et al., 1997. 'Filterers' are defined as all organisms that feed on suspended particulate matter (in the case of this analysis, only sponge groups are included in this FFG); 'predators' are defined as those organisms which 'kill and eat members of other feeding groups'; and 'collector-gatherers' are defined as those organisms which 'utilize fine and very fine particulate organic matter' (MacNeil et al. 1997). Relative abundance plots of each FFG on the five substrate groups were created in Microsoft Excel.

A similarity matrix was calculated using Bray-Curtis similarity with a fourth-root transformation. Such a large transformation was chosen because it made the relationships more clear graphically. A Multidimensional Scaling plot (in this case Kruskal's non-metric MDS procedure) was calculated for each site. This yields the relative similarities of the communities found on each substrate type in a graphical form, both in terms of family composition and number of individuals because it is based on a similarity matrix (Clarke and Warwick 2001).

RESULTS

The video taken by the ROV had very good clarity and was very useful for identification of individuals; however, the field of view was constantly changing because

it was difficult to keep the ROV, which is fairly light compared to a submersible, at a consistent distance from the bottom due to the currents. Also, the operators frequently used the zoom on the camera to get a better look at the sponges or the organisms living on the sponges. The field of view was also lessened in areas with a higher percentage of live and standing dead sponges; however, since all the video was taken on live reefs it was all in fairly complex habitat so it is unlikely that this factor biased the counts of organisms. The ROV did elicit an escape response when it approached organisms such as squat lobsters and rockfish but it did not appear to affect most of the organisms as long as it did not get too close.

Of the 28 families identified from the video, 10 are echinoderms, four are cnidarians, four are arthropods, four are chordates, three are poriferans, two are molluscs and one is an annelid. Of the echinoderm families, seven are sea stars (asteroids), which are generally fairly mobile and are predators which consume their prey by everting their stomachs and externally digesting tissue. The Asterinidae, Echinasterida, Goniasteridae, Poraniidae, Pterasteridae and Radiasteridae feed on surface dwellers and are known to especially prey on bivalves; however, bivalves were not seen in the video and were relatively scarce in the grab samples taken from the sponge reefs so these asteroids must also be preying on other macrofaunal groups. Several individuals of the Poraniidae appeared to be sitting on the bases of live *Aphrocallistes/Heterochone* although it was difficult to determine if they were actually sitting on live sponges. This observation along with the observation of round areas of dead skeleton at the base of several *Aphrocallistes/Heterochone*, such as those an everted stomach of an asteroid might leave, leads to the speculation that this family may actually feed on the reef-building sponges

themselves. This speculation is given further weight by the identification of a member of the Poraniidae sitting atop a live *Aphrocallistes/Heterochone* on Hecata Bank off the coast of Oregon (Natalie Strom, pers. comm.). Members of the last family of asteroids, the Luidiidae, are subsurface feeders which bury themselves in soft sediments and dig for bivalves. This family was relatively rare on the sponge reefs with only two individuals recorded. The ophiuroids (brittle stars) generally classed as detritus feeders and are often found in large concentrations on the seafloor, although some individuals were also observed inside standing dead sponge with their arms sticking out the former oscula. The Stichopodidae are a family of sea cucumbers (holothuroids) and are also detritivores, which scavenge across the seafloor. The final family of echinoderms are the Strongylocentrotidae, which are sea urchins (echinoids) and are therefore herbivores. At the sponge reef depths (150 to 230 metres), these scavengers of drift algae and can often be found in large groups on drift kelp that has caught on the reef-building sponges. This group was rare in the video collected in 2002, with only two individuals recorded.

The cnidarian families are divided into three families of sea anemones, the Actiniidae, Cerianthidae and Metridiidae, and one family of corals, the Caryophylliidae. All cnidarians are suspension feeders, capturing zooplankton with their feeding tentacles. Cnidarians were found only at the Fraser Ridge reef complex and were not very abundant with only 40 individuals recorded overall, with 34 of those being from the family Actiniidae.

The four families of arthropods were all crustaceans, with one family of shrimp, the Pandalidae, two families of crabs, the Lithodidae and Majidae, and one family of squat lobsters, the Galatheidae. All of these families are found from very shallow to very deep

benthic habitats. In shallow areas, they are sometimes known to feed on algae but at depths below the photic zone, such as sponge reef depths, they are thought to act as predators of zooplankton, other crustaceans and even fish (Jensen 1957 and Hart 1982); however, the Galatheidae have also been observed to act as collector-gatherers and possibly as filterers (Burd 1983). The Galatheidae have also been observed at act in a very defensive manner to aggressive behaviour by conspecifics and by competitors, usually by using a 'tail-flip' escape response (Antonsen and Paul 1997). This was also the escape response elicited when the ROV came too close to galatheids.

The four families of chordates include three families of bony fishes, the Scorpaenidae, Stichaeidae and Pleuronectidae, and one family of cartilangenous skates, the Rajidae. All these groups are known to be predators of crustaceans, other fish and benthic infauna. Only three individuals of the Rajidae were recorded and of the other three families, only the Scorpaenidae were abundant and were also the only family where juveniles were noted on the reefs.

The three families of poriferans include two demosponges, Demosponge 1 (which is likely in the family Desmacellidae, but since a sample was not obtained, this could not be confirmed just using video) and Pachastrellidae, and boot sponges of the family Rossellidae, which are also hexactinosidan sponges but do not have the same fused skeleton as the reef-building sponges. These are all filterers and would likely compete with the reef-building sponges for food resources. It was mentioned in the Methods section that demosponges can inhabit the skeleton of reef-building sponges and that these cannot be distinguished from live reef-building individuals. These demosponges have been identified to the family Desmacellidae in sponges sampled in Barkley Sound (Henry

Resiwig, pers. comm.). It is not known whether these demosponges inhabit already dead skeleton or whether they can kill the reef-building sponges in order to inhabit the skeleton.

The two mollusc families were the Cymatiidae, which are predatory snails known to prey on bivalves, and the Octopodidae which are predatory cephalopods, known to prey on crustaceans. Both were rare on the reefs, with only one individual of the Cymatiidae recorded at the Fraser Ridge reef complex and five individuals of the Octopodidae recorded at the Hecate Strait reef complexes. Both of these groups are quite cryptic, especially the Octopodidae, and their numbers may have been underestimated.

The only annelid family recorded was the Sabellidae, suspension feeding tube worms which usually require hard substrate for attachment. Only eight individuals of this family were recorded, although these were definitely underestimated on the video due to their size, as they were relatively abundant in the grab samples (see Chapter 4).

The total number of individuals utilizing each substrate is shown in Figure 3.3. Fallen and standing dead sponge are more heavily occupied than any category of live sponge. For example, at Site 2 there are 10.33 individuals per 100 meters of transect on the two dead sponge categories combined as opposed to 1.34 individuals per 100 m on the three live sponge categories. All sites follow this trend, although site 1 has less of a difference between the dead sponge categories and live sponge categories than the other sites (3.63 individuals per 100 meters on both dead sponge categories as opposed to 1.91 individuals per 100 meters on the live sponge categories).

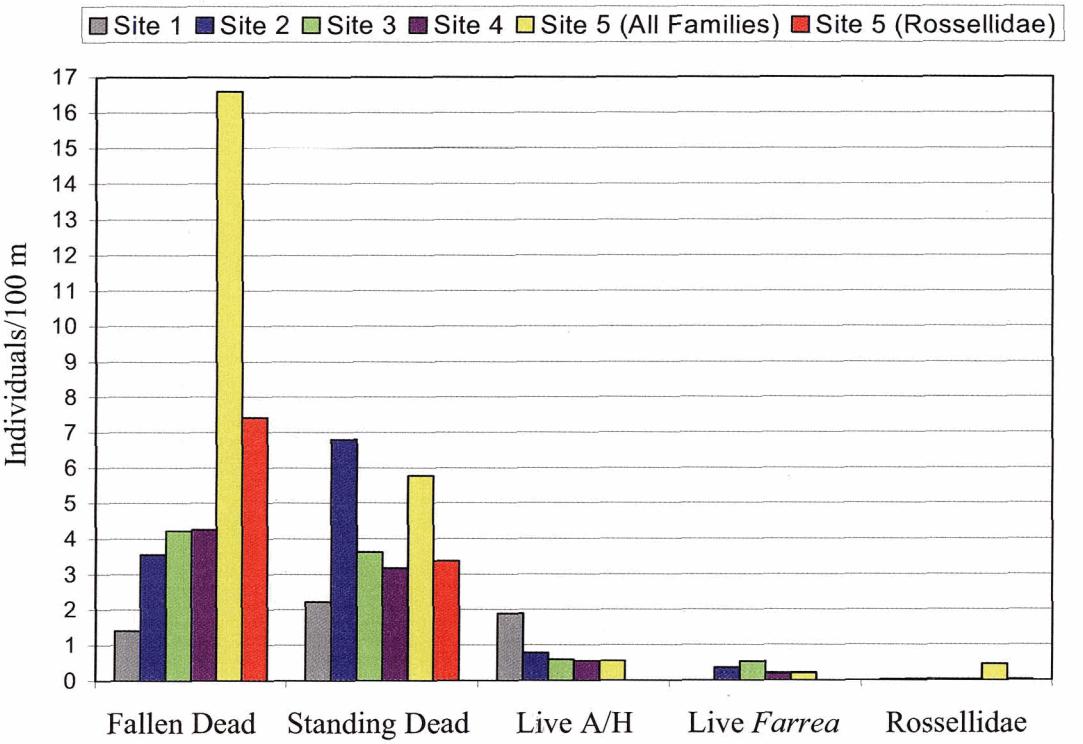

Figure 3.3: Total number of individuals per 100 linear meters of transect on each substrate type by site. Note that Site 5 has two bars, one with total individuals (including Rossellidae) and just the Rossellidae from Site 5.

It is also worth noting that Site 1 has lower abundances than the other sites on the two dead sponge categories, but has higher abundances than the other sites on the live *Aphrocallistes/Heterochone* sponge category.

Site 5 is subdivided into two categories: all families including the Rossellidae and the Rossellidae. It is clear that this site has far more rossellids than any other site and it is, therefore, no surprise that the rossellids have higher numbers of individuals utilizing them at Site 5 than at any other site (0.45 individuals per 100 meters as opposed to an average of 0.026 individuals per 100 meters at sites 1 to 4, with site 2 having the highest value at 0.030 individuals per 100 meters).

Figure 3.4 examines the relationship of taxonomic richness and diversity between the five substrate types. For taxonomic richness all sites show a distinct decrease from dead sponge to live sponge, except at Site 4 where richness is the same on live *Farrea* as on standing dead sponge (5 taxonomic groups on each). Shannon-Wiener Diversity (hereafter referred to as diversity) decreases from dead sponge to live sponge although it is not as marked as with the other measures, and there are distinct deviations at Sites 4 and 5. At Site 4, diversity actually peaks on live *Farrea* with a value of 1.56 while dead sponge averages only 0.88 between the two categories. At Site 5 diversity increases to the same value as standing dead sponge at live *Farrea* and live Rossellidae at 1.22, although fallen dead sponge is higher and live *Aphrocallistes/Heterochone* is lower.

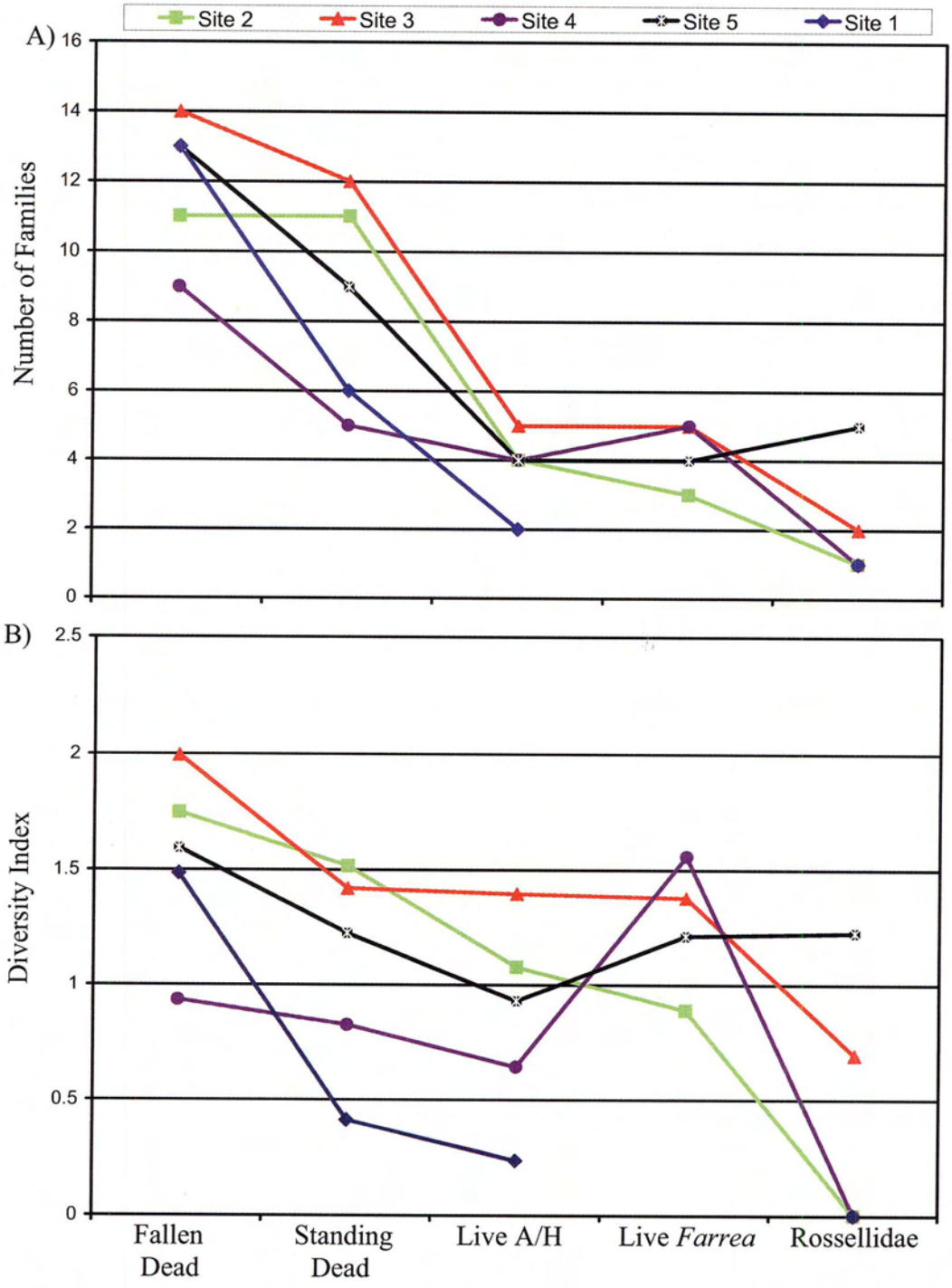

Figure 3.4: Family richness (A) and Shannon-Wiener Diversity Index (B) for each substrate type at each site.

Figure 3.5 examines how the 14 most abundant families occupy substrate on the reefs. Certain families utilize a larger number of substrates than others as well as in different relative amounts compared to other families. For example, at Site 3 more than 90% of the Galatheidae are found on fallen and standing dead sponge, while more than 95% of the Majidae are found on live A/H and *Farrea*. At the other Hecate Strait sites (2 and 4) these families show similar trends, with the Galatheidae utilizing slightly over 90% of both fallen and standing dead sponge combined. The Majidae utilize the standing dead sponge more at sites 2 and 4, with just over 75% on live sponge categories at Site 4 and just over 80% on live sponge categories at Site 2. Site 1 appears to be anomalous, with just over 60% of the Galatheidae on fallen and standing dead sponge. The Majidae at Site 1 are more consistent with the other sites, utilizing around 85% live sponge.

The Goniasteridae and Radiasteridae are found only on dead sponge at all sites where they occur, but their relative occurrence on fallen and standing dead sponge varies considerably between sites. For example, the Goniasteridae utilize 100% standing dead sponge at Site 4, just under 90% at Site 5, around 30% at Site 2 and only 20% at Site 3. The Radiasteridae show similar trends at the same sites.

The Ophiuroidea show no real trends among sites, sometimes utilizing all substrates (Site 5) and sometimes only one substrate (Site 4). The Scorpaenidae are mostly found on the dead sponge (between 50 and 70% at all sites) but also utilize all species of live reef-building sponges as substrate. Demosponge 1, an unidentified demosponge of which a sample was not obtained, but is likely *Desmacella* sp. cf. *vagabunda* (H. Reiswig, pers. comm.) is only found at Sites 3, 4 and 5 and was only noted on *Farrea occa*, including the dead sponge it was noted on at Site 3.

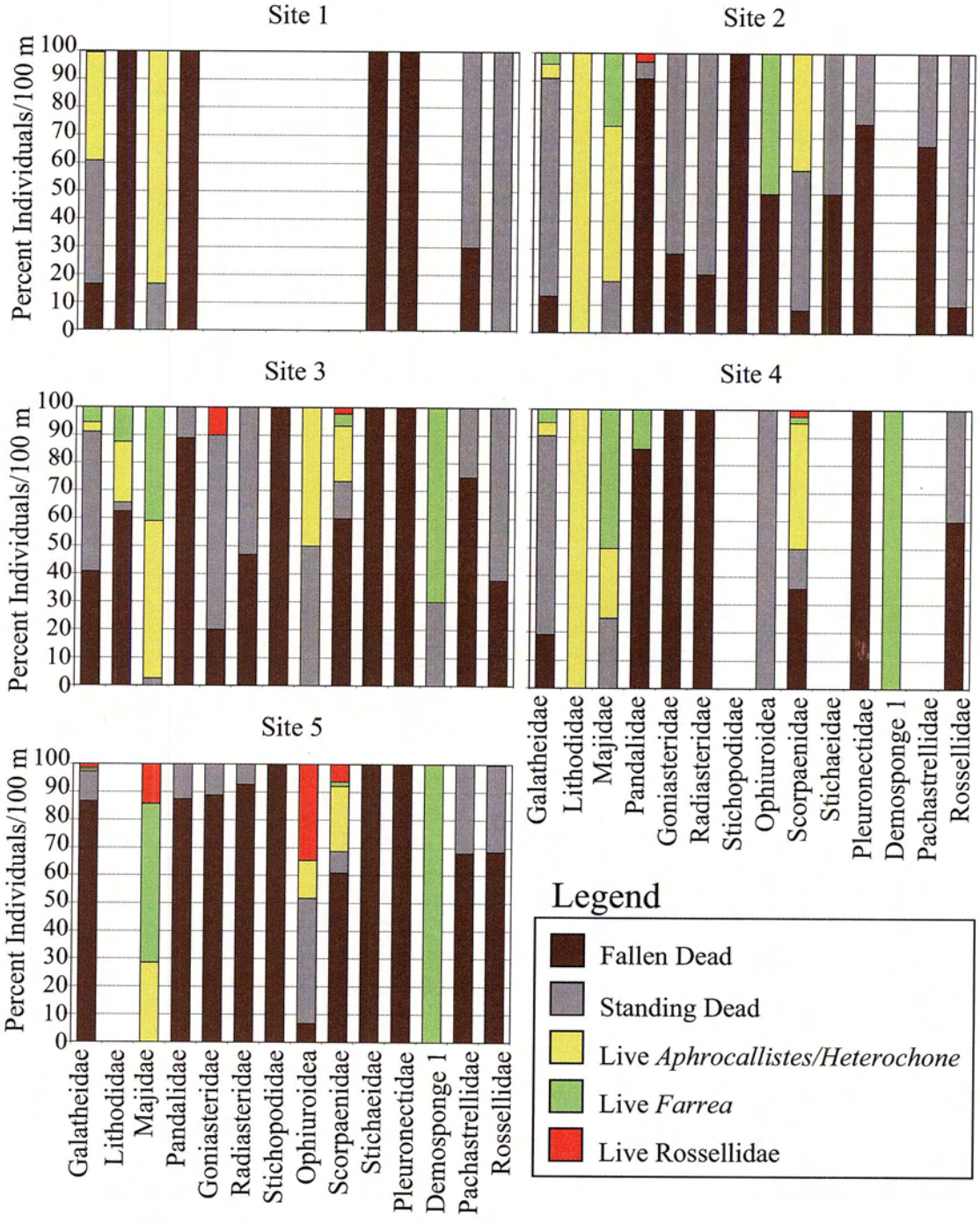

Figure 3.5: Relative abundance of 14 most common families (class in the case of the Ophiuroidea) per 100 meters of linear transect distance. Absence of a bar for a particular family indicates the family was not recorded on video at that site.

Several of the 14 most abundant families are absent from some sites, most notably at Site 1, the Fraser Ridge site, which is very different in form and current regime from the other sites. The Goniasteridae, Radiasteridae, Stichopodidae, Ophiuroidea, Scorpaenidae and Demosponge 1 are all absent from this site. Site 4 also has some notable absences: the Stichopodidae, Stichaeidae and Pachastrellidae. These families were all present at Sites 2 and 3, the other Hecate Strait sites.

The 14 most abundant families were each placed into a Functional Feeding Group (FFG) as defined in the Methods section based on their known feeding habits as discussed earlier in the results section. The Galatheidae were the only family found to fit into more than one FFG category and were separated from the other families which fit into only one category and given the category name 'Multiple', indicating they have multiple feeding strategies. The relative abundance of each FFG on the five substrate categories is shown in Figure 3.6. Note that several FFG's are missing from the 14 most abundant families. The most notable are the suspension feeders, which are the cnidarians and were only reported at Site 1 in low numbers as mentioned earlier.

As with the other measures reported, the trends in relative abundance of FFG's on the five substrate types are similar between the three complex A sites (2, 3 and 4) and anomalous at Site 1 and Site 5. At the complex A sites, predators have a relative abundance of between 58 and 75% on fallen and standing dead sponge, multiple strategists have a relative abundance of approximately 90% on fallen and standing dead sponge and filterers are found almost exclusively on fallen and standing dead sponge. Collector-gatherers were relatively more abundant on fallen and standing dead sponge but the most abundant substrate type varied between the complex A sites.

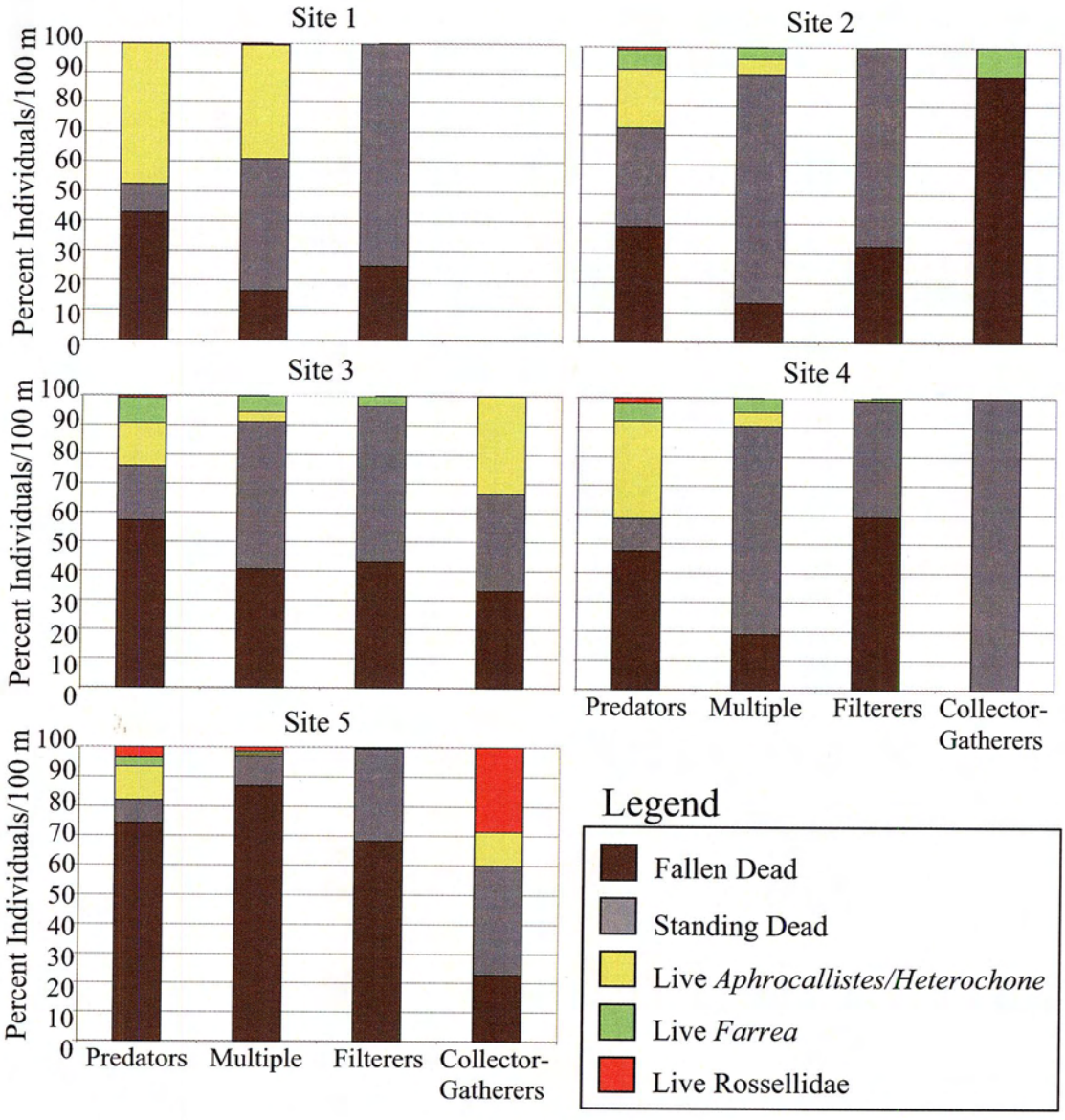

Figure 3.6: Relative abundance of Functional Feeding Groups (FFGs) of 14 most abundant families per substrate type per site. Absence of a bar for a particular FFG indicates that group was not recorded on video at that site.

At Site 1 predators, multiple strategists and filterers are more than 50% abundant on dead sponge; however, collector-gatherers, which in this case only includes the Ophiuroidea, are absent from the Fraser Ridge site. At Site 5, which is the northern Queen Charlotte Sound site, the trends are similar to the Hecate Strait sites for predators, multiple strategists and filterers, although the Rossellidae play more of a role at this site as with all the other measures. Collector-gatherers are again distributed over a larger number of substrates, with the Rossellidae playing a relatively larger role than at any other site.

An MDS plot was created for each site based on all the families and their standardized abundances at that site to determine if any substrate types grouped together in terms of community structure (Figure 3.7). Sites 2, 3 and 4 (all from reef complex A in Hecate Strait) show the same association of dead sponge types grouping together and the reef-building sponges grouping together. At Sites 1 and 5 deviations from this trend are apparent. At Site 5 (complex B in Queen Charlotte Sound), which has a very large number of rossellid sponges, the dead sponge groups still fall out together but the Rossellidae and the live *Aphrocallistes/Heterochone* group fall out together, leaving the live *Farrea* separate. At Site 1, where there is no *Farrea*, the standing dead sponge and the live reef-building sponges group together.

DISCUSSION

Different families have associations with the different categories of substrates on the sponge reefs, and these associations vary both between families and between sites.

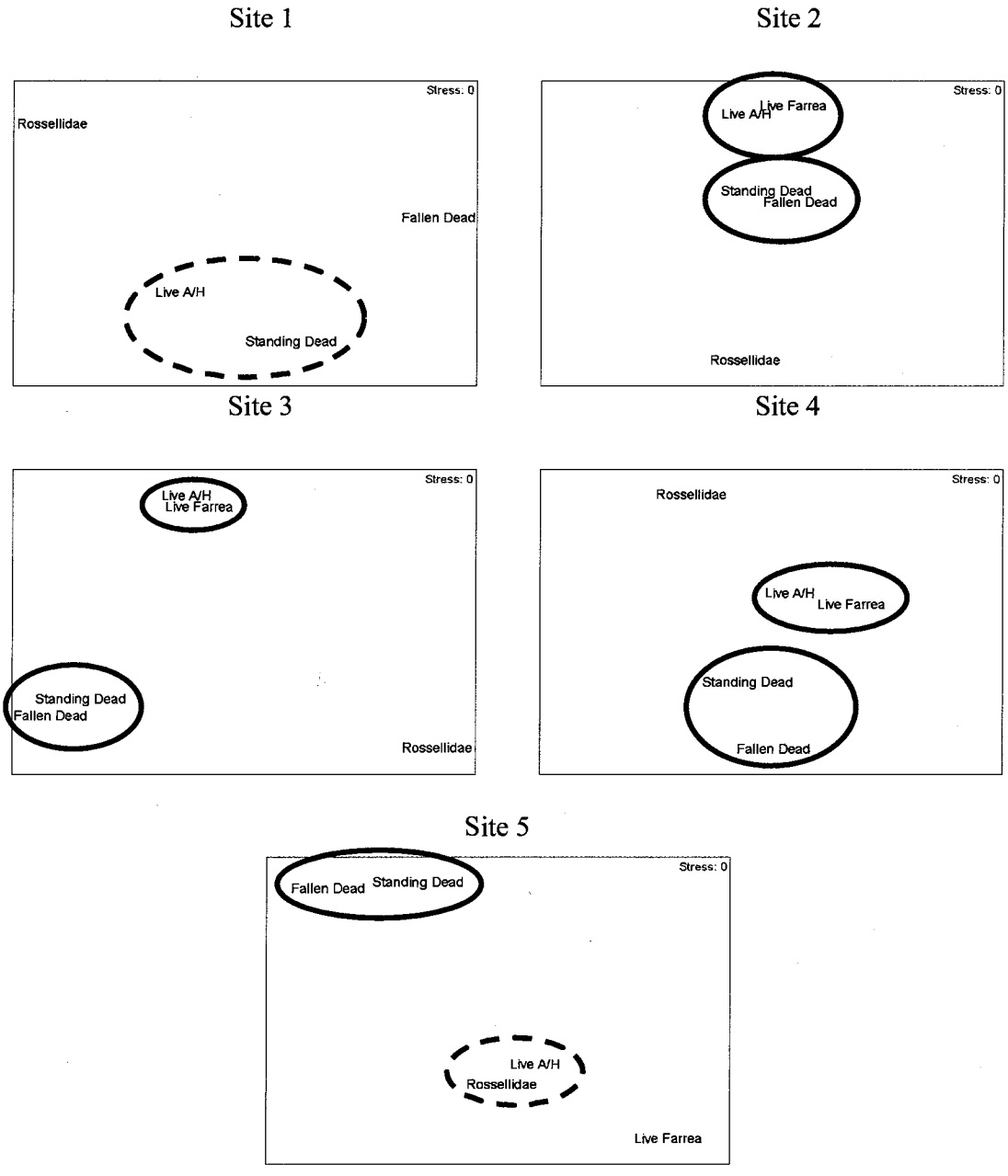

Figure 3.7: MDS plots for each site showing relative similarities in community structure between each substrate type. The solid circles show groupings that are consistent over most of the sites and the dashed circles indicate groupings that are considered anomalous or site-specific.

This is not an unexpected result as many other organisms have been shown to have strong substrate associations, such as brown trout (Shirvell and Dungey 1983), Devils River minnows (Gibson et al. 2004), Atlantic cod (Fraser et al. 1996, Cote et al. 2003), damselfishes (Ormond et al. 1996), Arc-Eye Hawkfish (DeMartini 1996), unionid mussels (Brown and Banks 2001), hermit crabs (Turra and Denadai 2002) and even larval blackflies (Grillet and Barrera 1997). In each of these studies, substrate associations were also measured with substrate availability and with other physical and biotic factors that might affect substrate choice, making their conclusions that associations do exist stronger than in the present study.

It is interesting that a heavy bias towards dead sponge exists among most of the families and Functional Feeding Groups recorded on the reefs. Taxonomic richness, abundance of individuals and diversity all generally show a decrease from dead sponge to live sponge, although this has some variation between sites. There are several potential reasons why this is the case. It may be due to the characteristics of the reef-building sponges themselves. All three species have an outer coating of silica spicules projecting from the live tissue which could potentially be injurious to animals with soft tissues (Reiswig 2002). In fact, Dr. W.C. Austin conducted an experiment which proved that the spicules from a live *Aphrocallistes vastus* would penetrate and remain in the relatively tender tube-feet of asteroids (W.C. Austin, pers. comm.). Families with hard exoskeletons, such as the Majidae and other Crustaceans, or other protective scales or plates, such as the Scorpaenidae and many of the Ophiuroidea, would be expected to be more able to utilize the live sponge, and potentially avoid competition with families unable to utilize that substrate.

Another potential reason why dead sponge has higher abundance of individuals and families is that there are more food resources on dead sponge, both in terms of non-predatory FFG's (i.e. organisms that could potentially be prey) and the macrofaunal organisms that are living on or attached to dead sponge fragments, because no macrofauna has been found on or attached to living reef-building sponges. Also, live reef-building sponges are feeding on bacteria and detrital phytoplankton and are therefore removing nutrients from the water column so that depletion of nutrients may be affecting abundance and diversity on live reef-building sponges.

Another trend is that abundance, richness and diversity are lower on standing dead sponge compared to fallen dead sponge. One possible explanation for this trend is that standing dead sponge is not as old as fallen dead sponge so there could potentially be more macrofauna on fallen dead sponge and therefore more food resources. Also standing dead sponge is harder to get to for some groups such as asteroids, sea cucumbers and ophiuroids because they have to climb vertical surfaces. There is also the potential bias of video sampling, because standing dead sponge is more complex than fallen dead sponge and megafauna may be able to hide more efficiently on the standing dead sponge.

Relative abundance of individuals from the 14 most abundant families showed that different families used the substrate on the sponge reefs in different ways, even though the families may have similar feeding strategies or food resource needs. One of the clearest examples of this was the difference between the Galatheidae and the Majidae, where the Galatheidae utilized a relatively higher percentage of dead sponge as substrate compared to the Majidae which utilized live sponge almost exclusively. Both the Galatheidae and Majidae are known to be predators, although the Galatheidae are also

known to have the ability to switch feeding modes (Burd 1983); in addition, the Galatheidae are known to be less aggressive and escape confrontation when possible (Antonsen and Paul 1997). In this case, the Majidae are likely out-competing the Galatheidae for use of the live sponge substrate which would bestow a number of advantages on predators of planktonic organisms, height above the bottom and access to currents being the two most obvious.

All trends noted had some variation between sites. Interestingly, in most cases, trends were consistent at the complex A sites (2, 3 and 4). When major exceptions were noted they were at Sites 1 (Fraser Ridge) and 5 (complex B). One of the most notable differences at Site 1 is the lack of all echinoderm families among the 14 most abundant families. A plausible explanation for this absence does not immediately suggest itself, although recruitment it obviously an issue a Site 1. This observation and possible explanations deserve further study.

The differences at Sites 1 and 5 could be due to differences in the physical characteristics of the reefs themselves. The complex A reef is mostly continuous biohermal habitat, while the complex B site is mostly discontinuous biohermal and biostromal habitat (Conway et al. 2001). Unfortunately, this complex has never been mapped with multibeam, so its differences from complex A in terms of physical characteristics are not yet fully known. The extremely high numbers of rossellid sponges at complex B indicate that some differences in physical structure are to be expected. Also, complex B is the only reef complex that has not been heavily trawled (Jamieson and Chew 2002), which can be expected to have a major impact on community structure.

Site 1 (Fraser Ridge) is situated in a very different current regime than complex A and B and has morphologically very different sponges (Conway et al. In Press)(see Chapter 1 for more details). It is also a small, isolated reef situated in a far more turbid habitat, being close to the Fraser River plume (Conway et al. 2004). The associated heavy sediment input and lower salinity in the upper water column could have a profound influence on the associated community.

CONCLUSIONS

- Dead sponge substrates are, overall, higher in abundance of individuals, family richness and diversity than living sponge.
- Major differences exist between megafaunal families in their occurrence on different substrate types; these differences vary between families and between sites.

Whether it is differences in availability of substrate, predation pressures, variance in competition, current regime, life-history stage or other physico-chemical factors that are responsible for the observed trends should be investigated if we are to further our understanding of the microhabitats offered by the sponge reefs on B.C.'s continental shelf.

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CHAPTER 4:
Polychaete Diversity

ABSTRACT

The objective of this study was to describe quantitatively the macrofaunal polychaete community of the British Columbia glass sponge reefs and compare it to that of the surrounding shelf community. Thirty on-reef and ten off-reef grab samples were taken during cruise PGC02004 in June 2002 using both Peterson and Shipek grabs. A total of 643 individual polychaetes could be identified to family and, of those, 430 could be further identified to 105 species. All counts were standardized by volume of the grab sample and these standardized values were used in all analyses. Univariate analyses used were richness (S), number of individuals (N), Pielou's Evenness Index (J') and Shannon-Wiener Diversity Index (H') which were calculated at both the species and family levels, as well as taxonomic diversity (Δ) and taxonomic distinctness (Δ^*) at the species level. The multivariate analyses used were SIMPER and ANOSIM. Rank abundance plots of the top 20 most abundant species in each habitat and all families as well as for feeding groups were created.

No significant differences for any univariate measure between on-reef and off-reef habitats could be detected at the species level, although richness and Shannon-Wiener Diversity were significantly higher on-reef at the family level. The ANOSIM was highly significant between habitat types ($p=0.001$) for both the species and family level and SIMPER showed a 93.99% dissimilarity between the communities at the species level and 74.43% dissimilarity at the family level.

The major conclusions are 1) polychaete richness and diversity are higher on-reef at the family level but not the species level, which underlines the importance of looking at different taxonomic levels when comparing macrofaunal communities and 2) on-reef and off-reef communities are very different in terms of community structure although there is overlap in the species and family composition.

INTRODUCTION

An important step in understanding any benthic ecosystem is the gathering of detailed knowledge of the macrofaunal community, which is a major element in many ecosystem processes such as nutrient cycling, food webs and bioturbation leading to burial and dispersion of nutrients, as well as being secondary producers in some systems (Sanvincente-Anorve et al. 2002, Snelgrove and Smith 2002). Important members of the soft-bottom macrofaunal community are the polychaete worms. High abundance of polychaetes and high species richness have been found at all depths, including continental shelves and abyssal plains (Knox 1977, Dauvin et al. 1994, Rouse and Pleijel 2001, Arvantidis et al. 2002, Glover et al. 2002, Perez-Mendoza et al. 2003, Rodriguez-Villanueva et al. 2003). Molluscs and crustaceans have also been found to be important contributors to soft-bottom benthic communities in terms of density, diversity and biomass (San Martin et al. 2000); however, the polychaete worms can be considered as the major taxonomic group in soft-bottom communities (Glover et al. 2002, Rodriguez-Villanueva et al. 2003).

Polychaetes are also abundant in hard-bottom habitats such as tropical coral reefs and rock walls in fjords (Levings et al. 1983, Santa-Isabel et al. 2000), although not many studies have been done on polychaete diversity on hard substrates due to the difficulties in sampling, especially in deeper waters. Polychaetes are also tolerant of many forms of stress including low oxygen concentrations caused by organic nutrient loading, and have even been known to shift feeding modes to accommodate such conditions (Levin 2000, Rodriguez-Villanueva et al. 2003).

Polychaetes were dominant in the grab samples obtained from the glass sponge reefs, accounting for 60 to 80% of the individuals in any given sample. The sponge reefs represent a unique habitat which is not directly comparable to either soft- or hard-bottom habitats due to the presence of the hexactinellid sponge skeleton fragments which remain intact after the sponges die and provide hard substrate for attachment of sessile organisms. This mix of soft sediment and hard biogenic substrate in one ecosystem is not common, with the spicule mats of the Antarctic and the deep-sea coral reefs of the Atlantic being potentially the most comparable habitats (Barthel 1992, Bett and Rice 1992, Fossa et al. 2002).

Another unique feature of the sponge reefs is the organic rich sediment that drops out of the water column by the baffling effect of the living sponges and buries the dead sponge fragments. This organic input leads to anoxic conditions beneath the surface-water interface (Krautter et al. 2001).

The objective of this study was to describe quantitatively the macrofaunal polychaete community of the glass sponge reefs in terms of species and family composition, richness, number of individuals and diversity, and to compare it to the polychaete community of the surrounding habitat to determine if, and how, the reef community differs. The hypothesis is that the sponge reef polychaete community would significantly differ from the off-reef community due to the differences in substrate, with glacial till and sediment off-reef and sediment mixed with dead sponge fragments on-reef.

METHODS

Grab samples were taken during cruise PGC02004 in June, 2002, using both Van Veen and Shipek samplers in both on-reef and off-reef locations between 172 and 237

metres depth (see Table 4.1 for grab sample information and Figure 4.1 for grab sample locations). Off-reef samples were between 0.75 and 4 km away from the sponge reefs. All samples were washed over a 2mm mesh screen and all macrofaunal organisms (those larger than 2mm) were collected and sorted into major taxonomic categories, although only polychaete worms were identified further for this study. For on-reef samples, each sponge skeleton fragment was examined by dissecting microscope at low magnification for attached organisms. Organisms located within the siliceous framework, which can be up to 10 mm thick and full of sediment, were not removed or counted due to time constraints. This will have biased the counts for some groups; for example, many individuals of the family Syllidae were noted partially projecting from a skeletal fragment, but could not be removed without destroying either the skeleton or the worm. It is difficult to estimate how much bias this introduced into the sampling. All polychaetes with heads intact were used in the analysis even if the rest of the individual was missing. All individuals were fixed in 4% formalin then stored in 70% ethanol.

In total, 643 individual polychaetes were picked from the samples; 213 could be identified only to family and 430 could be identified to species (105 species in 27 families in 12 orders) using appropriate literature (Banse and Hobson 1974, Fauchauld 1977, Hobson and Banse 1981, Kozloff 1996, Blake et al. 1997a, Blake et al. 1997b, Blake et al. 1997c, Blake et al. 1997d). Only 11 individuals could not be placed to family and were therefore not used in any analyses. See Appendix II for a full species list and individuals per sample.

Table 4.1: Sample information for grab samples taken on cruise PGC02004.

Sample Number*	Latitude °N	Longitude °W	Depth (m)	Reef Complex	Habitat	Surface Area (m^2)
32ab	53.10017	130.49800	179	A	On-reef	0.14
33ab	53.10213	130.49883	175.2	A	On-reef	0.14
34ab	53.10917	130.50283	177	A	On-reef	0.14
35a	53.10567	130.51067	179	A	On-reef	0.10
36a	53.10650	130.51117	179	A	On-reef	0.10
37ab	53.11633	130.51817	187	A	Off-Reef	0.14
38ab	53.11900	130.51150	179	A	On-reef	0.14
39ab	53.13017	130.51917	192	A	On-reef	0.14
41a	53.12150	130.52267	177	A	On-reef	0.10
41bb	53.12100	130.52300	179	A	On-reef	0.08
42b	53.12500	130.52633	191	A	On-reef	0.04
43ab	53.13533	130.53250	186	A	On-reef	0.14
44ab	53.13700	130.53450	190	A	On-reef	0.14
45b	53.10917	130.49350	192	A	On-reef	0.04
46ab	53.09667	130.48433	184	A	On-reef	0.14
47ab	53.10033	130.48333	180	A	On-reef	0.14
48ab	53.10433	130.48933	178	A	On-reef	0.14
49a	53.10033	130.49717	181	A	On-reef	0.10
50b	53.17333	130.42833	176	A	On-reef	0.04
51b	53.17700	130.43250	174	A	On-reef	0.04
52b	53.17300	130.44000	185	A	On-reef	0.04
53b	53.17967	130.44100	183	A	On-reef	0.04
55b	53.18350	130.44800	182	A	On-reef	0.04
56b	53.13667	130.54300	179	A	On-reef	0.04
83ab	53.14967	130.39933	204	A	Off-Reef	0.14
85a	53.15367	130.40633	207	A	Off-Reef	0.10
85b1	53.14733	130.39633	206	A	Off-Reef	0.04
87a	53.21150	130.48917	172	A	Off-Reef	0.10
92a	53.17750	130.62267	unknown	A	Off-Reef	0.10
94b	53.17117	130.62850	177	A	Off-Reef	0.04
96b	53.15617	130.59217	184	A	Off-Reef	0.04
98b	53.15283	130.58150	189	A	On-reef	0.04
99b	51.33833	128.76617	223	D	Off-Reef	0.04
100b	51.35030	128.78352	222	D	On-reef	0.04
101b	51.34983	128.80050	223	D	On-reef	0.04
102b	51.35083	128.81700	228	D	On-reef	0.04
103b	51.34983	128.83267	226	D	On-reef	0.04
104b	51.35033	128.84983	231	D	On-reef	0.04
105b	51.35050	128.86700	231	D	Off-Reef	0.04
106b	51.35117	128.88067	237	D	On-reef	0.04

***a = Peterson grab; b = Shipek grab; ab = both grabs used.**

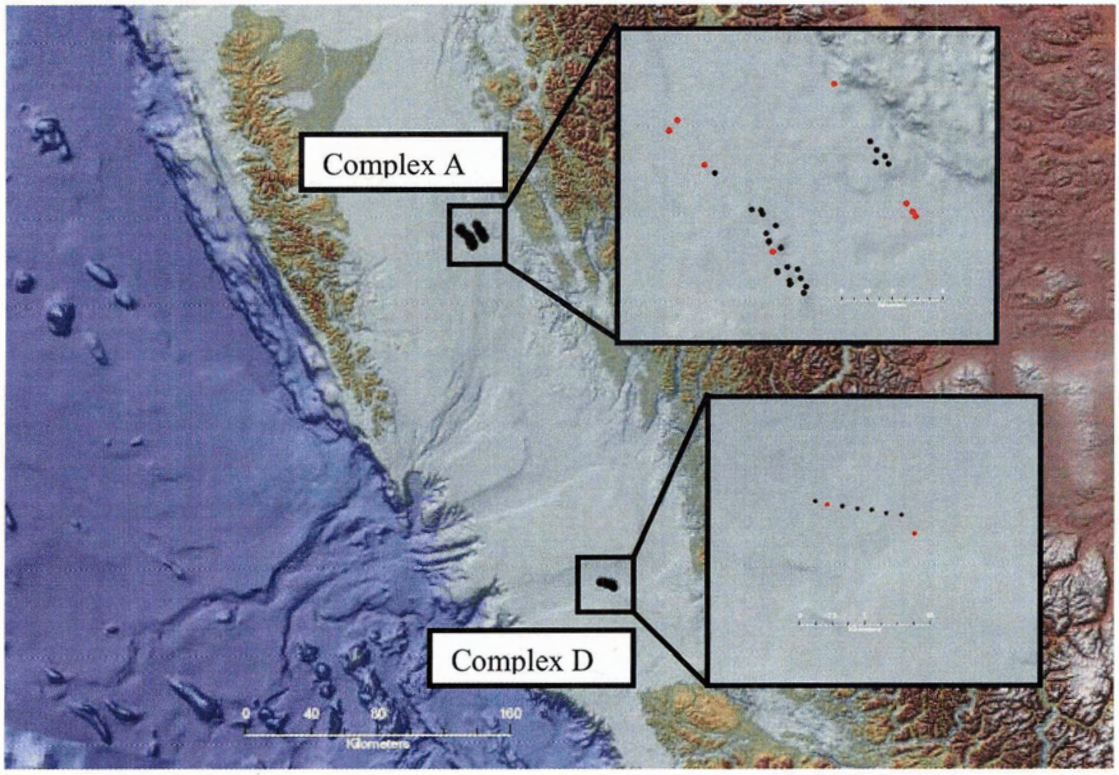

Figure 4.1: Locations of grab samples taken at reef complexes A and D in June 2002. Red indicates samples taken off-reef and black indicates samples taken on-reef.

For statistical analysis, all counts of organisms were standardized to the surface area of the grab (m^2). These standardized counts were used for all analyses. Species richness (S), number of individuals (N), Pielou's Evenness Index (J'), Shannon-Wiener Diversity Index (H'), Taxonomic Diversity (Δ) and Taxonomic Distinctness (Δ^*) were calculated using the statistical package PRIMER-E for the 430 individuals in 105 identifiable species. In PRIMER Pielou's Evenness Index has the formula: $J' = H'/\text{Log}(S)$ where H' is the Shannon-Wiener Diversity Index and S is species richness formula (Krebs 1989, Clarke and Warwick 2001). The Shannon-Wiener Diversity Index has the formula: $H' = -\sum(P_i\text{Log}(P_i))$ where P_i is the proportion of the total sample belonging to the *i*th species (Krebs 1989, Clarke and Warwick 2001). Taxonomic Diversity has the formula: $\Delta = (1-\sum_i p_i^2)/(1 - n^{-1})$ where $p_i=x_i/n_i$ and x_i is the abundance of the *i*th species and n is the total number of individuals in the sample (Clarke and Warwick 1998). This is essentially a derivation of Simpson's index with an element of taxonomic relatedness. As Clarke and Warwick (1998) explain, taxonomic diversity is "the expected path length between any two randomly chosen individuals from the sample." Taxonomic Distinctness has the formula: $\Delta^* = [\sum\sum_{i<j}\omega_{ij}x_ix_j]/[\sum\sum_{i<j}x_ix_j]$ where ω_{ij} is the 'distinctness weight' given to the path linking species *i* and *j*, and x_i is the abundance of the *i*th species and x_j is the abundance of the *j*th species (Clarke and Warwick 1998). This is the "expected (weighted) path length between any two randomly chosen individuals from the sample, conditional on them being from different species" (Clarke and Warwick 1998). For this analysis the path lengths in Δ^* were weighted so that the length between phylum and species equaled 100. The weighted path lengths were therefore: species = 16.667, genus = 33.333, family = 50, order = 66.667, class = 83.333 and phylum = 100.

Family richness (S), number of individuals (N), Pielou's Evenness Index (J') and the Shannon-Wiener Diversity Index (H') were also calculated for the 643 individuals identified to family. This was done because some studies have shown that changes in community structure in soft-bottom habitats were sometime more easily distinguished at the family rather than species level (Rodriguez-Villanueva et al. 2003).

Error bar plots giving the mean and 95% Confidence Intervals for each of the univariate measures for both habitats were plotted using the statistical software package SPSS 11.0. Each error bar represents a t-test comparison, meaning that error bars which do not overlap the mean of another error bar represent a significant comparison.

A rank abundance plot using the 20 most abundant polychaete species was created using SigmaPlot 8.0. This plot displays the percent average abundance of each species relative to the other species displayed. Usually all plots are ranked according to one factor, in this case, either on-reef or off-reef; however, in this case, one plot was created using the 20 most abundant species ranked according to on-reef abundances and one according to off-reef abundances. This was done to highlight the differences between the two communities. A rank abundance plot was also created for all families identified in the grab samples. Both plots were ranked by on-reef habitat. All families were also placed into a feeding group from information in Rouse and Pleijel (2001) and a rank abundance plot was created for those feeding groups ranked by on-reef abundance.

For the multivariate measures, a standardized data matrix (using individuals/m^2) was created for analysis with the PRIMER-E statistics package. Similarity percentages (SIMPER) were calculated to determine how dissimilar the habitat types are and to indicate which species or family contributes most to that dissimilarity and the percentage

of that contribution (Clarke and Warwick 2001). A similarity matrix was then calculated using Bray-Curtis similarity with a fourth-root transformation. This similarity matrix was used to perform an Analysis of Similarity (ANOSIM) to determine if the community, both in terms of species or family composition and number of individuals, differed between habitat types (Clarke and Warwick 2001). Fortunately, ANOSIMs are very robust to relatively unbalanced sample designs (Clarke and Warwick 2001), which is important for this study since 30 on-reef samples were available compared to only 10 off-reef samples. These multivariate measures were carried out for both species and family matrices. These measures were carried out in conjunction with the univariate measures because some studies have shown that changes in community structure can be detectable with multivariate measures even when not detectable with univariate measures (Rodriguez-Villanueva et al. 2003).

RESULTS

The grab samples from the reefs were highly stratified, with the sponge fragments projecting from the sediment having high numbers of attached individuals, and buried fragments having few or no attached macrofauna. Fragments from the deepest parts of the grab, < 30 cm beneath the surface, were usually discoloured with black and orange crusts and were devoid of attached organisms, except for a few bivalves of the genus *Thyasira* which are known to be tolerant of low oxygen levels (Krautter et al. 2001). This stratification is a phenomenon which was not examined in this study but which deserves further attention. The sediment matrix in which the fragments were buried was very fine greenish clay with a distinct sulphurous smell. The percentage of the grab

sample composed of sponge fragments ranged from approximately 20 to 90%, although the majority of the samples had more than 50% sponge fragments.

The off-reef samples had a wider range of sediment types, from all greenish clay to greenish clay mixed with sand and gravel, with the gravel size ranging from to cobbles. The sulphurous smell was noticeable in the all-clay samples, although it was not as pronounced as it was with the on-reef samples, but absent in the other off-reef samples. The gravel often had tube worms attached to it.

Polychaetes made up the majority of any sample and were the only organisms identified to species for this study, but many other groups were present. These include crustaceans, including squat lobsters, numerous amphipods and small shrimp; echinoderms, including brittle stars, sea cucumbers and even one sea star (which was *Henricia* sp.); brachiopods; bivalves including *Hiatella arctica* and *Thyasira* sp., some type of scallop and several others that were not immediately identifiable; numerous hydroids; bryozoans of both the encrusting and erect variety; foraminiferans of both the agglutinating and shelled variety; sipunculids, and even one pycnogonid. However, the most numerous group aside from the polychaetes were the encrusting and erect demosponges which often covered large portions of the hexactinellid skeleton fragments that had not been covered by sediment.

Analyses for Polychaete Species

Although some trends in the univariate measures are noticeable, none of the comparisons between habitats are significantly different from each other (Figure 4.2). In general, mean species richness, mean number of individual per metre, mean Shannon-Wiener diversity and mean taxonomic diversity are higher on-reef but these comparisons

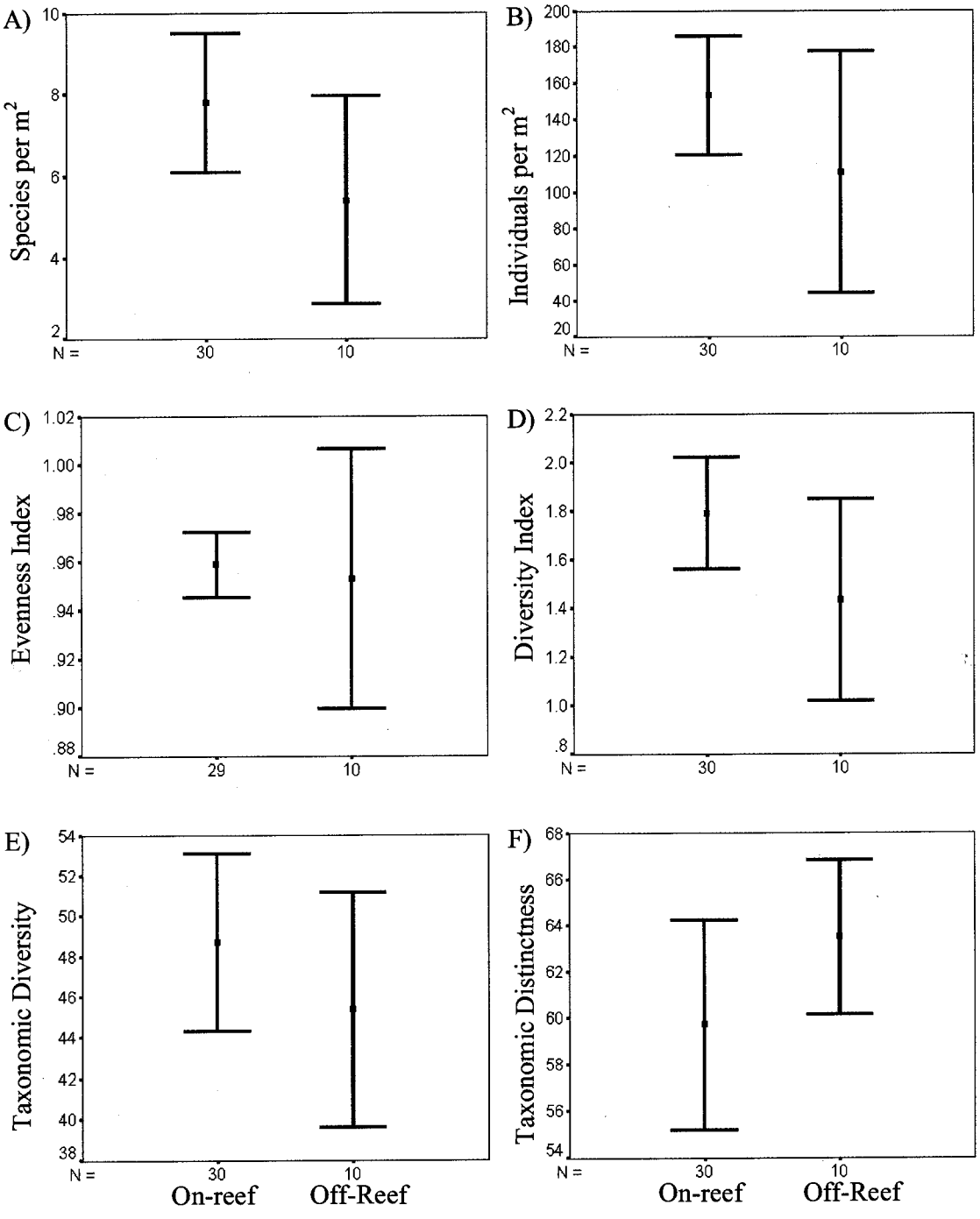

Figure 4.2: Polychaete species richness (A), number of individuals (B), Pielou's Evenness Index (C), Shannon-Wiener Diversity Index (D), Taxonomic Diversity (E) and Taxonomic Distinctness (F) summarized for habitat type in error bar plots with means and 95% Confidence Intervals (N = number of samples).

are not significant. No trend is noticeable for evenness. Mean taxonomic distinctness is higher off-reef, but again this comparison is not significant. The variability of the off-reef samples is higher than for the on-reef samples.

The rank abundance plots for the top 20 most common species from each habitat show that the species composition is very different between the two habitats (Figure 4.3). Only 6 species are common between the two plots. Two of those species are relatively more abundant on-reef (*Onuphis iridescens* and *Anobothrus gracilis*), two are relatively less abundant on-reef (*Notoproctus pacificus* and *Euclymene zonalis*) and two have approximately the same relative abundance between the two habitats (*Ninoe gemmea* and *Glycera tesselata*). The slopes of the curves are also different between habitats. The on-reef curve has a relatively consistent slope from the relatively most abundant to relatively least abundant species, while the off-reef curve has one dominant species (*Notoproctus pacificus*) and then flattens out.

The multivariate measures give different results from the univariate measures but agree better with the rank abundance curves. The ANOSIM comparison between habitats shows significant differences between on-reef and off-reef polychaete communities ($p=0.001$, $R=0.411$). The SIMPER analysis shows that the on-reef and off-reef communities are 93.99% dissimilar. Table 4.2 lists the species that cumulatively contribute 50% to this dissimilarity. None of the 20 species listed contributes more than 5.32% to dissimilarity and the average abundances are very different between the habitats for almost all the listed species, many being at least an order of magnitude different. There are also many similarities between the 20 species listed in the SIMPER analysis and the species in the rank abundance curves.

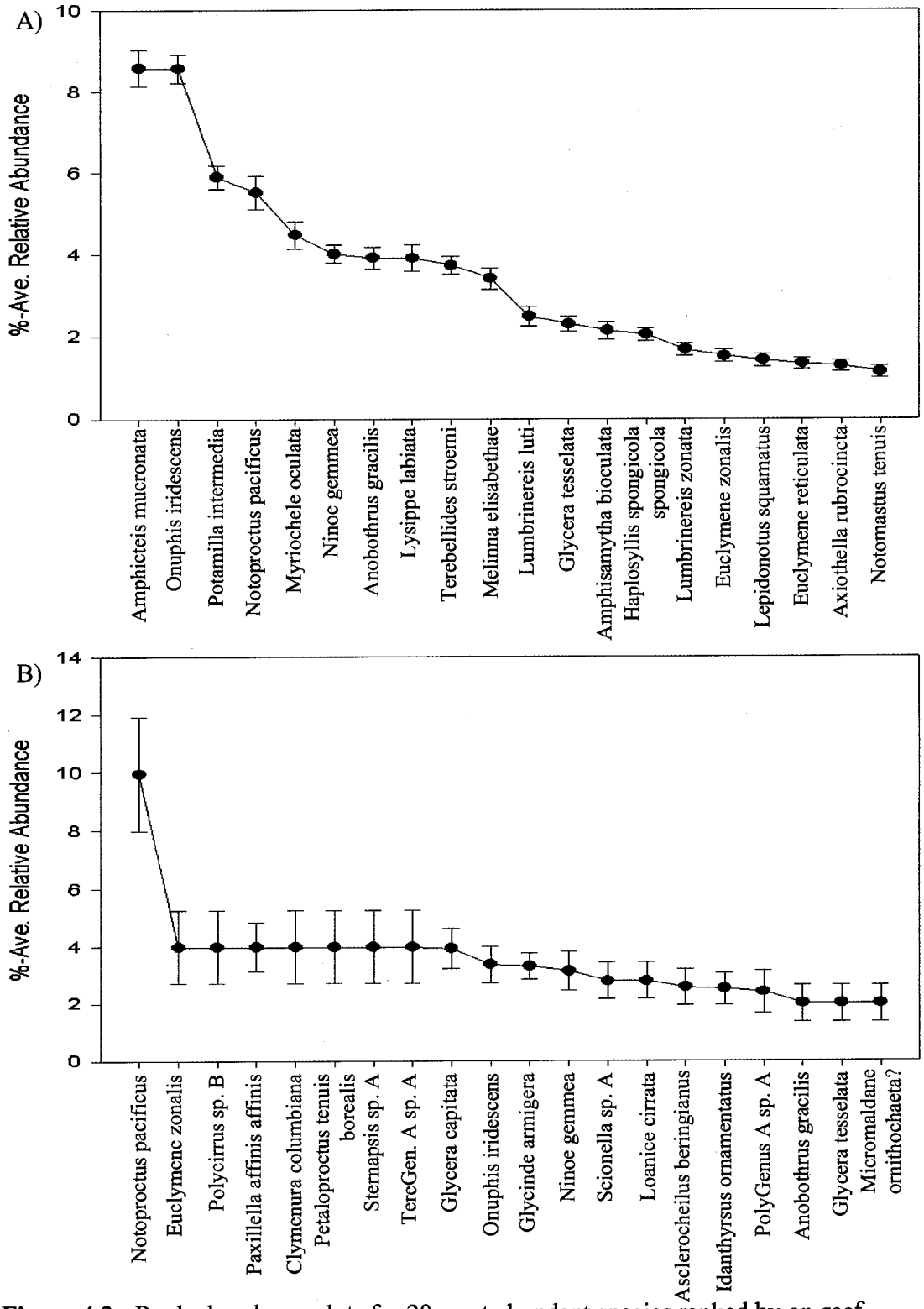

Figure 4.3: Rank abundance plots for 20 most abundant species ranked by on-reef habitat (N=30) (A) and off-reef habitat (N=10) (B).

Table 4.2: SIMPER results for comparison of species community between habitats. Only those species that cumulatively contribute 50% to the dissimilarity between the habitats are included.

Family	**Species**	**Ave. Species Abundance (on-reef / off-reef)**	**Contribution to % dissimilarity**
Onuphidae	*Onuphis iridescens*	13.52 / 1.71	5.32
Ampharetidae	*Amphicteis mucronata*	12.70 / 0.00	4.11
Maldanidae	*Notoproctus pacificus*	8.17 / 12.50	4.06
Lumbrineridae	*Ninoe gemmea*	5.93 / 3.93	3.81
Goniadidae	*Glycinde armigera*	0.83 / 4.14	3.68
Sabellidae	*Potamilla intermedia*	7.88 / 2.50	3.18
Ampharetidae	*Anobothrus gracilis*	6.62 / 0.00	2.64
Glyceridae	*Glycera capitata*	0.48 / 4.93	2.37
Lumbrineridae	*Lumbrinereis luti*	2.83 / 3.21	2.33
Spionidae	*Laonice cirrata*	0.00 / 3.50	2.09
Oweniidae	*Myriochele oculata*	6.62 / 0.00	2.02
Trichobranchidae	*Terebellides stroemi*	5.51 / 0.00	2.00
Ampharetidae	*Lysippe labiata*	5.77 / 0.71	1.95
Glyceridae	*Glycera tesselata*	4.23 / 0.00	1.89
Maldanidae	*Euclymene zonalis*	2.24 / 5.00	1.79
Maldanidae	*Micromaldane ornithochaeta?*	1.49 / 2.50	1.75
Ampharetidae	*Melinna elisabethae*	5.04 / 0.00	1.67
Ampharetidae	*Melinna cristata*	1.38 / 2.50	1.61
Terebellidae	*Scionella* sp. A	0.24 / 3.50	1.47
Capitellidae	*Notomastus tenuis*	0.83 / 2.50	1.42

Analyses for Polychaete Families

The univariate measures calculated for the polychaete family matrix (Figure 4.4) show some trends similar to those shown by the species matrix. Family richness and diversity are both higher on-reef; however, unlike the species matrix plots, these comparisons are significant for richness ($p=0.045$) and diversity ($p=0.055$). Number of individuals per square metre is higher on-reef but it is not a significant comparison. Evenness does not show any clear trend for family. The off-reef samples again show more variability than the on-reef samples.

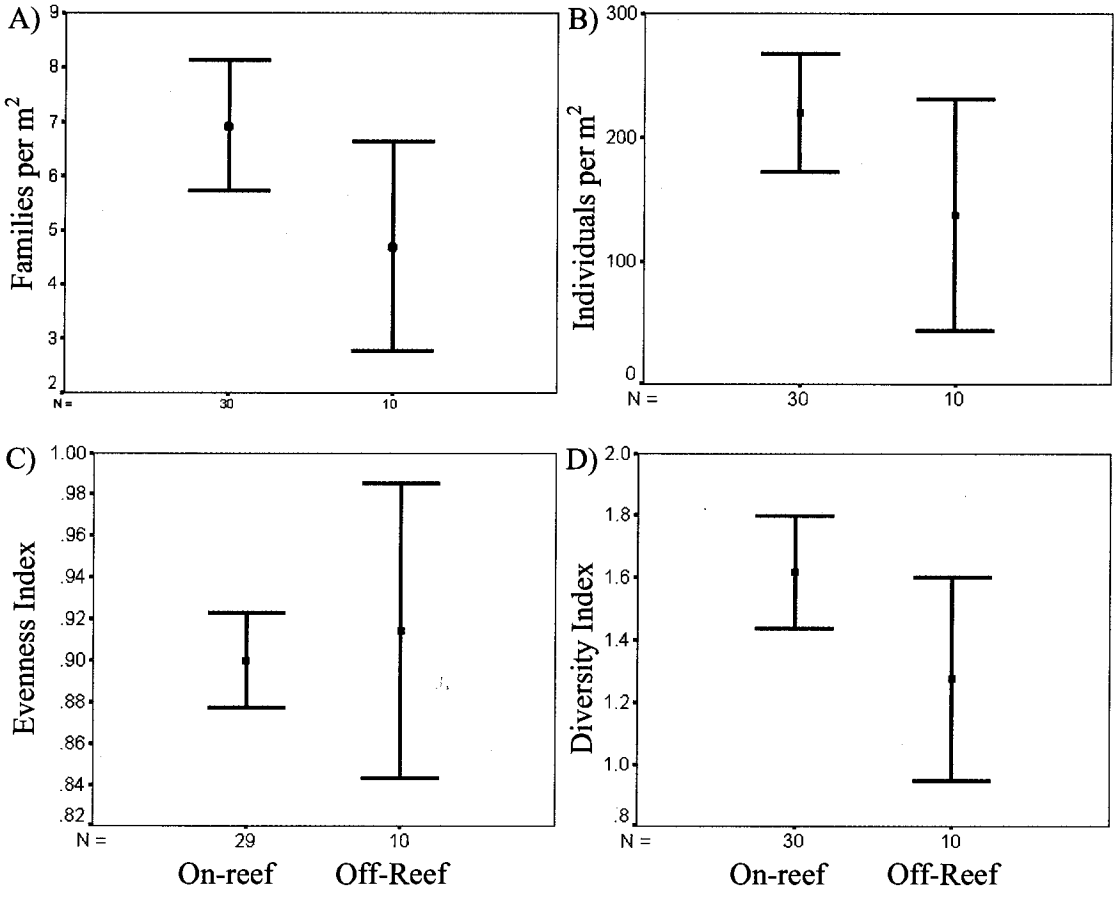

Figure 4.4: Polychaete family richness (A), number of individuals (B), Pielou's Evenness Index (C) and Shannon-Wiener Diversity Index (D) summarized for habitat type in error bar plots with means and 95% Confidence Intervals (N = number of samples).

The rank abundance plots for all 27 families identified in the samples (Figure 4.5) show that the family Maldanidae is dominant in both habitats, with a higher relatively abundance off-reef. The shape of the curves is different as well with a steep slope at the beginning of the on-reef curve that flattens out after nine families. The off-reef curve also has a steep slope at the beginning but flattens out much faster, except for a spike of higher relative abundance at the Terebellidae.

In order to determine whether there is an ecological significance as to why some of the univariate trends differ between species and family, the families were placed into feeding groups. These groups are a combination of lifestyle (tubiculous, predator, motile burrower, motile tubiculous or burrower) and feeding mode (deposit feeder, carnivore or filter feeder). Six feeding groups were identified: tubiculous, deposit feeders which are sedentary tube dwellers that feed on organic matter in the surrounding sediment (Maldanidae, Ampharetidae, Sabellidae, Terebellidae, Oweniidae, Trichobranchidae, Pectinariidae, Cirratulidae); predator, carnivores which are mobile individuals that feed on other animals (Syllidae, Polynoidae, Nereididae, Euphrosinidae); motile burrower, carnivores which move freely through the sediment and feed on animal matter (Lumbrineridae, Glyceridae, Goniadidae, Nephtyidae, Oenonidae); motile tubiculous, carnivores which are mobile tube-dwellers that feed on other animals (Onuphidae); burrower, deposit feeders which are build burrows in the sediment and remain relatively sedentary and feed on surrounding sediment, either on the surface or beneath it (Spionidae, Scalibregmatidae, Capitellidae, Paraonidae, Cossuridae); motile burrower, deposit feeders which move freely through the sediment and feed on organic matter in subsurface sediments (Sternaspidae); and tubiculous, filter feeders which are sedentary

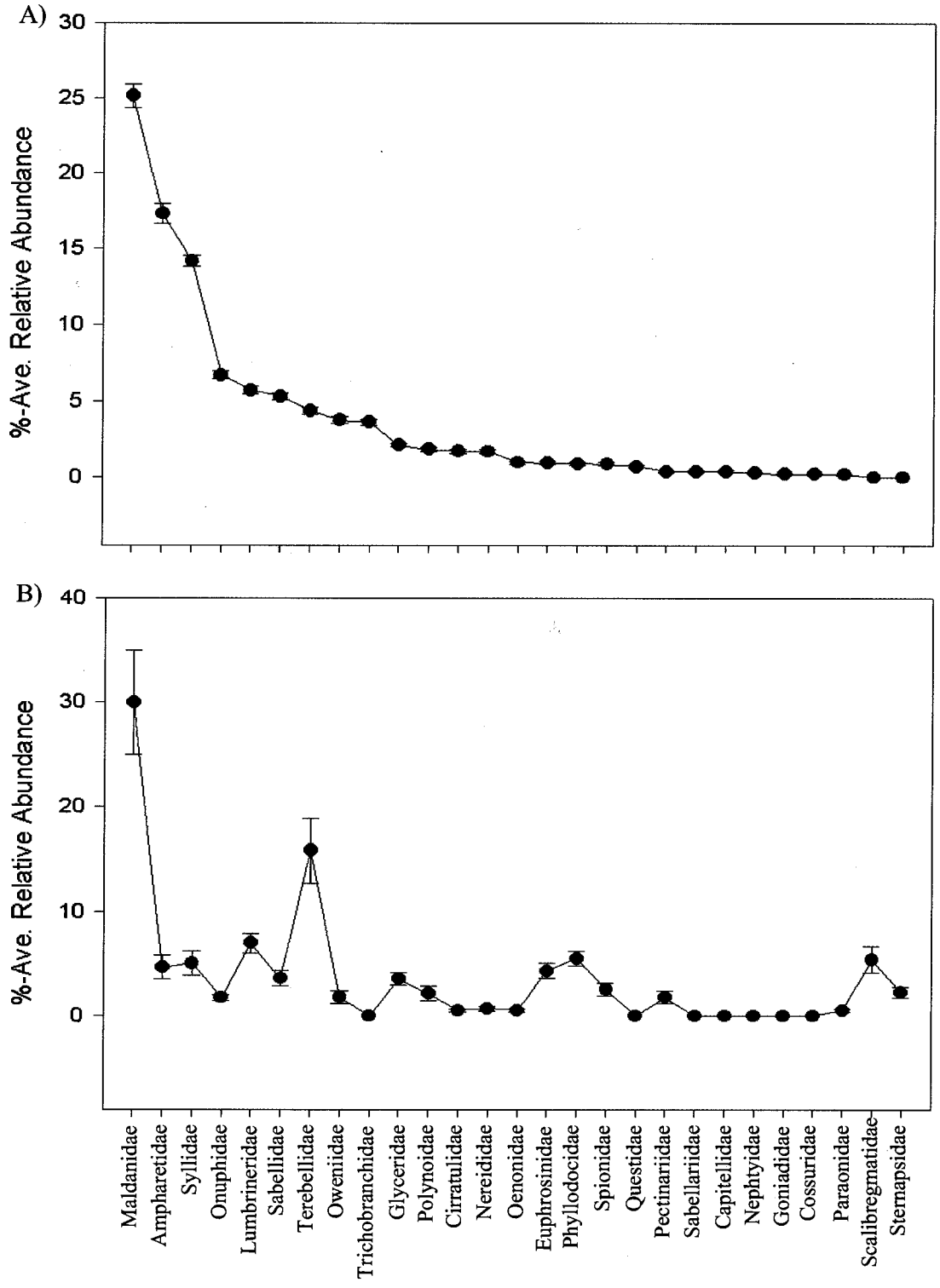

Figure 4.5: Rank abundance plots for all families identified in the grab samples for both on-reef (N=30) (A) and off-reef (N=10) (B). The families are ranked by on-reef habitat.

tube dwellers that filter food out of the water column using tentacles or other feeding appendages (Sabellariidae). There was insufficient information to place one family, Questidae, into a feeding group, so it was not used in the rank abundance plots for feeding groups.

The rank abundance plots for feeding groups (Figure 4.6) show that tubiculous deposit feeders are dominant in both habitats with about 60% relative abundance in each. The main differences between the habitats is in the predator, carnivore group which has a relative abundance approximately twice as high on-reef as off-reef and also in the carnivorous motile burrowers have higher relative abundance off-reef, the opposite trend from on-reef. Comparing the results from the feeding group rank abundance plots to the family rank abundance plots, it should be noted that 6 of the 10 relatively most abundant on-reef families and 4 of the 10 relatively most abundant families off-reef are tubiculous deposit feeders.

The multivariate analyses do not agree well with the trends shown in the univariate measures but, as with the species analyses, agree better with the rank abundance plots. The ANOSIM between habitats shows significant differences between the communities at the family level ($p=0.001$). The SIMPER analysis shows that the on-reef and off-reef family communities are 74.43% dissimilar. Table 4.3 shows that only 7 families out of the 27 identified cumulatively make up 50% of the dissimilarity between the habitats, although none of them contribute more than 9.80%.

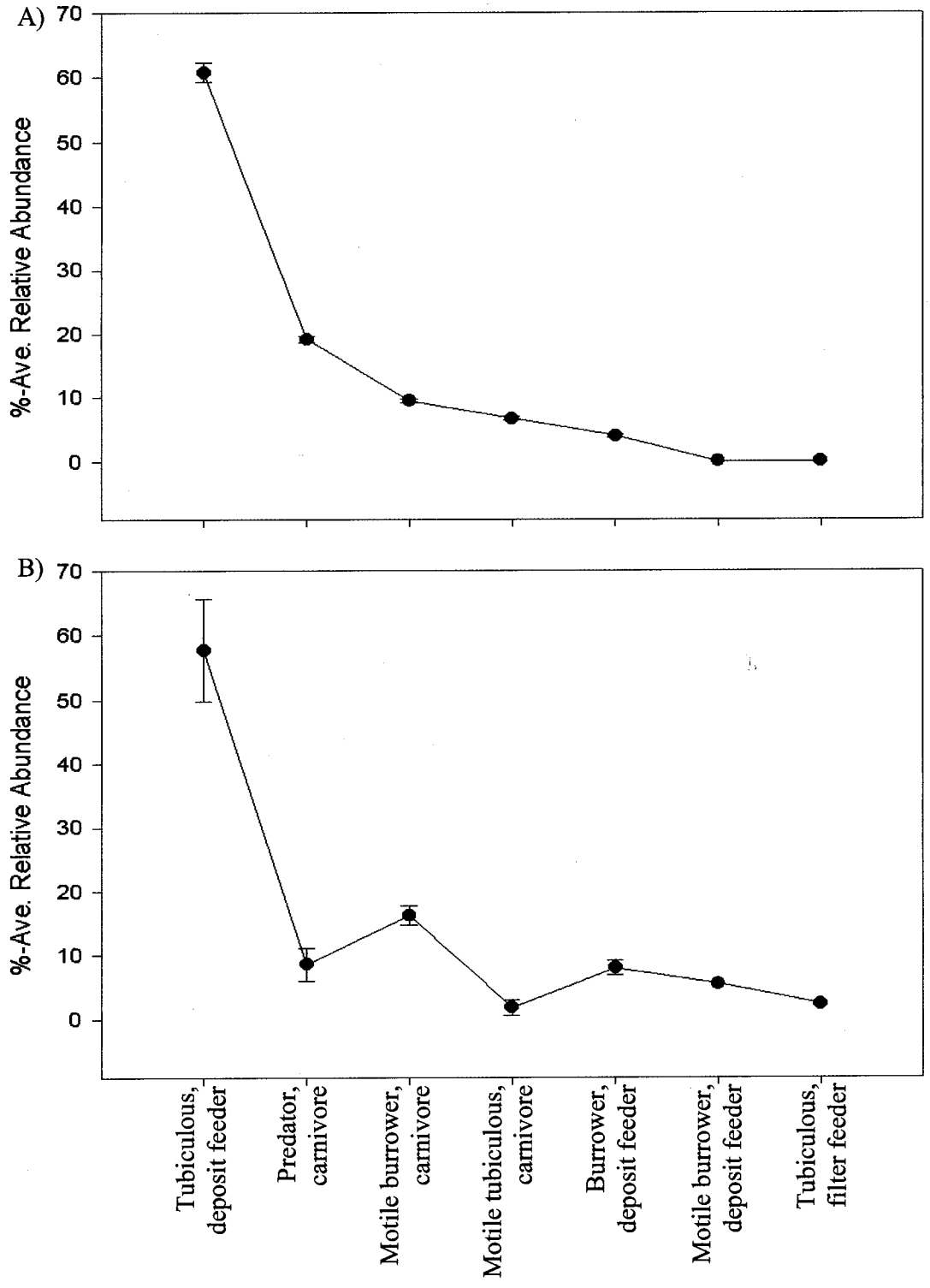

Figure 4.6: Rank abundance plots for feeding groups identified in the grab samples for both on-reef (N=30) (A) and off-reef (N=10) (B) habitats. The groups are ranked by on-reef habitat.

Table 4.3: SIMPER results for comparison of the family community between habitats. Only those families that cumulatively contribute to the upper 50% of the dissimilarity between the habitats are included.

Family	Ave. Family Abundance (on-reef / off-reef)	Contribution to % dissimilarity
Ampharetidae	38.04 / 6.43	9.80
Syllidae	31.15 / 7.00	9.04
Maldanidae	55.25 / 41.00	8.89
Lumbrineridae	12.55 / 9.64	6.77
Onuphidae	14.69 / 2.43	6.62
Goniadidae	2.00 / 7.64	6.14
Terebellidae	9.64 / 21.64	6.08

DISCUSSION

The results gathered from this data show the importance of looking at different taxonomic levels and using different methods of analysis to gain a complete picture of the differences between communities of macrofaunal organisms. The results for the polychaete species univariate analyses had no significant differences between habitats while richness and diversity at the family level showed significant differences, albeit borderline, between habitats. The rank abundance plots appear to disagree with the univariate analyses because they show different species communities between habitats and different relative abundances between families between the different habitats, indicating that the univariate measures are not giving a complete picture because they do not take species identity into account. This is where multivariate techniques can be useful because the entire community structure can be measured together instead of in parts as with the univariate measures. The ANOSIM results support what the rank abundance plots show, which is that the on-reef and off-reef communities are significantly different at both the species and family levels. The SIMPER analysis also supports the ANOSIM results, showing over 75% dissimilarity between the on-reef and

off-reef communities at both the species and family levels. It also appears that a small percentage of species and families are contributing the most to the dissimilarity between habitats because only 20 out of 105 species (19%) and 7 out of 27 families (26%) contribute 50% of the dissimilarity. It should be noted at this point that a large mesh size (2 mm) was used, and this may have allowed some of the smaller polychaetes to fall through. A smaller mesh size might yield a different result.

The question becomes why there is a significant difference between the polychaete community on-reef and off-reef at both the species and family level. Part of the answer to that question can be found in the feeding group analysis. The relatively most dominant feeding group is the same in both habitats but 60% of the 10 relatively most abundant families on-reef are in that group while only 40% of the 10 relatively most abundant families off-reef are in that group. There are also differences in the relative abundances of the three next most common feeding groups and the families making up those groups in each habitat. For example, predators are relatively more abundant on-reef than they are off-reef indicating a community with a greater food supply for them on-reef compared to off-reef habitat. Although biomass was not measured in this study, a higher relative percentage of predators could indicate higher biomass on-reef.

These factors indicate an ecological difference between the two habitats. This difference could be due to differences in the physical characteristics of the two habitats. For example, gravel makes up the hard substrate in off-reef habitats while porous skeletal fragments make up the hard substrate on-reef. Other physical parameters were not measured for this study, but some of the parameters that could influence the macrofaunal community could include percent organic composition of the sediment, the width of the

benthic boundary layer which could be influenced by the presence of the sponges and anoxic conditions within the sediment, which were especially noted in on-reef samples and which could cause a reducing layer to form.

Still looking at the univariate measures, it is interesting that while neither taxonomic diversity nor taxonomic distinctness are significantly different between the two habitats, they show opposing trends, with mean taxonomic diversity higher on-reef and mean taxonomic distinctness higher off-reef. The difference between these two measures is essentially that taxonomic distinctness is weighted so that it reflects pure taxonomic relatedness rather than a mix of taxonomic relatedness and evenness of abundance like taxonomic diversity. So higher taxonomic distinctness off-reef indicates that any two randomly chosen individuals in a sample will be more closely related than in an on-reef sample. Higher taxonomic diversity on-reef indicates that the samples are in some way more even in abundance of species while also mixing in some indication that any two randomly chosen individuals will be more closely related. In some ways these two results are contradictory but since neither was significant, it does not truly tell us anything about the differences between the habitats.

Another observation from the results is that off-reef samples are more variable than on-reef samples according to the univariate measures. One possible explanation for this is that there are fewer off-reef samples but it could also be due to the greater variability in substrate off-reef compared to on-reef samples which are only made of sediment and dead sponge fragments as opposed to varying amounts of sediment and gravel of differing sizes.

A habitat comparable to the sponge reefs is difficult to identify for comparing with the univariate and multivariate measures obtained in this study. The spicule mats in the northeast Atlantic (Bett and Rice 1992) have abundant polychaete macrofauna but are at abyssal depths (>1500 meters) and are therefore not truly comparable. However, polychaete abundance was found to be correlated to the area of sponge spicule mats that were encrusted with foraminiferans, but not with total area of the spicule mats (Bett and Rice 1992). Agglutinating and other types of foraminiferans were also very common on the sponge fragments in the grab samples in this study and were invariably more abundant on the fragments closest to the surface-water interface which is where most of the macrofaunal organisms were found. Perhaps foraminiferans are a good indicator for the more highly oxygenated areas of the sponge fragments. This may explain why Bett and Rice (1992) found a correlation between those spicule mats with foraminiferans but not with total area of the spicule mats (most of which were probably beneath the surface-water interface and therefore in areas of lower oxygen). It would be interesting to examine if a similar correlation could be found in the grab samples from the glass sponge reefs of British Columbia.

The *Oculina* reefs off Florida are another potentially comparable habitat since these deep-water coral reefs are built in much the same way as the sponge reefs, although they are in shallower water (70 to 100 meters) (Reed 2002). A study of the macrofaunal invertebrate community of the *Oculina* reefs showed a very different community to those on the sponge reefs, one dominated by molluscs (230 species), although it does have a fairly comparable number of polychaete families (23 families from 42 samples) (Reed 2002).

The fjords of British Columbia could potentially provide a comparable habitat to the sponge reefs, with large piles of dead hexactinellid sponge at the base of the walls from dead sponges that have fallen off fragments (mostly from *Aphrocallistes vastus* and *Heterochone calyx*, two of the reef-builders that live individually on the fjord walls)(Levings et al. 1983). Unfortunately, no details of the macrofaunal community were provided in the paper, except to state the presence of *Thelepus cincinnatus*, a terebellid polychaete that builds its tubes out of sponge spicules. A terebellid polychaete that builds its tube out of sponge spicules was also identified in the grab samples from the sponge reefs but was identified as *Scionella* sp. A, since it did not fit the description of any *Scionella* species currently known in British Columbia. A comparison of these sponge fragment mounds in the fjords and the sponge reefs would be highly relevant and is currently being undertaken (S. Leys, pers. comm.).

Another potentially relevant study is a census of the benthic macrofauna of Hecate Strait conducted by Burd and Brinkhurst (1987), where the major reef complexes are located. Two of the areas surveyed were of comparable depth to the off-reef samples in this study. One had fine sandy silt substrate and the other had a range of substrates from cobble and pebble to sandy silt. Polychaetes were the most abundant macrofauna at both stations with the species *Lumbrinereis luti, Prionospio steenstrupi, Spiophanes berkleyorum, Galathowenia oculata, Euclymene zonalis, Owenia fusiformis, Polycirrus* sp., and *Mediomastus* sp. being most abundant at the first site and *Spiochaetopterus costarum, Galathowenia oculata, Owenia fusiformis, Myriochele heeri* and *Odostomia* sp. being most abundant at the second site. Aside from *Lumbrinereis luti, Prionospio steenstrupi,* and *Owenia fusiformis,* none of these species were found at the off-reef sites

in this study although some of the other genera were found on-reef. Burd and Brinkhurst (1987) found that all four sites studied in Hecate Strait were significantly different from each other in terms of community structure, with substrate type as an important factor in determining that structure. Substrate type is considered an important factor in determination of any macrofaunal polychaete community, as is the level of organic carbon input (Santa-Isabel et al. 2000, Rodriguez-Villanueva et al. 2003) and depth (San Martin et al. 2000, Perez-Mendoza et al. 2003). Unfortunately Burd and Brinkhurst (1987) did not use any of the univariate measures calculated in this study, therefore no direct comparison of the community structure as described by them and that in this study can be made.

CONCLUSIONS

- Polychaete richness and diversity are significantly higher in on-reef habitat at the family level, but not at the species level.
- On-reef and off-reef habitats are different in terms of overall polychaete community structure, including species and family composition and abundance but there is also some overlap in species and family composition.
- Tubiculous deposit feeders are the dominant taxa at both on-reef and off-reef sites.

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CHAPTER 5:
Conclusions and Future Work

In summation, the major conclusions reached in this thesis are:

- Live reef habitat has significantly higher taxonomic richness than dead reef or off-reef habitat and higher abundance of individuals without the boot sponges or demosponges included.
- Trends noted in comparisons of abundance of individuals between habitats, within a taxonomic group, depend on the group and its particular physiological characteristics.
- Live reefs are nursery habitats for juvenile rockfish.
- The community structure of live reef and off-reef habitats are significantly different.
- High complexity areas have significantly higher richness and abundance of individuals when boot sponges and demosponges are removed from the analyses.
- High complexity, off-reef areas have the highest richness and abundance of individuals of any shelf habitats possibly due to the combination of physical rugosity and biological complexity in those areas
- Some evidence points to the conclusion that dead reef areas are caused by bottom trawling and are therefore impacted habitats.
- Dead sponge substrates are, overall, higher in abundance of individuals, family richness and diversity than living sponge.
- Major differences exist between megafaunal families in their occurrence on different substrate types; these differences vary between families and between sites.
- Polychaete richness and diversity are significantly higher in on-reef habitat at the family level, but not at the species level.

- On-reef and off-reef habitats are different in terms of overall polychaete community structure, including species and family composition and abundance but there is also some overlap in species and family composition.
- Tubiculous deposit feeders are the dominant taxa at both on-reef and off-reef sites.

The conclusions reached from the studies performed in this thesis are a first step toward understanding the ecology of these unique and relatively unknown ecosystems; however, some issues related to the data collection for these studies need to be taken into consideration to understand the implications of these conclusions. One issue is the difference between on-reef, off-reef and dead reef. Classifying samples into one of these categories is not difficult from video; however, all off-reef video was relatively close to live reefs due to the sampling design, meaning these off-reef areas could be influenced by the on-reef community through propagule exchange or migration of individuals. To ensure truly different habitats are being compared, off-reef areas of similar depth that are not adjacent to live reefs should be sampled and compared to on-reef samples. For the grab samples, distinguishing off-reef was relatively easy due to the absence of dead sponge fragments; however, live reef samples and dead reef samples could not be distinguished because neither sidescan sonar nor multibeam have yet been able to distinguish between live and dead reef. The macrofaunal community could potentially be different on dead reef compared to live reef, so visual confirmation of the habitat of any grab samples should be undertaken.

The definition of dead reef habitat is another issue. It was defined for the purposes of this thesis as a flat area of broken, dead sponge fragments covered in sediment and organic 'fuzz', with no reef-building sponges growing on it and little, if any, standing

dead sponge. It was also noted that the origin of dead reef habitat is unknown and could potentially be the product of natural reef disintegration or bottom trawling. This is an important distinction and needs to be established for future studies, especially what natural processes could cause disintegration of a sponge reef mound. It is also possible that some of the lower complexity off-reef areas have been trawled, something that could not be established from video observation, and may also have biased results from those areas.

Another issue to consider is that counts of megafaunal organisms will be biased in areas of higher complexity because the organisms have more places to hide. This is an unfortunate consequence of studying ecosystems at depths where the use of submersibles or ROVs are necessary, and there is no way at present to overcome this bias; however, it must still be taken into account when analyzing data collected using these methods.

The taxonomic level of identification at which the communities were analyzed also needs to be considered. In the megafaunal community comparison, all different taxonomic levels were lumped together, while in the megafaunal substrate use analysis only the family level was considered. In the macrofaunal polychaete community analysis both the species and family levels were analyzed with differing results which indicates that taxonomic level can affect the outcome of a community analysis. The most appropriate taxonomic level is not always clear for a particular study, although a level that has some ecological significance is always to be desired. When using video, species level identification is not often possible so perhaps family level should be used in future studies involving video, since there is still a degree of physiological relatedness at that level that generally indicates similar ecological niches or requirements. Family level

gave clearer results for the macrofaunal polychaete analysis, at least in terms of univariate measures, which indicates it could also be the most useful taxonomic level for megafaunal analyses.

The last major issue that needs to be considered is that each of these studies gives us only a snapshot of the ecosystems being studied at that particular point in time. It gives no idea of how the community of each of these ecosystems may alter with the seasons or with year to year variability, such as with an El Nino event or other event that affects water conditions or climate. Studies during different seasons and over a number of years need to be conducted to understand the seasonal and annual fluctuations that are a natural part of any ecosystem. Also, only two of the four complexes in the Queen Charlotte Basin have been surveyed by video, and only the Fraser Ridge reef complex has been properly surveyed in the Georgia Basin. Differences between the reef complexes and between the different reef forms, biostromal or biohermal, need to be studied in order to get a more complete picture of the reef community.

Keeping the aforementioned issues in mind, there are still a few implications that can be drawn from the conclusions presented in this thesis. These implications have mostly to do with fisheries management on and around the sponge reefs. The reef community is unique and is a nursery habitat for juvenile rockfish, some of which are commercially important species. Although the reefs have already been protected from bottom trawling, the implications of these conclusions indicate that a greater degree of protection is warranted, not only to protect the rockfish fishery in the northern part of B.C. but also to ensure the health of a globally unique ecosystem. This protection could be in the form of a marine protected area or, as has also been suggested, as a UNESCO World Heritage

Site (Manfred Krautter, pers. comm.). The exact implications and proper management actions cannot be defined from this first, descriptive study of the sponge reefs; therefore, a further implication is that a study more directed to specific questions of importance to fisheries management is required. One of the major questions is how resilient are the sponge reefs to bottom trawling or other disturbances, natural or anthropogenic? What is the time-frame for recovery of a sponge reef from such disturbance, especially considering that growth rates and many other biological attributed of the hexactinellid sponges themselves are still unkown?

Some other questions that have arisen from this thesis are what makes the live sponge reefs good nursery habitat for juvenile rockfish? Are they just a place to hide from predators or do they also provide food and other resources? How important are the reefs to the maintenance of healthy populations of commercially important rockfish species? Do adult rockfish spawn on the reefs or do the juveniles migrate to the reefs from off-reef spawning grounds? What are the characteristics of the taxonomic groups that are found in higher abundances on the reefs that make them more suited to that habitat? How important are the sponge reefs in overall shelf productivity? How are the various microhabitats or niches that the reefs provide defined and how are they utilized by the organisms that live on the reefs, beyond substrate?

There is another implication for fisheries management from the conclusions reached in this thesis, but it does not relate to the reefs themselves. The conclusion that off-reef areas of high physical and biological complexity have the highest richness and abundance of individuals of any of the shelf communities compared in this thesis also has implications for fisheries management on the continental shelf in general. The

implication is that these areas are also potentially nursery habitats as well as potential areas of high productivity from a fisheries standpoint and need to be identified and protected. It also raises the question, is it the combination of physical and biogenic complexity that makes the off-reef, high complexity areas higher in richness and abundance of individuals, and how important is that combination in overall shelf productivity? Further study of the importance of complexity in terms of community structure and productivity is indicated.

APPENDIX I – Megafaunal organisms identified during cruise PGC02004 and used in on reef substrate use analysis.

Phylum: Class	Family	Species
Annelida: Polychaeta	Sabellidae	Unidentified Tube Worm
Arthropoda: Malacostraca	Majidae	*Chorilia longipes*
Arthropoda: Malacostraca	Lithodidae	*Lopholithodes foraminatus*
Arthropoda: Malacostraca	Lithodidae	*Lopholithodes* sp.
Arthropoda: Malacostraca	Galatheidae	*Munida quadrispina*
Arthropoda: Malacostraca	Pandalidae	*Pandalus platyceros*
Arthropoda: Malacostraca	Lithodidae	*Placetron wosnessenskii*
Arthropoda: Malacostraca	Majidae	*Pugettia* sp.
Arthropoda: Malacostraca	Majidae	*Scyra acutifrons*
Chordata: Chondrichthyes	Rajidae	*Raja rhina*
Chordata: Chondrichthyes	Rajidae	*Raja* sp.
Chordata: Osteichthyes	Pleuronectidae	*Hippoglossus stenolepis*
Chordata: Osteichthyes	Scorpaenidae	*Sebastes alutus*
Chordata: Osteichthyes	Scorpaenidae	*Sebastes babcocki*
Chordata: Osteichthyes	Scorpaenidae	*Sebastes crameri*
Chordata: Osteichthyes	Scorpaenidae	*Sebastes elongatus*
Chordata: Osteichthyes	Scorpaenidae	*Sebastes helvomaculatus*
Chordata: Osteichthyes	Scorpaenidae	*Sebastes* sp.
Chordata: Osteichthyes	Scorpaenidae	*Sebastolobus* sp.
Chordata: Osteichthyes	Stichaeidae	Unidentified Stichaeidae
Cnidaria: Anthozoa	Actiniidae	*Cribrinopsis fernaldi*
Cnidaria: Anthozoa	Metridiidae	*Metridium giganteum*
Cnidaria: Anthozoa	Cerianthidae	*Pachycerianthus* sp.
Cnidaria: Anthozoa	Caryophylliidae	Poss. *Lophelia californica*
Echinodermata: Asteroidea	Asterinidae	*Asterina miniata*
Echinodermata: Asteroidea	Goniasteridae	*Ceramaster patagonicus*
Echinodermata: Asteroidea	Goniasteridae	*Ceramaster* sp.
Echinodermata: Asteroidea	Radiasteridae	*Gephyreaster swifti*
Echinodermata: Asteroidea	Echinasterida	*Henricia* sp.
Echinodermata: Asteroidea	Luidiidae	*Luidia foliolata*
Echinodermata: Asteroidea	Poraniidae	*Porianopsis inflatus inflatus*
Echinodermata: Asteroidea	Pterasteridae	*Pteraster tesselatus*
Echinodermata: Echinoidea	Strongylocentrotidae	*Allocentrotus* sp.
Echinodermata: Holothuroidea	Stichopodidae	*Parastichopus leukothele*
Echinodermata: Ophiuroidea	Ophiuroids	Class Ophiuroidea
Mollusca: Cephalopoda	Octopodidae	*Octopus* sp.
Mollusca: Gastropoda	Cymatiidae	*Fusitriton oregonensis*
Porifera: Demospongiae	Demosponge 1	Likely Desmacellidae
Porifera: Demospongiae	Pachastrellidae	*Vulcanella tenuilaminaris*
Porifera: Hexactinellida	Rossellidae	Unidentified Rossellid

APPENDIX II: Species list for grab samples from cruise PGC02004. Used in polychaete diversity analyses.

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Ampharetidae	*Amage anops* (Johnson, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Ampharete finmarchica* (Sars, 1864)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Amphicteis mucronata* Moore, 1923	0	0	1	1	2	0	0	0	0	5	2	0	0	2	0	3	0	1	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ampharetidae	*Amphicteis* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ampharetidae	*Amphisamytha bioculata* (Moore, 1906)	3	0	0	0	0	0	0	0	0	3	0	0	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Anobothrus gracilis* (Malmgren, 1866)	0	3	0	2	0	0	1	0	0	0	0	0	4	2	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ampharetidae	*Eclysippe*? sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Lysippe labiata* Malmgren, 1866	0	0	0	0	0	0	0	1	0	3	2	0	3	0	0	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Lysippe mexicana*?	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Melinna cristata* (M. Sars, 1851)	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ampharetidae	*Melinna elisabethae* McIntosh, 1922	0	0	0	1	0	0	0	0	0	1	0	0	3	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Capitellidae	*Mediomastus* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitellidae	*Notomastus giganteus* Moore, 1906	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Capitellidae	*Notomastus tenuis* Moore, 1909	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Cirratulidae	*Monticellina tesselata*?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Cirratulidae	*Tharyx multifilis* Moore, 1909	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cossuridae	*Cossura bansei*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphrosinidae	*Euphrosine arctica* Johnson, 1897	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Glyceridae	*Glycera capitata* Oersted, 1843	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Glyceridae	*Glycera tesselata* Grube, 1863	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Goniadidae	*Glycinde armigera* (Moore, 1911)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0	0	1	0	0	
Goniadidae	*Glycinde picta* (Berkley, 1927)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Goniadidae	*Goniada brunnea* (Treadwell, 1906)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Goniadidae	*Goniada maculata* (Oersted, 1843)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineridae	*Lumbrinereis luti* Berkeley & Berkeley, 1945	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0
Lumbrineridae	*Lumbrinereis* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineridae	*Lumbrinereis zonata* (Johnson, 1901)	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Lumbrineridae	*Ninoe gemmea* Moore, 1911	1	1	0	1	0	0	0	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0
Maldanidae	*Asychis similis* (Moore, 1906)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Axiothella rubrocincta* (Johnson, 1901)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Maldanidae	*Clymenura columbiana* (Berkeley, 1929)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Maldanidae	*Euclymene reticulata* Moore, 1923	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Euclymene zonalis* (Verrill, 1874)	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Maldane sarsi sarsi* Malmgren, 1865	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Maldane* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Maldanidae	*Maldanella harai* (Izuka, 1902)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Maldanidae	*Micromaldane ornithochaeta* ?	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Nicomache lumbricalis* (Fabricius, 1780)	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Notoproctus pacificus* (Moore, 1906)	0	0	2	6	1	5	0	1	0	0	0	0	0	1	1	3	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0
Maldanidae	*Notoproctus* sp. A	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Paxillura* sp. A	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Petaloproctus tenuis borealis* Arwidsson, 1907	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Maldanidae	*Praxillella affinis affinis* (Sars, 1872)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Maldanidae	*Praxillella affinis pacificus* Berkeley, 1929	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Praxillella gracilis* (Sars, 1861)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Maldanidae	*Praxillella praetermissa* (Malmgren, 1866)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtyidae	*Aglaophamus rubella anops* Hartman, 1950	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nereididae	*Cheilonereis* poss. *cyclurus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae	*Nereis procera* Ehlers, 1868	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae	*Nereis* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae	*Nereis wailesi* Berkeley & Berkeley, 1954	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae	*Nereis zonata* Malmgren, 1867	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereididae	*Platynereis bicanaliculata* (Baird, 1868)	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oenonidae	*Drilonereis longa* Webster, 1879	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oenonidae	*Drilonereis* nr. *falcata*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onuphidae	*Onuphis geophiliformis* (Moore, 1903)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onuphidae	*Onuphis iridescens* (Johnson, 1901)	1	5	2	3	2	0	2	2	0	0	0	8	1	0	1	1	3	2	0	0	0	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Onuphidae	*Onuphis* poss. *affinis*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Oweniidae	*Myriochele oculata* Zachs, 1923	0	1	0	3	4	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oweniidae	*Owenia fusiformis* delle Chiaje, 1841	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Paraonidae	*Aricidea simplex* (Day, 1963)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paraonidae	*Paraonella platybranchia* (Hartman, 1961)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinariidae	*Pectinaria californiensis* Hartman, 1941	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pectinariidae	*Pectinaria moorei* Annenkova, 1929	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phyllodocidae	*Clavadoce* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	*Eteone* sp. A	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	*Eteone* sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	*Phyllodoce medipapillata* Moore, 1909	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Polynoidae	*Lepidonotus squamatus* (Linnaeus, 1767)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Polynoidae	PolyGenus A sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0
Questidae	*Questa caudicirra* Hartman, 1966	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellariidae	*Idanthyrsus ornamentatus* Chamberlain, 1919	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	*Eudistylia catharinae* Banse, 1979	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	*Potamilla intermedia* Moore, 1905	0	5	2	0	4	0	0	3	0	2	0	2	3	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Sabellidae	*Potamilla myriops* Marenzeller, 1884	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Sabellidae	*Potamilla neglecta* (M. Sars, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sabellidae	*Sabella media* (Bush, 1904)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	*Sabellastarte* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	*Sabellastarte* sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	SabGenus A sp. A	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scalibregmatidae	*Asclerocheilus beringianus* Ushakov, 1955	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Scalibregmatidae	*Scalibregma inflatum* Rathke, 1843	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Spionidae	*Laonice cirrata* (Sars, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	
Spionidae	*Prionospio steenstrupi* Malmgren, 1867	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Spionidae	*Spiophanes* sp. A	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Sternapsidae	*Sternaspis fosser* Stimpson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Sternapsidae	*Sternaspis* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
Syllidae	*Exogone dwisula*?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Syllidae	*Haplosyllis spongicola spongicola* (Grube, 1855)	0	0	2	0	1	0	0	0	0	1	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Syllidae	*Odontosyllis phosphorea* Moore, 1909	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Syllidae	*Sphaerosyllis pirifera* Claparede, 1868	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	

Family	Species	32ab	33ab	34ab	35a	36a	37ab	38ab	39ab	41a	41bb	42b	43ab	44ab	45b	46ab	47ab	48ab	49a	50b	51b	52b	53b	55b	56b	83ab	85a	85b1	87a	92	94b	96	98	99	100	101	102	103	104	105	106
Terebellidae	*Amaena occidentalis* (Hartman, 1944)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Terebellidae	*Artacama conifera* Moore, 1905	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellidae	*Neoamphitrite robusta* (Johnson, 1901)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellidae	*Pista cristata* (O.F. Muller, 1776)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Terebellidae	*Pista hansei* Saphronova, 1988	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellidae	*Polycirrus* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Terebellidae	*Polycirrus* sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Terebellidae	*Scionella* sp. A	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Terebellidae	TereGen. A sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Terebellidae	*Thelepus japonicus* Marenzeller, 1884	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellidae	*Thelepus setosus* (Quatrefages, 1865)	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Trichobranchidae	*Terebellides* sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichobranchidae	*Terebellides stroemi* M. Sars, 1835	0	0	0	1	0	0	0	1	0	1	0	4	4	0	0	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Trichobranchidae	*Trichobranchus glacialis* Malmgren, 1866	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0