

**THE EFFECTS OF TRAWLING ON BENTHIC HABITATS: AN ANALYSIS OF
RECOVERY IN THE WESTERN GULF OF MAINE CLOSURE**

By

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Thesis Advisor: Dr. Leslie Watling

An Abstract of the Thesis Presented
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Otter trawling, a common method to catch commercially valuable groundfish, has been shown to reduce benthic habitat complexity by the direct reduction of abundance levels of epifaunal and infaunal species. Such reductions in benthic biodiversity may have long-term consequences for ecosystem resilience and function of benthic habitats. In the Gulf of Maine, in order to address concerns of declining groundfish stocks while simultaneously conserving benthic habitats, marine protected areas (MPA) have been designated that restrict groundfish trawling. One such MPA, the Western Gulf of Maine Closure (WGOMC), encompasses regions that, as of 2004, had been closed to trawling for 6 and 4 years, respectively. Such a time frame allows the question, how have benthic communities responded to the cessation of chronic groundfish trawling? To address this question, an observational study was conducted where the community composition of coarse sediments in the WGOMC at different times were compared to coarse sediment community composition of an actively trawled fishing ground (the Kettle) at a similar depth. Video transects of epifaunal communities were taken in the WGOMC in August

2002 (2-year closed sites). Video transects of the epifaunal community and grab samples of the infaunal community were taken in the Kettle in August of 2003 (Open 2003), and resampled in August 2004 (Open 2004). Finally, video transects and grab samples were taken again in the WGOMC in August 2004 in what were the 2-year closed sites (now the 4-year closed sites), and in the 6-year closed region of the WGOMC (6-year closed sites). Multivariate analysis showed significant differences in benthic community composition between the Kettle and the WGOMC which could be attributed to the cessation of chronic trawling disturbance. In general, benthic communities in the Kettle were dominated by more disturbance tolerant, opportunistic families, while communities in the WGOMC were dominated by more disturbance intolerant, sessile families.

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INTRODUCTION

The direct effects of mobile fishing gear on continental shelf benthic communities have been well documented (Dayton *et al.* 1995; Auster *et al.* 1996; Jennings and Kaiser 1998; Auster and Langton 1999; Watling and Norse 1998; Hall 1999; Kaiser and de Groot 2000). Trawling has been shown to reduce biotic habitat complexity by removing sensitive organisms, resulting in a loss of biological and structural diversity. However, the long-term effects of biodiversity loss on ecosystem function in subtidal coarse bottoms remains largely unknown. While the acute impacts of trawling appear to be a good predictor of the cumulative impacts of chronic trawling (Auster and Langton 1999), there are few data on how impacted communities will change in composition and abundances over time following the cessation of trawling. Given the growing appreciation of the value of biodiversity as essential to the health of marine ecosystems (Bengtsson *et al.* 1997; Costanza *et al.* 1997; Freckman *et al.* 1997; Gray 1997; Schlapfer and Schmid 1999), there is now a growing need to understand and sustain biodiversity as a part of any fisheries management plan.

Biodiversity has been found to be positively associated with habitat complexity (Tokeshi 1999). Habitat complexity has two components, 1. habitat heterogeneity, or the patchiness of habitat types across a seascape, and 2. habitat structure, or the physical or architectural structure of a habitat. Abiotic structure in benthic habitats, such as rocks and boulders, increases the surface area of available attachment space for sessile epifauna such as corals, sponges, brachiopods, and bryozoans. The presence of sessile epifauna then increases microhabitat diversity through added vertical relief, which attracts symbionts that utilize various parts of epifaunal growth forms or colonies. Sessile

epifauna and abiotic structures also create spaces within and between them that increase shelter space resulting in patches of inquilinous species that otherwise, could not coexist (Huffaker 1958).

Infaunal species enhance biodiversity by increasing heterogeneity within the sediments. For example, the movements of infauna through the sediments can create resource patchiness by altering chemical gradients. Bioturbating infauna may also regulate the release of ammonium back into the water column, an essential nutrient for photosynthesis. The presence of worm tubes near the sediment-water interface creates three dimensional structures on the surface of mixed sediments, and provides refuge to free-living infauna from predation (Woodin 1981; Auster *et al.* 1997). Oxygen content and penetration depth into the sediments is also deeper in the area of the tubes themselves (Aller 1982; Reise 1987; Meyers *et al.* 1987).

The complexity of benthic habitats can then provide ecosystem services to higher trophic levels. Firstly, the presence of structure provides refuge for benthic predators from which they entrap their prey. Refuge plays a large role in the strength of the link between benthic habitats and demersal fish because infaunal and inquilinous species serve as important prey items for adult demersal fish. Secondly, the presence of structure decreases the vulnerability of 0-year fish to predation (Lough *et al.* 1989; Tupper and Boutilier 1995a, b; Collie *et al.* 1997; Lindholm *et al.* 1999;). In such cases, habitat structures whose interstices are small relative to predator body size confer excellent refuges for 0-year fish and other such prey species (Bell and Woodin 1984; Witman 1985).

Trawling may reduce the structural and biological complexity of subtidal benthic habitats more than any other disturbance, natural or anthropogenic, in areas that are heavily fished and deeper than storm surge (Watling and Norse 1998). Subtidal coarse bottoms are often highly diverse, because they are generally dominated by organisms that enhance habitat complexity such as upright sessile epifauna and tube-builders (Collie et al. 1997). Such organisms are often more vulnerable to disturbance, thus trawling may jeopardize long-term ecosystem function by selecting against those organisms that play the greatest role in enhancing biodiversity. To assess the abilities of these organisms to fulfill their roles in ecosystem function, species richness and population abundances must be considered. If resident populations of seafloor communities are so low they are beyond the threshold at which they are able to fulfill their ecosystem roles, they can be considered functionally extinct (Thrush and Dayton 2002). Furthermore, many of the species that add to the physical structure of a given habitat, and some that benefit from added structure, show positive density-dependent population dynamics. Whether or not communities on and within coarse bottoms are anywhere near functional extinction is unknown. In fact, little is known about ecosystem function in these environments prior to trawling.

In order to detect how communities may change following the cessation of trawling, studies must address the connection between habitat complexity and diversity over time. The spatial and temporal patterns of recovery in communities after fishing will be variable, depending on biological and physical characteristics of the environment under study (Auster and Langton 1999). The ecological roles that component organisms play are determined by attributes of the resident species themselves as exhibited by their life

histories, interactions between component species and broad-scale and local chemical and physical dynamics, and interactions between different species populations, such as competition for food and space. These community dynamics then make up the provision of ecosystem services available to higher trophic levels such as demersal fish, which function in the ecosystem as large predators.

In this study, changes in the composition of benthic communities were investigated on and within coarse sediments at different times following the cessation of trawling in the WGOMC, a habitat MPA. Changes in benthic community composition from sites in the WGOMC were assessed by comparing current community states in regions of the WGOMC that have been closed to trawling for different amounts of time to sites of similar substrate and depth in the Kettle, an actively trawled fishing ground. Because sediment type and depth of sampling sites were comparable and greater than what is affected by storm surge, differences in benthic community composition and abundances that could be attributed to release from chronic trawling disturbance were anticipated.

A meta-analysis conducted on results of 39 published fishing impact studies by Collie *et al.* (2000b) found that the total number of individuals in actively trawled areas are most reduced in more stable biogenic habitat types, namely coarse sediments of gravel, mud, and sand with interspersed stones and boulders. Among infaunal communities, increases in diversity in the 4- and 6-year closed sites were not expected as much as shifts in community dominance from more disturbance tolerant, mobile, opportunistic families in the Kettle to sessile, slower-reproducing families in the WGOMC. Sessile polychaetes and crustaceans stabilize sediments by creating semi-permanent tubes near the sediment-water interface. Not only do these organisms tend to

have longer life spans than more mobile families of the same class, they also spend most of their lives in their tubes and reproduce less often, which makes them more vulnerable to direct damage from trawls, and less likely to recover in the interim between frequent trawling disturbances (Jenkins *et al.* 2001).

Among epifaunal assemblages, community states in the 6-year closed sites were expected to differ significantly from not only the Kettle, but also the 2-year closed sites, which were sampled again 2 years later when the same region had been closed for 4 years (4-year closed sites). Epifaunal communities of coarse sediment types often support a wide variety of attached sessile groups such as poriferans, cnidarians, bryozoans, brachiopods, and tunicates, as well as many mobile groups such as various crabs, shrimp, and sea stars. Sessile upright epifauna such as poriferans and anthozoans, which can dominate on coarse sediments, are vulnerable to direct damage from trawls (Lindholm *et al.* 2004), especially branched growth forms of porifera (Sainsbury 1993; Sousa 2001; Wassenberg 2002). Poriferans also exhibit no escape response, unlike some anthozoans, such as *Cerianthis*, which can retreat into its tube when disturbed. Life history strategies of poriferans indicate that communities of these organisms may take years to fully recover, thus evidence of recovery was not anticipated until the 6-year closed sites (Bergman *et al.* 2000; Collie *et al.* 2000a; Collie *et al.* 2005).

Human activities such as groundfishing have altered continental shelf seafloor habitats for a long time, and consequently there are few bottom areas that can be deemed pristine, or “natural”. The widespread use of trawls to catch demersal fish thus challenges scientists to identify ecological thresholds without an undisturbed reference for comparison. On the most basic level, the recovery of any ecosystem from disturbance

depends on the temporal and spatial constraints that disturbance imposes on recovery processes. If the frequency of disturbance is greater than the time it takes the system to recover, and a large proportion of seascape is affected, the community may cross a threshold and become unstable, and shift into a different trajectory (Turner *et al.* 1993; Thrush and Dayton 2002; Thrush *et al.* 2005). In ecological theory, community recovery via succession implies a predictable progression of species composition and abundance until a climax community state is reached (Connell 1989; Bell *et al.* 1991). However, if the ratio of disturbed to undisturbed area is too large, shifts in local community states may be disturbance mediated and lottery based, which can result in shifts that are unpredictable because they are based on a pool of recruits available in the water column at the time that niche space is available (Horn 1976; Auster and Langton 1999). In essence, how much is too much, and how does the system respond following the cessation of chronic trawling disturbance? With this project, changes in family diversity and abundances following the cessation of trawling disturbance, one aspect of the structural component of ecosystem function, were addressed.

METHODS

Study Site Location and Description

The Western Gulf of Maine Closure (WGOMC) is located in the southwestern region of the Gulf of Maine, running from 43°15'N latitude south to 42°15'N, and west to east from longitude 70°15'W to 69°45'W (Figure 1). As of May 2004, it had been closed a little over 6 years west of the 70° line, and 4 years east of the 70° line. The 6-year region of the WGOMC was initially established May 1, 1998 with the sole purpose of conserving depleted demersal fish stocks by the New England Fisheries Management

Council as part of Framework Adjustment 25 to the Northeast Multi-species Fishery Management Plan. At that time, mobile bottom tending gear and gill netting were banned within the closure, with the exception of shrimp trawls. In May 2000, the 4-year region of the WGOMC was established with the same fishing restrictions as the 6-year region. In May 2004, the entire WGOMC was reclassified as a habitat closure with the expressed purpose of not only conserving demersal fish stocks, but also allowing recovery of benthic habitats that may have been affected by past trawling. Currently, all mobile bottom tending gear, including shrimp trawls and gill netting, are banned, and as a habitat closure, the WGOMC is now closed to groundfishing indefinitely, rather than until depleted demersal fish stocks recover. Worth noting, however, is that lobster traps, mid-water trawls, research bottom trawling, and recreational fishing have always been, and are still, permitted in the WGOMC.

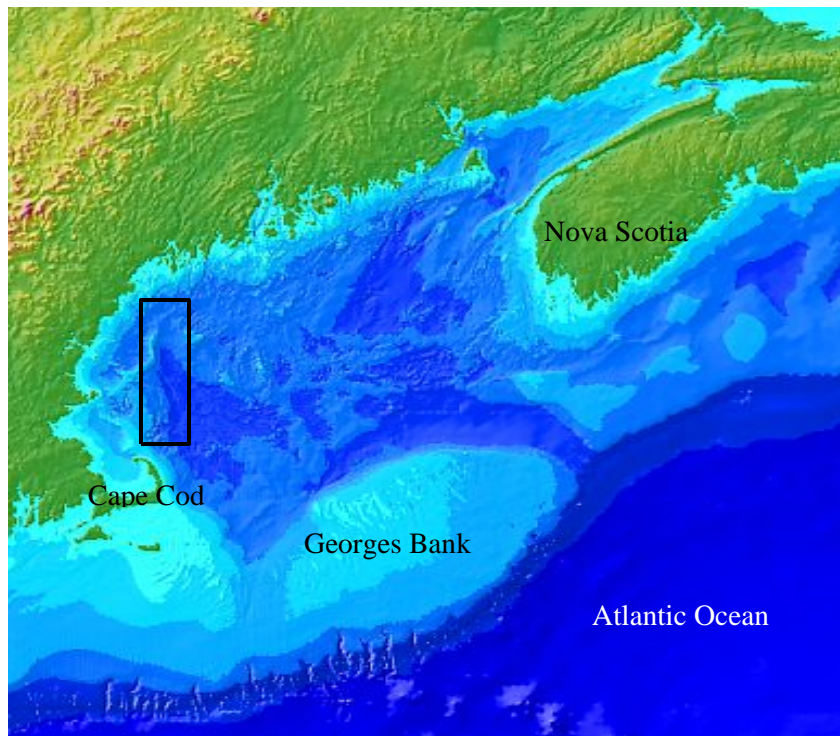


Figure 1. Map of the Gulf of Maine, boxed area represents the Western Gulf of Maine Closure.

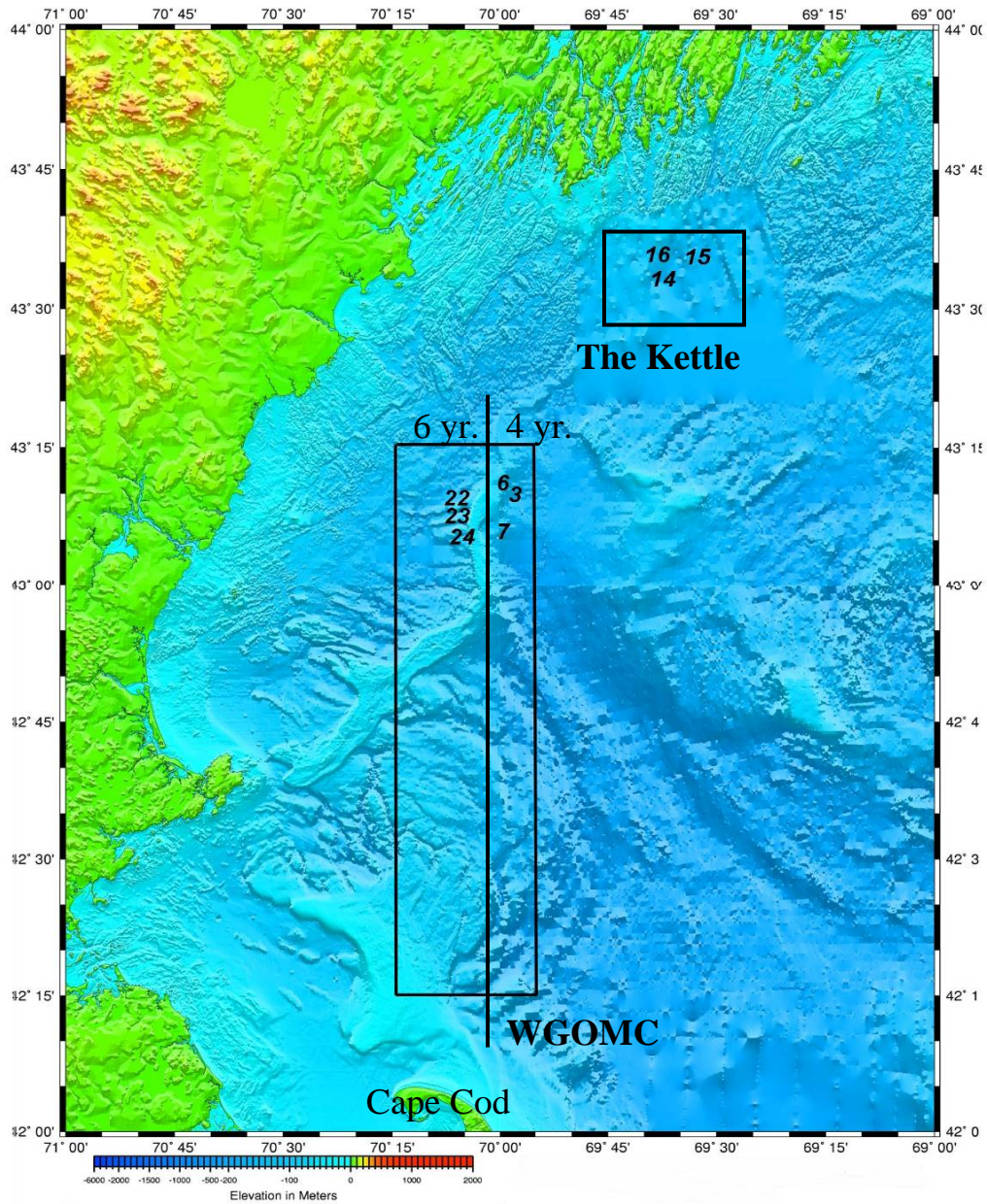


Figure 2. Study sites: WGOMC: sites west of the 70° line had been closed for 6 years, sites east of the 70° line had been closed 4 years. The Kettle: sites located roughly 16 nautical miles northeast of sites in the WGOMC.

Study Design

This study was an observational field study conducted using a block design where the treatment variable, the presence of demersal fish trawling, was assigned with *a priori* knowledge of fishing activity (Van Dolah et al. 1987; Riemann and Hoffman 1991).

Study sites in the WGOMC were located in the northern region of the closure surrounding Jeffrey's Ledge (Figure 2), a rocky outcrop that runs from the northern tip through the mid-region of the WGOMC. Study sites on the eastern side of Jeffrey's Ledge were also east of the 70° line within the closure, therefore in the 4-year region of the WGOMC. Study sites on the western side of Jeffrey's Ledge were also west of the 70° line within the closure, therefore in the 6-year region of the WGOMC. All actively trawled study sites were located in a fishing ground known as the Kettle. Study sites were chosen based on three criteria: 1. substrate type, 2. depth, and 3. fishing activity. Sediment type sampled was a coarse mix of gravel, mud, and sand with interspersed stones and boulders. To avoid the potentially confounding effects of winter storm surge on results, all study sites were located between 100 – 130 m depth. Study sites in the WGOMC, prior to being closed in May, 1998, were within formerly productive fishing grounds frequently targeted by fishermen. The Kettle is an historic fishing ground that continues to be fished intensely. Study sites in both the WGOMC and the Kettle specifically were chosen based on recommendations by Cameron McClellan, a fifth generation fisherman and Captain of F/V *Adventurer*, who, along with much of the downeast Maine groundfishing fleet, used to fish study sites in the WGOMC, and currently fishes study sites in the Kettle.

Sampling of study sites began in August of 2002, and continued each August through 2004. In August of 2002 in the WGOMC, the region west of the 70° line had been closed for 4 years, and east of the 70° line had been closed for 2 years. The first 2 summers of the sampling regime were spent attempting to properly survey benthic communities in an attempt to find study sites that would match the above stated sampling criteria. The goal of this sampling strategy was to obtain multiple samples of the infaunal and epifaunal components of benthic communities in order to encompass as much of the natural variation within benthic populations as possible (Thrush *et al.* 2001). Within each region, sites were identified where it would be possible to take at least three video transects with one grab sample nested in each transect (Table 1).

Table 1. Sampling sites, treatment levels, and community component sampled each August from 2002 through 2004.

Sampling Sites	Treatment levels	Sampled for:	Sites (figure 2)	Year Sampled:
Open 2003	Trawled	Epifauna/Infauna	14, 15, 16	Aug. 2003
Open 2004	Trawled	Epifauna/Infauna	14, 15, 16	Aug. 2004
2-yr closed sites	Untrawled	Epifauna	6, 3, 7	Aug. 2002
4-yr closed sites	Untrawled	Epifauna/Infauna	6, 3, 7	Aug. 2004
6-yr closed sites	Untrawled	Epifauna/Infauna	22,23, 24	Aug. 2004

In August of 2002, video transects of the epifaunal component of benthic communities of 3 study sites in the 2-year region of the WGOMC (sites 6, 3, and 7) were performed. In August of 2003, infaunal and epifaunal components of benthic communities of 3 study sites in the Kettle (sites 14, 15, and 16) were surveyed. Finally, in August of 2004 the infaunal and epifaunal components of all previously sampled study sites in the Kettle and the WGOMC (sites 3, 6, 7, 14, 15, and 16) were resampled, with sites 3, 6, and 7 in the WGOMC then having been closed to groundfishing for 4 years rather than just 2. Resampling all previously sampled sites would also allow consideration of possible year effects on population dynamics of resident families. Furthermore, in August of 2004, the

infaunal and epifaunal components of 3 study sites (sites 22, 23, and 24) located in the 6-year region of the WGOMC were also sampled.

Each study site of all regions sampled consisted of 3 sampling stations; each station comprising one video transect of the epifaunal community, and one grab sample of the infaunal community taken at the same location of that video transect, with the exception of the 2-year region of the WGOMC. The 2-year region of the WGOMC, sampled in August 2002, was only sampled for epifauna; therefore each study site consisted of 3 video transect stations only.

Sampling of the Benthic Community

A 0.1-m² Smith-McIntyre bottom grab was used to collect sediment samples. Grab samples were sieved into a 500 micron sieve and preserved in 10% buffered formalin solution. Upon return to the lab all samples were transferred into 70% ethyl alcohol. Infauna were identified to the level of family and enumerated for each sample.

The Phantom 300 remotely operated vehicle (ROV: Deep Ocean Engineering, San Leandro, California) was used to conduct all video transects. The ROV was configured to collect video, which were recorded onto mini-DV format tapes aboard the ship. While the ship was anchored, transects were recorded at each station that were approximately 10 to 15 minutes in length. In order to get the ROV to the bottom, a drop weight was attached to the tether approximately 100 feet from the ROV itself. Once on the bottom, the ROV had roughly 50 feet to roam, and the ROV was driven with its skid bars in contact with the bottom as much as possible in a lawn-mower type fashion back and forth over the bottom. Upon return to the lab, organisms were identified to lowest taxonomic

level possible and enumerated in all non-overlapping frames where the ROV was on the bottom (Auster *et al.* 1988).

Grain-size analysis

Approximately 10 g of sediment was collected from the upper 5 cm of the surface of each bottom grab in the 6-year closed sites and Open 2004. Particle size analysis was carried out following Folk (1973). In the laboratory, each sample was rinsed and homogenized, then shaken and centrifuged at 23,400 RCF for 15 minutes to remove salts and disaggregate the sediment grains. Samples were then put through a series of wet sieves to separate out the gravel (>2mm) and sand (>62.5 microns) fractions and to collect the mud (<62.5 microns) fraction. Gravel and sand fractions were placed in the oven to dry (110°C) for 24 h. To separate silt and clay, each mud fraction was placed into a 1 L graduated cylinder, and brought up to 1 L with 0.002 M solution sodium pyrophosphate. Solutions were then homogenized, and 20 ml of the suspension was immediately removed using a pipette and placed in the oven to dry. This portion represented the weight of silt + clay in 1 L of suspension. Using Stokes's law and Waddell's shape correction, the settling velocity of clay (2 microns) was obtained as $2.3 \times 10^{-4} \text{ cm s}^{-1}$ at 22°C. Using this settling velocity, the time for clay particles to settle 5 cm was calculated as 3.42 h. After 3.42 h, a second 20-ml aliquot was taken 5 cm deep from each cylinder, and placed into the oven to dry. This portion represented the weight of clay in 1 L of solution. Dry weights were used to calculate percent gravel, sand, silt and clay in each sample.

Multivariate Analysis

The multivariate statistical package PRIMER 5.0 (Clarke and Warwick 1994) was used to analyze both infaunal and epifaunal data. Non-metric multidimensional scaling (MDS) using the Bray-Curtis similarity coefficient was applied to fourth-root-transformed infaunal abundance data to indicate patterns in community assemblages. The fourth-root transformation was used to lessen the contribution of a few very abundant taxa and weight more heavily the rarer taxa. No transformation was applied to epifaunal abundances, however numbers were standardized to 50 sequential frames due to unequal number of frames in some transects.

A one-way analysis of similarities (ANOSIM) was performed to test the significance of the effects of the treatment factor on population abundances. The treatment factor levels were determined by fishing history. For infaunal community data, treatment factor levels were: 1.) Open 2003, referring to samples taken from the Kettle in August 2003, 2.) Open 2004, referring to sites resampled in the Kettle in August 2004, 3.) the 4-year closed sites, referring to sites sampled in the 4-year region of the WGOMC, and 4.) the 6-year closed sites, referring to sites sampled in the 6-year region of the WGOMC. For epifaunal community data, treatment factor levels included all above stated study sites as well as the 2-year closed sites, referring to sites sampled in the WGOMC in August 2002, when east of the 70° line within the closure had only been restricted for 2 years. When a significant difference ($p < 0.05$) was detected, a similarity percentage breakdown (SIMPER) was conducted to determine which taxa were primarily responsible (make up 90% of the difference between factor levels) for the observed

differences. Research into family life histories of significantly abundant taxa was done to interpret the results of the SIMPER breakdown.

Univariate analysis

The PRIMER function DIVERSE was used to calculate taxonomic richness (s), taxon abundance (N), Pielou's evenness (J'), and Shannon-Wiener diversity ($H'(\log e)$) for each sample.

RESULTS

Infauna

A total of 41,472 individuals were sampled in all study sites. In Open 2003, 10,261 individuals were sampled, in Open 2004, 10,234 were sampled, in the 4-year closed sites, 9,447 individuals were sampled, and in the 6-year closed sites, 11,530 individuals were sampled. Individuals were identified to the family level (71 families) with the exception of five groups (Oligochaetes, Caprellid, Tanaidacea, Sipunculida, and Chaetodermomorpha). All sites were dominated by annelids (Open 2003: 69%; Open 2004: 60%; 4-yr closed: 64%; 6-yr closed: 60%). Following annelids, Closed sites were dominated by molluscs (4-yr closed: 13%; 6-yr closed: 14%), then arthropods (4-yr closed: 11%; 6-yr closed: 13%), while Open sites were dominated by arthropods (Open 2003: 13%; Open 2004: 23%), then molluscs (Open 2003: 8%; Open 2004: 7%).

Univariate Diversity Indices

Univariate diversity indices were calculated to recognize overall differences in community attributes (see Appendix D). Overall, the 6-year closed sites showed the highest average taxonomic richness, abundance, and dominance (Table 2), while Open 2004 showed the highest average taxonomic evenness and diversity (Table 3).

Table 2. Ranked average diversity indices for taxonomic richness, abundance, and dominance.

	Richness		Abundance		Dominance
	S		N		d
6-yr cl	40.89	6-yr cl	1281.1	6-yr cl	5.58
4-yr cl	38.22	Open '03	1140.1	4-yr cl	5.37
Open '04	34.5	Open '04	1111.1	Open '04	4.78
Open '03	30.89	4-yr cl	10.49.7	Open '03	4.27

Table 3. Ranked average diversity indices for taxonomic evenness and diversity.

	Evenness		Diversity
	J'		H'(loge)
Open '04	0.71	Open '04	2.49
Open '03	0.69	4-yr cl	2.44
4-yr cl	0.67	6-yr cl	2.42
6-yr cl	0.65	Open '03	2.37

Multivariate Analyses

A 2-D, non-metric, multidimensional scaling (MDS) plot of infaunal familial and group abundance similarities, sorted by treatment, indicated that the communities could be separated based on treatment group (Figure 3).

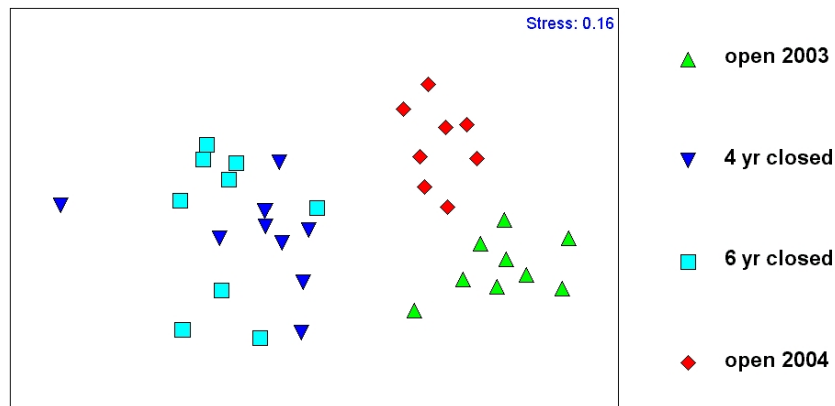


Figure 3. Non-metric multidimensional scaling (MDS) ordination for infaunal community assemblages based on Bray-Curtis similarity coefficient of 4th root-transformed abundances.

A one-way ANOSIM indicated the separation based on treatment to be significant ($R = 0.759$; $p = 0.001$). Pairwise tests (Table 4) indicated that while Open 2003 and Open 2004 were significantly different, they were more similar to each other in taxon composition and abundance than to either the 4- or 6-year closed sites. Pairwise tests also indicated a significant difference between the 4- and 6-year closed sites; however, they were more similar to each other in taxon composition and abundance than to either Open 2003 or Open 2004 sites.

Table 4. Pairwise comparisons of infaunal community assemblages. Lower half of the triangle matrix contains ANOSIM values while upper half contains corresponding p values.

Groups	Open 2003	Open 2004	4 yr closed	6 yr closed
Open 2003		0.001	0.001	0.001
Open 2004	0.636		0.001	0.001
4 yr closed	0.916	0.839		0.004
6 yr closed	0.961	0.951	0.252	

SIMPER analysis of similarity (see Appendix B) between stations within sites used average abundances of all taxa that contributed significantly and consistently to the composition of communities in each area sampled. All significantly contributing taxa were then divided into three abundance groups for organizational purposes. High abundance taxa (community dominants) were those that averaged >100 individuals/sample; moderate abundance taxa were those that averaged 10-100 individuals/sample, and low abundance taxa were those that averaged 1-10 individuals/sample. The number of taxa making up each group were then enumerated (Figure 4). A large number of taxa contributed significantly to the composition of communities in each area; the purpose of dividing these taxa by average abundances was

to better organize the taxa into generalized groups that might give an abundance context in which to place taxa when named throughout the paper.

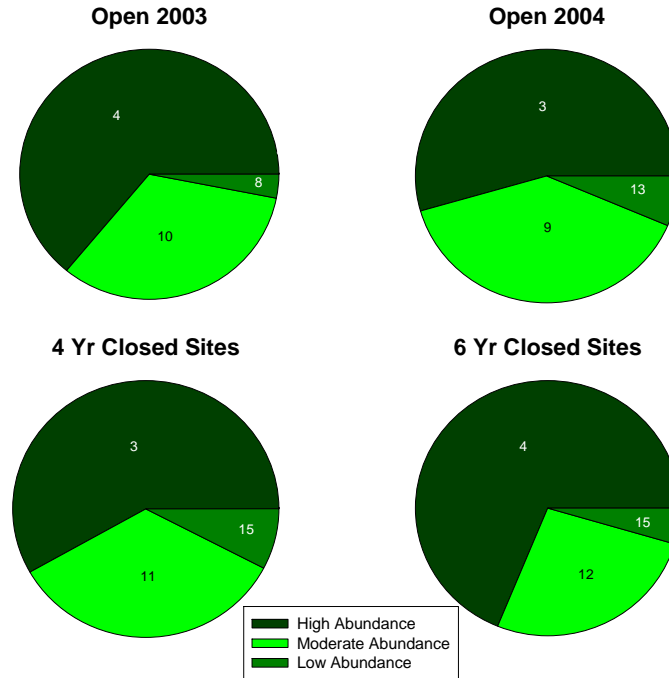


Figure 4. Breakdown of average abundances of taxa that significantly contributed to community composition into High abundance (on average >100 individuals/sample), Moderate abundance (on average 10-99 individuals/sample), and Low abundance (on average 1-9 individuals/sample) groups at all study sites. Numbers represent number of taxa making up each group.

The high abundance group was dominated by 3 or 4 families of polychaetes in each area, however different families dominated based on treatment. Open 2003 and Open 2004 were largely dominated by the polychaete family Spionidae, while the 4- and 6-year closed sites were largely dominated by the polychaete family Sabellidae. High contributions to the moderate abundance group of Open 2003 and Open 2004 were made by the polychaete Lumbrineridae, and the crustacean Halacaridae. At corresponding contributions in the moderate abundance group of the 6- and 4-year closed sites were the polychaetes Maldanidae and Paraonidae, and the bivalve Astartidae. There was roughly

double the number of low abundance taxa in the 4- and 6-year closed sites and Open 2004, as there was in Open 2003. The low abundance group of Open 2003 was dominated by the crustaceans Tanaidacea and Leuconidae, and the polychaete Nereididae. Open 2004 and the 4- and 6-year closed sites included these families, as well as the crustaceans Isaeidae, Munnidae, and Stenothoidae in Open 2004, and the polychaetes Terebellidae, Goniadidae, Opheliidae, and Flabelligeridae, and the bivalve Cardiidae in the 4- and 6-year closed sites.

Taxa were divided into functional feeding groups based on past literature and general knowledge of the biological capabilities of all taxa present (Bousfield 1973; Fauchald and Jumars 1979; Ruppert, Fox, and Barnes 2004). Generalized definitions of feeding groups are listed in Table 5.

Table 5. Generalized definitions of infaunal functional feeding groups.

Non-selective deposit feeders	consume sediment in bulk
Selective deposit feeders	consume sediment but not in bulk
Carnivores	predators/scavengers of animal material
Suspension feeders	feed on suspended particles

When plotted by functional feeding groups, the 2-D, non-metric MDS also showed a separation of treatment groups (Figure 5), indicated to be significant by ANOSIM ($R = 0.578$; $p = 0.001$).

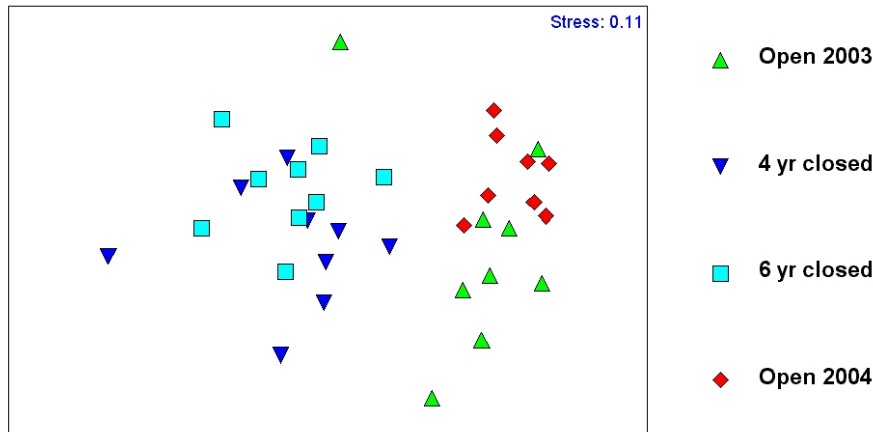


Figure 5. Non-metric multidimensional scaling (MDS) ordination for infaunal functional feeding group assemblages in open and closed sites (based on Bray-Curtis similarity coefficient of 4th root-transformed abundances).

Pairwise testing among treatment groups indicated significant differences between all groups along the lines of separation shown previously based on taxa (Figure 3; Table 4), however divisions between sites based on feeding groups were weaker between Open 2003 and Open 2004, and between the 6- and 4-year closed sites (Table 6).

Table 6. Pairwise comparisons of infaunal functional feeding groups. Lower half of the triangle matrix contains ANOSIM values while upper half contains corresponding p values.

Group	Open 2003	Open 2004	4 yr closed	6 yr closed
Open 2003		0.0026	0.001	0.001
Open 2004	0.173		0.001	0.001
4 yr closed	0.601	0.875		0.065
6 yr closed	0.751	0.937	0.123	

SIMPER analysis of similarity indicated that Open 2003 and Open 2004 were largely dominated by non-selective deposit feeders and carnivores. The 4- and 6-year closed sites were largely dominated by non-selective deposit feeders and suspension feeders (approximately 60% cum.), followed by carnivores and selective deposit feeders (Figure 6).

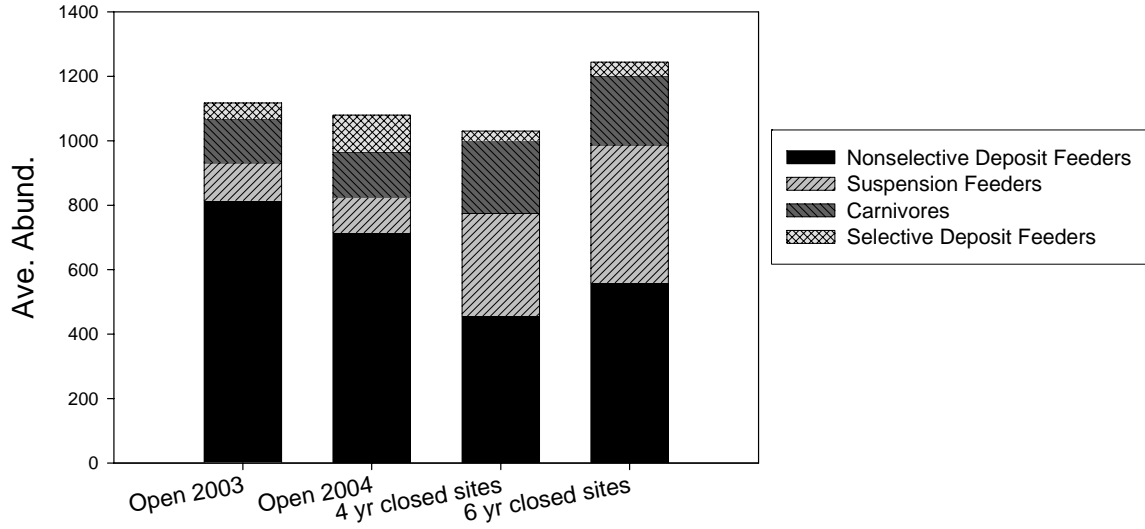


Figure 6. Shifts in feeding group dominance in infaunal community assemblages.

SIMPER analysis of dissimilarity (see Appendix C) was used to determine % contributions of taxa that significantly and consistently contributed to differences between all sampling sites. Between Open 2003 and Open 2004, 43 taxa made up approximately 90% of observed differences. No one group contributed more than 6% to observed differences. The largest contributions to differences between the two areas were made by moderate and low abundance taxa (Table 7).

Table 7. SIMPER analysis of dissimilarity, the top ten contributing taxa to community differences between Open 2003 and Open 2004.

Taxa		Open '03 Av. Ab.	Open '04 Av. Ab.	Contrib%	Cum%
Isaeidae	crustacean	0	6.25	5.24	5.24
Oligochaete	annelid	28.89	1.25	5.12	10.36
Caprellidea	crustacean	0	2.38	3.64	14
Mesodesmatidae	bivalve	0	3.75	3.62	17.62
Owenidae	polychaete	13	5.63	3.14	20.76
Stenothoidae	crustacean	0.33	2.25	3.11	23.87
Dorvilleidae	polychaete	4.22	9.38	2.76	26.64
Diastylidae	crustacean	2.11	6.88	2.61	29.25
Opheliidae	polychaete	4	2.5	2.59	31.84
Unciolidae	crustacean	1	0	2.57	34.41

Forty-seven taxa made up approximately 90% of the observed differences between communities in Open 2003 sites and 4-year closed sites, and 46 taxa made up approximately 90% of the differences between Open 2004 and the 4-year closed sites. A diversity of groups contributed to differences between the 4-year closed sites and the Open sites, with no one family contributing more than 5% to observed differences. For the most part, differences were made up by groups showing higher average abundances in the 4-year closed sites. The highest contribution to community differences between the Open sites and the 4-year closed sites was made by moderate and low abundance families (Tables 8, 9).

Table 8. SIMPER analysis of dissimilarity, the top ten contributing taxa to community differences between the 4-year closed sites and Open 2003.

		Open '03	4 yr cl		
Taxa		Av. Ab.	Av. Ab.	Contrib%	Cum%
Mesodesmatidae	bivalve	0	8.56	4.34	4.34
Oligochaete	annelid	28.89	0.44	3.95	8.29
Caprellid	crustacean	0	3.78	3.59	11.89
Spionidae	polychaete	297.89	70.33	3.43	15.31
Terebellidae	polychaete	1.33	8.33	3.14	18.45
Leuconidae	crustacean	4.44	0.11	3.09	21.53
Sabellidae	polychaete	82.33	260.33	2.92	24.46
Cuspidaridae	bivalve	0	2.78	2.76	27.22
Goniadidae	polychaete	0.22	2.78	2.48	29.69
Halacaridae	crustacean	42.89	10.67	2.42	32.12

Table 9. SIMPER analysis of dissimilarity, the top ten contributing taxa to community differences between the 4-year closed sites and Open 2004.

		4 yr cl	Open '04		
Taxa		Av. Ab.	Av. Ab.	Contrib%	Cum%
Halacaridae	crustacean	10.67	92.75	4.06	4.06
Terebellidae	polychaete	8.33	0.25	3.55	7.61
Munnidae	crustacean	0.22	5	3.3	10.92
Spionidae	polychaete	70.33	247.5	3.19	14.11
Sabellidae	polychaete	260.33	64.5	3.1	17.21
Leuconidae	crustacean	0.11	4.5	2.98	20.19
Isaeidae	crustacean	0.56	6.25	2.95	23.14
Stenothoidae	crustacean	0	2.25	2.93	26.06
Cuspidaridae	bivalve	2.78	0	2.89	28.95
Goniadidae	polychaete	2.78	0.13	2.79	31.74

Forty-eight taxa made up approximately 90% of the differences between communities in the 6-year closed sites and Open 2003, and between the 6-year closed sites and Open 2004. No one family contributed more than 5% to observed differences between the three areas. Unlike the 4-year closed sites vs. Open 2003 and Open 2004, where the highest contributors to community differences were moderate and low abundance groups, high abundance taxa contributed the highest percentages to community differences between the 6-year closed sites and the Open sites (Tables 10, 11).

Table 10. SIMPER analysis of dissimilarity, top ten contributing taxa to community differences between the 6-year closed sites and Open 2003.

Taxa		Open '03	6 yr cl	Contrib%	Cum%
		Av. Ab.	Av. Ab.		
Spionidae	polychaete	297.89	35.78	5.03	5.03
Sabellidae	polychaete	82.33	351.11	3.41	8.44
Caprellidea	crustacean	0	7.44	3.4	11.84
Arcidae	bivalve	0	3	3.12	14.96
Sipunculida	sipuncula	0.22	6.33	3.1	18.06
Oligochaete	annelid	28.89	3.67	3.03	21.1
Leuconidae	crustacean	4.44	0.33	2.78	23.87
Terebellidae	polychaete	1.33	4.89	2.63	26.5
Mesodesmatidae	bivalve	0	8.56	2.61	29.11
Goniadidae	polychaete	0.22	2.78	2.51	31.62

Table 11. SIMPER analysis of dissimilarity, top ten contributing taxa to community differences between the 6-year closed sites and Open 2004.

Taxa		6 yr cl	Open '04	Contrib%	Cum%
		Av. Ab.	Av. Ab.		
Spionidae	polychaete	35.78	247.5	4.82	4.82
Sabellidae	polychaete	351.11	64.5	3.62	8.44
Isaeidae	crustacean	0.33	6.25	3.44	11.88
Halacaridae	crustacean	14.67	92.75	3.2	15.08
Terebellidae	polychaete	4.89	0.25	2.94	18.02
Arcidae	bivalve	3	0.13	2.89	20.91
Goniadidae	polychaete	2.78	0.13	2.82	23.73
Leuconidae	crustacean	0.33	4.5	2.64	26.37
Diastylidae	crustacean	0.67	6.88	2.57	28.94
Stenothoidae	crustacean	0.11	2.25	2.45	31.39

The largest contributions to community differences were made by the high abundance polychaete families Sabellidae and Spionidae. Increases in contributions to community differences from the 4- to 6-year closed sites coincided with changes in abundances of Sabellidae and Spionidae over time (Figure 7).

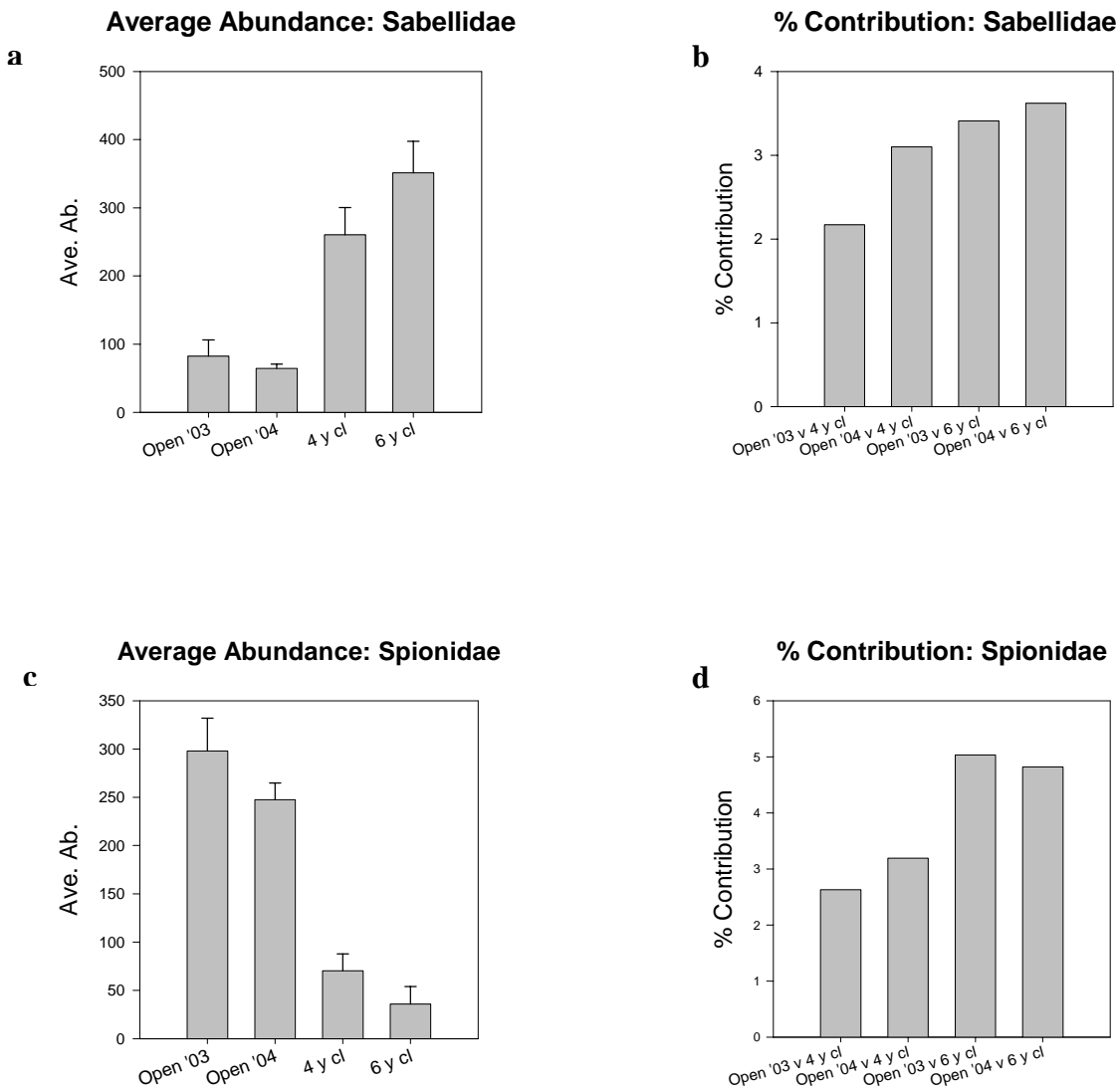


Figure 7. Shifts in dominance, Sabellidae and Spionidae. *a*: shifts in average abundances of Sabellidae over time. *b*: shifts in % contribution to differences by Sabellidae abundances between Open and Closed sites over time. *c*: shifts in average abundances of Spionidae over time. *d*: shifts in % contribution to differences by Spionidae abundances between Open and Closed sites over time.

Fifty-one taxa made up approximately 90% of observed differences between the 4- and 6-year closed sites. No one taxa contributed more than 4% to observed differences. Almost all significant differences between the 4- and 6-year closed sites were due to taxa showing higher abundances in the 6-year closed sites, however the greatest contribution to community differences was due to decreases in the polychaete Spionidae (Table 12.)

Table 12. SIMPER analysis of dissimilarity, top ten contributing taxa to community differences between the 4- and 6-year closed sites.

		4 yr cl	6 yr cl		
		Av. Ab.	Av. Ab.	Contrib%	Cum%
Spionidae	polychaete	70.33	35.78	3.23	3.23
Mesodesmatidae	bivalve	8.56	8.56	2.97	6.2
Ampeliscidae	crustacean	0.56	2.89	2.72	8.92
Ischyroceridae	crustacean	0.78	5.78	2.52	11.45
Oligochaete	annelid	0.44	3.67	2.49	13.94
Cuspidaridae	bivalve	2.78	1.11	2.48	16.42
Cirratulidae	polychaete	74.89	177.67	2.34	18.76
Mytilidae	bivalve	0	3.78	2.3	21.06
Opheliidae	polychaete	9.44	3.67	2.26	23.32
Nannastacidae	crustacean	1.56	0.33	2.23	25.55

Grain Size Analysis

Sediment grain size analysis was performed on Open 2004 and 6 year-closed sites (see Appendix E). Open 2004 contained more silt (ave. 38.4%) than the 6-year closed sites (ave. 11.9%), while the 6 year closed sites contained more gravel (ave. 22.8%) and sand (ave. 47.6%) than Open 2004 (gravel: ave. 8.5%; sand: ave. 31.2%).

Epifauna

A total of 25,987 individual organisms were identified in all ROV video transects. Analysis of all transects was performed on identifications at the lowest possible taxonomic level that could be consistently determined in all videos. All sites were dominated by the ascidian *Molgula sp.* (2-yr closed: 74%; Open 2003: 46%; Open 2004:

46%; 4-yr closed: 77%; 6-yr closed: 65%). Following *Molgula sp.*, the 2-year closed sites, Open 2003, and Open 2004 were dominated by the northern shrimp *Pandulus borealis* (2-yr closed: 13%; Open 2003: 41%; Open 2004: 34%), while the cnidarian *Cerianthis borealis* followed in the 4-year closed sites (8%), and porifera followed in the 6-year closed sites (26%).

Univariate Diversity Indices

Univariate diversity indices (see Appendix D) were calculated to recognize overall differences in community attributes (Table 13).

Table 13. Average diversity values for taxonomic richness, abundance, dominance, evenness, and diversity for all sampling sites, highest values are in bold.

	Richness	Abundance	Dominance	Evenness	Diversity
	S	N	d	J'	H'(loge)
6-yr cl	7.93	1490.3	0.97	0.5	1.02
4-yr cl	6.11	668.89	0.8	0.46	0.99
2-yr cl	6.57	284.57	0.99	0.54	0.82
Open 2004	6.56	536.44	0.74	0.62	1.14
Open 2003	5.38	351.13	0.62	0.63	0.99

Multivariate Analyses

A 2-D, non-metric, multidimensional scaling (MDS) plot of epifaunal group abundance similarities, sorted by treatment, indicated that the communities could be separated based on treatment group (Figure 8). A one-way ANOSIM indicated the separation based on treatment to be significant ($R = 0.412$; $p = 0.001$). Pairwise tests (Table 14) indicated that Open 2003 and Open 2004, and the 2-year closed sites and Open 2003 were not significantly different. There appeared to be weakly significant differences between the 2-year closed sites and Open 2004, the 2-year closed sites and the 4-year closed sites, and the 4-year closed sites and Open 2003, and Open 2004. The

6-year closed sites showed significant differences from all areas sampled, however, they were more similar to the 4-year closed sites than any other area sampled.

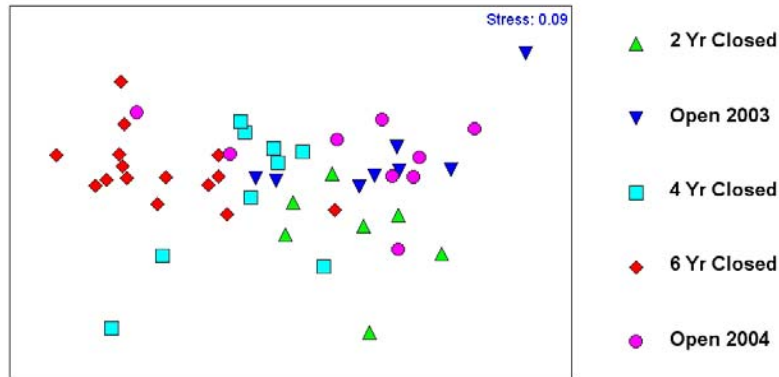


Figure 8. Non-metric multidimensional scaling (MDS) ordination for epifaunal community assemblages based on Bray-Curtis similarity coefficient of standardized untransformed abundances.

Table 14. Pairwise comparisons of epifaunal community assemblages, the lower half of the triangle matrix contains ANOSIM values, while the upper half contains corresponding p value.

Groups	Open 2003	Open 2004	2 yr closed	4 yr closed	6 yr closed
Open 2003		0.757	0.113	0.009	0.001
Open 2004	-0.05		0.026	0.004	0.001
2 yr closed	0.126	0.213		0.021	0.001
4 yr closed	0.229	0.288	0.236		0.002
6 yr closed	0.7	0.61	0.754	0.323	

All taxa identified and enumerated from video transects were then classified as mobile or sessile, and analyzed for possible treatment differences in the number of mobile predators and attached suspension feeders. Table 15 comprises taxa making up mobility groups. A 2-D, non-metric, multidimensional scaling plot was created of epifaunal group abundances sorted into sessile and mobile categories (Figure 9). A one-way ANOSIM indicated that differences based on treatment were significant ($R = 0.411$; $p = 0.001$).

Table 15: Mobility Classifications of Epifauna

Phylum	Taxa	Mobility
Cnidaria	<i>Cerianthis borealis</i>	Sessile
Porifera	Porifera	Sessile
Chordata	<i>Molgula</i> sp.	Sessile
Cnidaria	Bolocera tuediae	Sessile
Porifera	<i>Polymastia</i> sp.	Sessile
Lophophorata	<i>Terebratulina septentrionalis</i>	Sessile
Chordata	<i>Boltenia ovifera</i>	Sessile
Cnidaria	<i>Urticina feline</i>	Sessile
Porifera	<i>Haliclona</i> sp.	Sessile
Cnidaria	Umbellula	Sessile
Porifera	St. Sponge	Sessile
Arthropoda	<i>Pandulus borealis</i>	Mobile
Echinodermata	<i>Porania insignis</i>	Mobile
Echinodermata	<i>Henricia sanguinolenta</i>	Mobile
Arthropoda	Cancriidae	Mobile
Arthropoda	<i>Pagarus</i> sp.	Mobile
Arthropoda	Majidae	Mobile
Arthropoda	Pycnogonid	Mobile

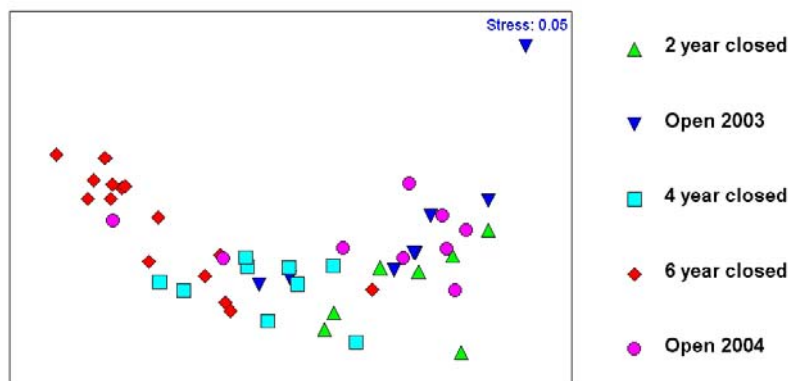


Figure 9. Non-metric multidimensional scaling ordination for epifaunal community assemblages sorted into sessile and mobile categories based on Bray-Curtis similarity coefficient of standardized untransformed abundances.

Pairwise tests generated by a one-way ANOSIM intensified similarities and differences observed previously in analysis based on taxa identifications (see Table 5). The 2-year closed sites did not differ significantly from Open 2003 or Open 2004. However, the 2-year closed sites and the 4-year closed sites, and the 4-year closed sites and both Open sites now differed more strongly than was previously observed. Finally, the 6-year closed sites differed significantly from all sites, however were more similar to the 4-year closed sites than anywhere else.

Table 16. Pairwise comparisons of epifaunal mobility groups, lower half of the triangle matrix contains ANOSIM values, while the upper half contains corresponding p values.

Groups	Open 2003	Open 2004	2 yr closed	4 yr closed	6 yr closed
Open 2003		0.876	0.556	0.006	0.001
Open 2004	-0.062		0.377	0.002	0.001
2 yr closed	-0.027	0.005		0.001	0.001
4 yr closed	0.343	0.394	0.519		0.004
6 yr closed	0.696	0.569	0.777	0.341	

SIMPER analysis of dissimilarity (see Appendix C) was used to identify all taxa that significantly contributed to community differences between all sampling sites. Pairwise tests indicated no significant differences between Open 2003 and Open 2004, and SIMPER analysis identified the same taxa as dominating both areas. Pairwise tests indicated no significant differences between the 2-year closed sites and Open 2003, and weakly significant differences between the 2-year closed sites and Open 2004, thus indicating that the 2-year closed sites may have been more similar to Open 2003 than Open 2004. SIMPER analysis of dissimilarity indicated this may be due to the appreciably higher average abundances in Open 2004 than both Open 2003 and the 2-year closed sites.

Pairwise tests indicated weakly significant differences between the 4-year closed sites and Open 2003 and Open 2004. This suggested that ongoing recovery may have occurred over time in the 4-year closed sites. The 4-year closed sites were a resampling of the 2-year closed sites after they had been closed for 4 years, and the 2-year closed sites were more similar to both Open sites than the 4-year closed sites. This was most likely due to increases in porifera in the intervening years between sampling of the 2-, and later the 4-year closed sites. Porifera did not contribute significantly to differences between the 2-year closed sites and Open sites, however, porifera made up approximately 25% and 23% respectively of the differences between the 4-year closed sites and Open sites (Tables 17, 18).

Table 17. SIMPER analysis of dissimilarity, top two contributing taxa to community differences between Open 2003 and 2-year closed sites, and Open 2004 and 2-year closed sites.

	Open '03	2 yr cl		
Taxa	Av. Ab.	Av. Ab.	Contrib%	Cum%
Molgula sp.	193.25	197.84	50.45	50.45
Pandulus borealis	90.73	38.24	20.86	71.31
	Open '04	2 yr cl		
Taxa	Av. Ab.	Av. Ab.	Contrib%	Cum%
Molgula sp.	314.98	197.84	47.08	47.08
Pandulus borealis	107.58	38.24	22.5	69.59

Table 18. SIMPER analysis of dissimilarity, top two contributing taxa to community differences between Open 2003 and 4-year closed sites, and Open 2004 and 4-year closed sites.

	Open '03	4 yr cl		
Taxa	Av. Ab.	Av. Ab.	Contrib%	Cum%
Molgula sp.	193.25	394.11	51.99	51.99
Porifera	20.24	153.54	25.21	77.19
	Open '04	4 yr cl		
Taxa	Av. Ab.	Av. Ab.	Contrib%	Cum%
Molgula sp.	314.98	394.11	51.04	51.04
Porifera	42.76	153.54	22.57	73.61

The 6-year closed sites showed significant differences from both Open 2003 and 2004. Two taxa made up approximately 85% of the differences by showing higher average abundances in the 6-year closed sites than in either of the Open sites (Table 19).

Table 19. SIMPER analysis of dissimilarity, top two contributing taxa to community differences between Open 2003 and 6-year closed sites, and Open 2004 and 6-year closed sites.

	Open '03	6 yr cl		
Taxa	Av. Ab.	Av. Ab.	Contrib%	Cum%
Molgula sp.	193.25	879.7	55.83	53.83
Porifera	20.24	444.55	32.06	85.88
	Open '04	6 yr cl		
Taxa	Av. Ab.	Av. Ab.	Contrib%	Cum%
Molgula sp.	314.98	879.7	52.49	52.49
Porifera	42.76	444.55	30.3	82.79

The third species to contribute significantly to community differences was also the only species to have higher average abundances in Open sites, the northern shrimp *Pandulus borealis* contributed approximately 5% to observed community differences.

Among all Closed sites, ongoing recovery may have caused the 4-year closed sites to be more similar to the 6-year closed sites than the 2-year closed sites. Pairwise tests indicated weakly significant differences between the 2- and 4-year closed sites, and it appeared that the 2-year closed sites were more similar to both Open sites than the 4-year closed sites. The 4-year closed sites were also not as different from the 6-year closed sites as the 2-year closed sites were. SIMPER analysis showed that more than 80% of all differences were due to increases in abundances from the 2-, to 4-, to 6-year closed sites (Table 20).

Table 20. SIMPER analysis of dissimilarity, changes in abundances of the top two contributing taxa to community differences in the 2-, 4-, and 6-year closed sites.

	2 yr cl	4 yr cl	6 yr cl
Taxa	Av. Ab.	Av. Ab.	Av. Ab.
Molgula sp.	197.84	394.11	879.7
Porifera	9.34	153.54	444.55

Possible directionality in recovery was further reflected in the overall average dissimilarity coefficient calculated between all communities, which was 66.86 between the 2- and 6-year closed sites, and 48.07 between the 4- and 6-year closed sites. Particularly significant were increases in abundances of porifera in the 4-, and 6-year closed sites (Figure 10a). While the colonial ascidian *Molgula sp.* contributed the most to community differences, the contribution of porifera to community differences actually increased over time in conjunction with abundance increases (Figure 10b).

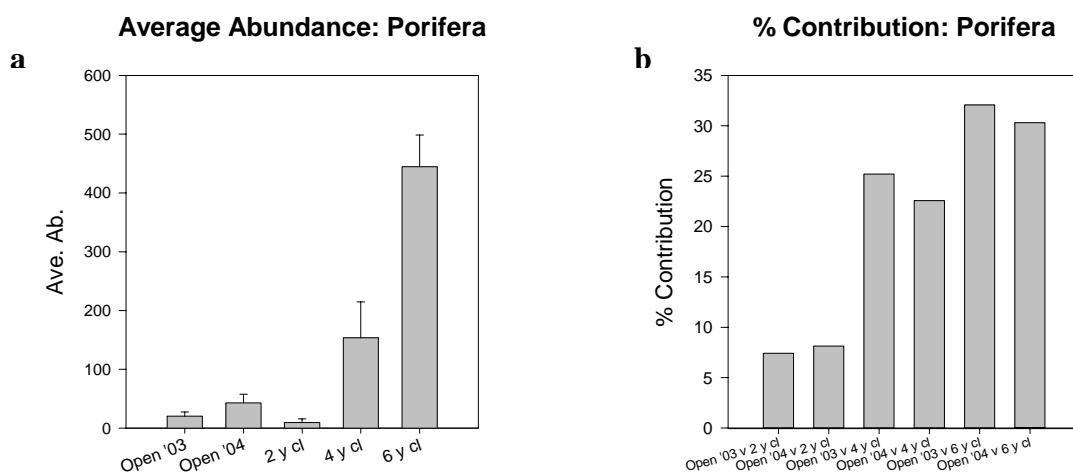


Figure 10. Shifts in dominance, porifera. *a*: Shifts in average abundance of porifera over time. *b*: Shifts in % contribution of porifera to community differences over time.

DISCUSSION

This study looked at the response of benthic communities on coarse bottoms in the WGOMC to the cessation of trawling at different times: 1. epifaunal communities in 2-year closed sites in August 2002, 2. epifaunal/infaunal communities in 4-year closed sites in August 2004 (resampling of 2-year closed sites), and 3. epifaunal/infaunal communities in 6-year closed sites in August 2004. Benthic communities of the WGOMC were then compared to an actively trawled fishing ground known as the Kettle: 1. epifaunal/infaunal communities in Open 2003, and 2. epifaunal/infaunal communities in Open 2004 (resampling of Open 2003).

Response of infaunal assemblages to the cessation of trawling

Results indicated changes in the composition of infaunal community assemblages in the WGOMC following the release of chronic trawling disturbance. In general, rather than observing presence/absence differences between most taxa in Open and Closed sites, the data demonstrated shifts in community dominance that reflected the interaction of fishing disturbance with the life history strategies of resident organisms. It appeared over time the % contribution to community differences shifted from low and moderately abundant taxa between the Open sites and the 4-year closed sites toward the dominant high abundance taxa between the Open sites and the 6-year closed sites.

One of the most striking differences between all Closed and Open sites were the shifts from the dominance of the polychaete Spionidae in the Open sites to Sabellidae in the Closed sites. Furthermore, it appeared there was some directionality in changes of average abundances of these polychaetes over time. Spionidae decreased from an average abundance per sample of approximately 297 and 247 in Open 2003 and 2004,

respectively, to 70 individuals/sample in the 4-year closed sites, and 35 individuals/sample in the 6-year closed sites. Sabellidae, on the other hand, appeared to increase over time from roughly 82 and 65 individuals/sample in Open 2003 and 2004, respectively, to roughly 260 individuals/sample in the 4-year closed sites, and 351 individuals/sample in the 6-year closed sites. Changes in abundances of these families over time was then reflected in increased % contributions of Sabellidae and Spionidae to community-wide differences from between the Open sites and the 4-year closed sites, to between the Open sites and the 6-year closed sites (Figure 7).

Chronic trawling disturbance has been shown to select for species with more vulnerable life history characteristics (Collie *et al.* 2000). Sabellids are sessile suspension feeding tube-builders that build permanent tubes just below the sediment-water interface, where their feather-like radiolar crowns can protrude into the water column and feed on suspended particles. Thus, Sabellidae are vulnerable to direct mortality from trawls. Spionids also build tubes; however they are more motile and do not necessarily spend their entire lives in their tubes, therefore Spionids most likely suffer lower mortality from trawls. Spionids also are most likely better able to recover between trawling disturbances. They are opportunistic r-strategists relative to Sabellids, which means they are characterized by shorter life-spans, many more reproductions per year, higher recruitment, and a higher death rate. This most likely makes them better adapted to disturbed environments in general. Sabellids, on the other hand, are most likely unable to adapt well to a chronically trawled environment. Suspension feeders generally feed best in relatively clear water (Loosanoff 1962). Resuspension of the upper layers of the sediments due to trawls (Caddy 1973; Black and Parry 1994; Pilskaln *et al.* 1998;

Palanques *et al.* 2001) would clog the feeding apparatuses of Sabellids, especially juveniles, and bury settling larvae.

SIMPER analysis of similarity also indicated shifts over time in the polychaete family Maldanidae. In Open 2003 and 2004, average abundances of Maldanidae stood around 27 and 33 individuals/sample, respectively, but increased in the 4- and 6-year closed sites to 43 and 54 individuals/sample. Increases in abundance of Maldanidae was not reflected in SIMPER analysis of dissimilarity, however, for Maldanidae was not listed as contributing significantly to differences between the Open and Closed sites. The fact that Maldanidae did not contribute significantly to differences between the Open and Closed sites highlights an important aspect of the difference between the information that can be revealed by SIMPER analysis of similarity and dissimilarity. Firstly, taxonomic richness and abundance were on average higher in the Closed sites, thus Maldanidae was not listed as contributing significantly to community differences because even at lower average abundances in the Open sites, it still contributed roughly the same percentage to community composition as it did in the Closed sites at higher abundances. Trends in population abundances, however, can matter. Maldanidae is a deposit feeder that lives head-down in the sediments in semi-permanent tubes, thus adding to the physical structure and heterogeneity of habitats through tube construction. Increased populations of tube-builders in general often stabilize the sediments, creating favorable environmental conditions for further growth of conspecifics and other families of tube-builders. Furthermore, if tube-builders are able to successfully establish high enough densities and bind up the sediments with tubes, they often inhibit burrowing species by limiting space and access to food and oxygen (Woodin 1974). Secondly, Maldanidae did contribute to

community differences when functional feeding groups were analyzed by accounting for a much greater percentage of the non-selective deposit feeders in the Closed sites, but not the Open sites where Spionidae dominated.

At increased abundances in the moderate abundance group in the Open sites was the crustacean Halacaridae and the polychaete Lumbrineridae. Both these organisms are most likely more disturbance tolerant as they are mobile and less likely to experience direct damage from trawls. Furthermore, they may even benefit from trawling disturbance. Firstly, Lumbrinerids are opportunistic carnivores and carrion-feeders, and may be attracted to other dead or damaged organisms within the upper 2 cm of the sediment in the wake of trawls. However, while Lumbrinerids may be better able to take advantage of ephemeral resources than other carnivores, it is worth noting that analysis of functional feeding groups revealed that the abundance of carnivores as a group was not lower in the Closed sites. It is possible that with decreases in permanent tube-builders in Open sites, limiting resources within the sediments such as food and space would be open for burrowers in general to take advantage of, and Lumbrineridae may have been best at doing this. Halacarids, on the other hand, are tiny deposit feeding mites that live on the sediment surface. They are highly mobile, and often attach themselves to sediment “fluff” on the sediment-water interface. In the Open sites, the “fluff” layer was most likely maintained by the settling out of resuspended materials and higher water content in the upper layers of the sediment due to chronic trawling. The presence of this fluff layer possibly created more favorable environmental conditions for hordes of Halacarids. In fact, in Open 2004 particularly, Halacarids were the 4th most abundant organism.

The 4- and 6-year closed sites also showed an increase in the influence of bivalves on community structure, particularly in the low abundance group. Between Open 2003 and the 4-year closed sites, for example, Mesodesmatidae, which was not found in Open 2003, contributed the highest % difference to community composition. Significant contributions to community differences were also made by Yoldiidae, whose abundances increased between all Open and Closed sites. Mesodesmatidae and Cardiidae, which were consistently present in low abundances in both the 4- and 6-year closed sites and not present in Open 2003, were not significantly present in Open 2004 either. Nearly all of the bivalves collected are sessile filter-feeders with the exception of Yoldiidae, which is also capable of deposit feeding. These organisms live sessile in the sediments with their siphons extended to the sediment-water interface to collect particles. In this study, bivalve populations most likely lived very near the sediment-water interface and were highly vulnerable to direct mortality from trawls because siphon length is positively correlated with the depths at which the species lives in the sediment, and nearly all bivalve specimens were < 1 cm in size. Furthermore, as filter-feeders, bivalves were likely to have their siphons clogged by resuspended materials in the Open sites, much like the polychaete Sabellidae.

Results also produced some interesting shifts among the low abundance taxa. Open 2004, and the 4- and 6-year closed sites all had double the number of low abundance taxa consistently contributing to community differences than Open 2003. Low abundance taxa in Open 2004 appeared to have accounted for the year differences between Open 2003 and Open 2004. Both sites were dominated by the same taxa; however in Open 2004, the crustaceans Isaeidae and Caprellid, which were not found in

Open 2003, contributed the greatest percentages to community differences between these sites and contributed significantly to community composition in Open 2004. Differences between the Open sites and the 4-year closed sites were dominated by low abundance taxa. Between Open 2003 and the 4-year closed sites, differences were reflected in increases in abundances of the bivalve Mesodesmatidae, the crustacean Caprellidea, and the polychaete Terebellidae in the 4-year closed sites, which were not significantly present in Open 2003. The only significantly contributing low abundance taxa that increased in Open 2003 was the crustacean Leuconidae. Between Open 2004 and the 4-year closed sites, differences were reflected in increases in abundances of Halacaridae and Munnidae in Open 2004, and increases in Terebellidae in the 4-year closed sites.

Trends in analysis of functional feeding groups reflected shifts in community composition from non-selective deposit feeders towards suspension feeders. The Open sites were largely dominated by non-selective deposit feeders, but the 4- and 6-year closed sites showed increases in abundances of suspension feeder that nearly equaled non-selective deposit feeders (Figure 6). Much of this shift was represented by increases in the polychaete Sabellidae and filter-feeding bivalves in the Closed sites. While these results then reflect mechanisms discussed earlier, overall trends in trophic group separation may also reveal other facets of infaunal community structure. Suspension feeders prefer more stable bottoms, thus often dominate coarser bottoms while non-selective deposit feeders reach high densities in less stable substrate such as muddy bottoms (Rhoads and Young 1970). Chronically trawled sites such as the Kettle may cause long-term shifts in environmental conditions that ultimately favor a community dominated by non-selective deposit feeders.

In the Open sites, where suspension feeders most likely suffer greater mortality from the direct effects of trawling, chronic reworking and resuspension of the upper layers may also inhibit their recovery while favoring non-selective deposit feeders. Over time, once more disturbance tolerant non-selective deposit feeders, such as Spionidae, are able to successfully establish, they may also inhibit the recovery of suspension feeders. Reworking of the sediment by non-selective deposit feeders through feeding and movement destabilizes the upper layers of the sediment by producing fecal pellets and larger clasts of semi-consolidated sediment, and increasing water content in the upper layers of the sediment (Rhoads and Young 1970). While deposit feeding polychaetes are generally inefficient at doing this, combined with the destabilizing effects of chronic trawling, shifts in community composition from community states dominated by suspension feeders towards those dominated by non-selective deposit feeders were most likely produced and maintained in the Open sites. A resuspended cloud and a fluidized fluff layer at the sediment-water interface were often observed on ROV video transects in the Open sites. Such physical instability in the sediments is stressful to suspension feeders. Firstly, as previously mentioned, a constant resuspended cloud may clog the filtering structures of suspension feeders, especially larvae and juveniles. Secondly, unstable sediments may discourage larvae from settling, and any newly settled larvae are probably buried or resuspended themselves. Thirdly, many sessile suspension feeders are probably unable to maintain a firm connection or build a permanent tube in an unstable bottom.

Response of epifaunal assemblages to the cessation of trawling

Analyses of epifaunal assemblages indicated a possible directionality in community differences between Open and Closed sites. Open 2003 and 2004 did not differ significantly from each other; however the Closed sites appeared to show a more complex relationship. The 2-year closed sites did not differ significantly from Open 2003; however differed weakly from Open 2004. The 2-year closed sites also differed weakly from the 4-year closed sites, and the 4-year closed sites differed significantly from both Open sites suggesting recovery had occurred in the 2 years between sampling the 2- and 4-year closed sites. This result was later magnified in multivariate analyses of mobility classifications, where the significance levels increased between the 4-year closed sites and Open sites, and between the 2- and 4-year closed sites. The 6-year closed sites differed significantly from all sites; however the 4- and 6-year closed sites were more similar than the 6 year closed sites and anywhere else.

When taxonomic differences were analyzed, it appeared that community differences reflected a process of recovery over time that may be ongoing in the WGOMC. From the Open and 2-year closed sites to the 4-, to the 6-year closed sites, there was a rise in the influence of sessile suspension feeders, particularly porifera . Not only did the abundances of porifera continually increase from the Open and 2-year closed sites, to the 4-, to the 6-year closed sites, but the % contribution of porifera to community differences increased as well (Figure 10). The growth form of those categorized under porifera in this study were highly branched, springing out of multiple bases, which most likely made them vulnerable to at least breakage under disturbance (Sainsbury 1993; Sousa 2001; Wassenberg 2002). Recovery of such animals is on the order of years due to

slow reproductive and growth processes, which was most likely why abundances did not seem to increase until after at least 4 years. The increases in the 6-year closed sites appeared dramatic, but really the most significant is that of increases in the 4-year closed sites because they were a resampling of the 2-year closed sites, thus the only direct measure of changes occurring over time.

Abundance-wise, *Molgula sp.* was the dominant organism of all sites, and contributed the most to differences among areas. While abundances increased over time (the 6-year closed sites saw the highest abundances of *Molgula sp.*), the % contribution of *Molgula sp.* to community differences stayed the same, at approximately 50%. This may have been in part due to the increasing % contribution of porifera to community differences over time. In the Open sites, any trawling occurring in the vicinity of boulders is most likely with rockhopper gear. This gear modifies groundgear on the lower lip of the mouth of the net to make it more buoyant, allowing the gear to skip over the bottom rather than continuously scrape. Fishermen use rockhoppers in areas of boulders and other complex relief in order to keep their nets from getting torn or caught. Colonial forms common on hard substrates such as *Molgula sp.* were most likely fragmented by trawling disturbances, rather than cleared completely. Thus, it would have been difficult for another organism to invade any open spaces enclosed by *Molgula sp.* because they already had a reproductive advantage being in such close proximity to newly available space. Furthermore, *Molgula sp.* are filter-feeders and were a major component to populations of invertebrates on hard substrates in all Open and Closed sites. They may have inhibited the establishment of other species in any open patches by

collectively depleting suspended food resources and ingesting other dispersing propagules (Young and Gotelli 1988).

Consistent contributions to similarity between stations within Open sites, and to community differences between Open and Closed sites were made by the northern shrimp *Pandulus borealis*. From the Open sites and 2-year closed sites, to the 4- and 6-year closed sites, the abundances of *Pandulus borealis* went down. It is unclear why northern shrimp populations decreased in the 4- and 6-year closed sites. One possibility is that the disturbed conditions in the Open sites may have been more ideal for *Pandulus borealis*. They are mobile predators and scavengers (Shumway *et al.* 1985), and trawling may have enhanced their food sources through damage to other organisms. Much past research has observed increases in mobile scavengers into trawled plots to feed on dead or damaged organisms (Kaiser and Spencer 1994; Hill *et al.* 1999; McConnaughey *et al.* 2000; Cryer *et al.* 2002). Upright, attached epifauna generally also sustain damage from trawls, possibly reducing cover for potential prey. However, had this been the case, increased abundances of other mobile predators and scavengers in the Open sites might have been observed. Furthermore, in studies where dead or damaged organisms being fed upon by mobile scavengers were observed in the wake of a trawl, the increased abundances of scavengers only lasted as long as the presence of the ephemeral resources that initially attracted them (Kaiser and Spencer 1994). After years of trawling, many organisms that suffer high mortality in the wake of a trawl are eventually lost from the community. Another possibility is that *Pandulus borealis* were a more competitively dominant mobile species relative to others in taking advantage of the long term unstable community state maintained in the Open sites. *Pandulus borealis* are a food source for many species of

fish, including demersal fish (Shumway *et al.* 1985). It is possible that chronic trawling significantly reduced predation pressure on *Pandulus borealis* in the Open sites. Exact reasons for increases *Pandulus borealis*, however, remain unclear because *Pandulus* is also extremely sensitive to bottom temperatures, thus it is equally possible that community differences were due to slight changes in bottom temperatures (Shumway *et al.* 1985).

Conclusions

Overall, the infaunal and epifaunal communities in the WGOMC following the cessation of trawling began a process of recovery that led to community states dominated by slower-growing, more disturbance-intolerant taxa. Fishing effort, however, was not experimentally controlled, and more importantly, sites may have differed in characteristics other than fishing intensity that could have influenced differences in community composition (Hall 1999). That said, subtidal benthic communities in coarse bottoms at >100 m depth are not acclimated to physically stressful conditions such as strong current flow or storm surge, thus it is reasonable to assume that such communities should be dominated by more stable sessile species in the absence of anthropogenic disturbance.

In the infaunal communities, environmental conditions that might alter composition between Open and Closed sites were differences in substrate type, namely grain size, sediment dynamics, rugosity, and related seabed features. Past studies have found that habitat type can be a relatively more important consideration than inside/outside Closed sites (Link *et al.* 2005). However, in the Kettle, a chronically trawled fishing ground, it was possible that alterations in habitat type as a result of

trawling drove long-term compositional differences between Open and Closed sites as well as direct mortality of more fragile organisms. Strong correlations were observed in compositional differences between Open and Closed sites that, according to the life histories of resident infauna, may have been related to the presence of trawling disturbance. Furthermore, differences between the Open and Closed sites persisted from the 4- to 6-year closed sites with continually increasing abundances of more stable taxa, namely the polychaete Sabellidae. Among epifaunal communities, it appeared there was a trend of ongoing recovery over time from the 2-, to 4-, to 6-year closed sites. There were sharp increases over time of nearly all organisms, especially *Molgula sp.* and porifera. In the 6-year closed sites, porifera were more numerous than in any other site, and appeared to be larger, and more evenly distributed.

It appears that recovery of both infaunal and epifaunal communities takes at least 6 years in the WGOMC as abundance increases were still being observed in the 6-year closed sites. It is also likely that epifaunal communities recover at a slower rate than infaunal communities, because the dominant epifauna, namely porifera, show slow growth, and are very long-lived. Bradshaw *et al.* (2000) and Collie *et al.* (2005) both projected that recovery of epifauna on gravel habitats to be on the order of 10 years; however it is impossible to project recovery time to any kind of endpoint as there were no untrawled control sites to compare Open and Closed sites to. It can be stated that recovery of benthic communities on coarse bottoms of the WGOMC must be more than 6 years, and epifaunal communities clearly showed slower recovery dynamics than infaunal communities.

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APPENDIX A

ABUNDANCE COUNTS

INFAUNAL TAXA

Table A1. Infaunal Abundance: List of all infaunal individuals identified at all Open and Closed sites for years 2003 and 2004.

TAXA	Open '03	Open '04	4 yr cl	6 yr cl	TOTALS
Ampeliscidae	2	11	5	26	44
Ampharetids	1773	1537	1397	1469	6176
Amphilochidae	0	2	0	0	2
Anthuridae	0	0	1	7	8
Apistobranchidae	0	0	0	1	1
Arcidae	0	1	9	27	37
Astartidae	223	225	206	422	1076
Capitellidae	50	26	7	15	98
Caprellid	0	19	34	67	120
Cardiidae	16	22	73	95	206
Chaetodermomorpha	2	7	5	16	30
Cirratulids	955	1175	674	1599	4403
Corophiidae	0	0	0	5	5
Cossuridae	218	279	207	302	1006
Cuspidariidae	0	0	25	10	35
Diastylidae	19	55	9	6	89
Dorvilleidae	38	75	51	46	210
Eunicidae	0	0	5	3	8
Eurycopidae	4	1	1	2	8
Eusiridae	0	0	0	1	1
Featherduster	1	1	16	2	20
Flabelligeridae	7	6	10	23	46
Gnathiidae	0	1	1	11	13
Goniadidae	2	1	25	25	53
Halacaridae	386	742	96	132	1356
Isaeidae	0	50	5	3	58
Ischyroceridae	21	6	7	52	86
Janiridae	2	9	10	17	38
Leuconidae	40	36	1	3	80
Lilljeborgidae	0	0	5	1	6
Lumbrinderidae	394	393	161	140	1088
Lysianassidae	0	5	10	3	18
Maldanidae	241	270	393	486	1390
Melitidae	3	0	1	2	6
Mesodesmatidae	0	30	77	77	184
Munnidae	21	40	2	8	71

Table A1. continued:

Myidae	5	0	0	0	5
Mytilidae	2	0	0	34	36
Nannastacidae	3	4	14	3	24
Nephtyidae	34	26	18	16	94
Nereididae	36	47	24	32	139
Oedicerotidae	0	0	2	2	4
Oligochaete	260	10	4	33	307
Opheliidae	36	20	85	33	174
Ophiactidae	3	8	19	20	50
Ophiolepidae	6	0	5	7	18
Orbinidae	1	0	0	0	1
Owenidae	117	45	99	117	378
Paraunidae	1000	440	436	492	2368
Pectinidae	0	1	1	1	3
Phoxocephalidae	110	83	89	161	443
Phyllodocidae	4	5	3	8	20
Pilargidae	0	0	0	1	1
Pleustidae	4	9	8	2	23
Podoceridae	0	1	9	3	13
Rissoidae	2	7	10	9	28
Sabellidae	741	516	2343	3160	6760
Scalibregmidae	20	38	61	43	162
Sigalionidae	6	17	20	8	51
Sipunculidea	2	12	19	57	90
Spionidae	2681	1980	633	322	5616
Stegocephalidae	0	0	0	2	2
Stenothoidae	3	18	0	1	22
Sternaspidae	0	0	0	2	2
Syllidae	658	461	1634	1457	4210
Tanaidacea	56	63	167	209	495
Terebellidae	12	2	75	44	133
Tironidae	0	0	0	1	1
Trochochaetidae	0	0	0	0	0
Unciolidae	9	0	2	3	14
Yoldiidae	32	51	138	143	364
TOTALS	10261	8889	9447	11530	40127

EPIFAUNAL TAXA

Table A2. Epifaunal Abundance: List of all epifaunal individuals identified at all Open and Closed sites for years 2002, 2003, and 2004.

TAXA	Open '03	Open '04	2 yr cl	4 yr cl	6 yr cl	TOTALS
Bolocera tuediae	164	268	48	78	178	736
Boltenia ovifera	0	3	0	0	0	3
Cancer crab	1	1	0	0	0	2
Cerianthis borealis	88	83	121	299	539	1130
Haliclona Sp	0	0	0	0	0	0
Henricia sanguinolenta	1	6	58	4	13	82
Lophophorata	0	0	1	2	382	385
Majidae	1	0	0	0	1	2
Molgula sp.	1104	1871	1395	2341	8709	15420
Pagarus sp.	0	0	1	0	3	4
Pandulus borealis	604	639	312	325	462	2342
Pennatula aculeata	0	0	0	0	0	0
Polymastia sp.	10	60	3	3	28	104
Porania insignis	1	1	4	8	7	21
Porifera	94	254	61	912	4401	5722
Pycnogonid	0	0	1	0	0	1
St. Sponge	0	0	0	0	19	19
Umbellula	0	0	0	1	12	13
Urticina felina	0	0	1	0	0	1
TOTALS	2068	3186	2006	3973	14754	25987

APPENDIX B

SIMPER ANALYSIS OF SIMILARITY

SIMPER analyses show the taxa responsible for 90% of the similarities between stations within sites for infaunal assemblages at all Open and Closed sites. Columns in each table list the average abundance per station (Av. Ab.), the average similarity between stations within each sites (Av. Sim.), a measure of how consistently individual taxa contribute to the overall similarity (Sim/SD), the percentage each individual taxa contributes to the total similarity (Contrib%), and the cumulative percentages down the table (Cum%).

INFAUNAL TAXA

Table B1. Open 2003 Infauna: SIMPER Analysis of Similarity between stations for infaunal assemblages at Open 2003 sites.

Av. Sim.: 80.22					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Spionidae	297.89	6.71	13.81	8.37	8.37
Ampharetidae	197	5.82	10.24	7.26	15.63
Cirratulidae	106.11	5.08	9.15	6.33	21.96
Paraonidae	111.11	4.8	11.15	5.99	27.95
Sabellidae	82.33	4.54	13.17	5.66	33.61
Syllidae	73.11	4.51	8.72	5.63	39.24
Lumbrineridae	43.78	4.17	11.26	5.19	44.43
Halacaridae	42.89	3.79	5.18	4.72	49.15
Maldanidae	26.78	3.7	7.99	4.62	53.76
Astartidae	24.78	3.63	10.68	4.52	58.28
Cossuridae	24.22	3.41	8.62	4.25	62.54
Phoxocephalidae	12.22	2.99	10.47	3.73	66.27
Owenidae	13	2.8	9.03	3.49	69.76
Tanaidacea	6.22	2.34	8.19	2.91	72.68
Oligochaete	28.89	2.33	1.78	2.9	75.78
Nereidae	4	2.31	7.91	2.88	78.46
Capitellidae	5.56	2.11	4.54	2.64	81.09
Nephtyidae	3.78	2.06	6.58	2.56	83.66
Leuconidae	4.44	1.7	1.81	2.12	85.77
Cardiidae	1.78	1.39	1.79	1.74	87.51
Yoldiidae	3.56	1.3	1.14	1.62	89.13
Opheliidae	4	1.21	1.13	1.51	90.64

Table B2. Open 2004 Infauna: SIMPER Analysis of Similarity between stations for infaunals assemblages at Open 2004 sites.

Av. Sim.: 81.62					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Spionidae	247.5	5.98	16.57	7.33	7.33
Ampharetidae	192.13	5.5	17.56	6.74	14.07
Cirratulidae	146.88	5.12	18.11	6.28	20.35
Halacaridae	92.75	4.47	10.71	5.48	25.83
Sabellidae	64.5	4.19	17.45	5.13	30.96
Syllidae	57.63	4.03	14.85	4.94	35.9
Lumbrineridae	49.13	3.97	22.12	4.86	40.76
Paraonidae	55	3.96	12.85	4.85	45.61
Cossuridae	34.88	3.62	17.77	4.43	50.04
Astartidae	28.13	3.45	20.6	4.23	54.27
Maldanidae	33.75	3.4	9.44	4.16	58.43
Phoxocephalidae	10.38	2.64	11.93	3.24	61.67
Dorvilleidae	9.38	2.49	6.52	3.05	64.72
Tanaidacea	7.88	2.3	10.42	2.82	67.54
Nereidae	5.88	2.13	11.2	2.62	70.16
Isaeidae	6.25	2.12	5.65	2.59	72.75
Scalibregmatidae	4.75	2.09	10.31	2.57	75.32
Yoldiidae	6.38	2.08	6.03	2.55	77.86
Munnidae	5	1.93	5.58	2.37	80.23
Diastylidae	6.88	1.59	1.57	1.95	82.18
Nephtyidae	3.25	1.46	1.63	1.78	83.96
Stenothoidae	2.25	1.28	1.64	1.57	85.53
Sigalionidae	2.13	1.25	1.64	1.53	87.06
Caprellid	2.38	1.25	1.67	1.53	88.59
Leuconidae	4.5	1.16	1.05	1.43	90.01

Table B3. 4-Yr Closed Sites Infauna: SIMPER Analysis of Similarity between stations for infaunal assemblages at 4-yr closed sites.

Ave. Sim.: 79.68					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Sabellidae	260.33	5.55	18.43	6.96	6.96
Syllidae	181.56	5.29	17.43	6.64	13.6
Ampharetidae	155.22	4.83	6.54	6.07	19.67
Cirratulidae	74.89	4.2	18.02	5.27	24.94
Spionidae	70.33	3.81	7.61	4.78	29.72
Paraonidae	48.44	3.62	7.99	4.54	34.25
Maldanidae	43.67	3.51	8.43	4.41	38.66
Astartidae	22.89	2.9	8.66	3.64	42.3
Tanaidacea	18.56	2.9	11.2	3.63	45.93
Lumbrineridae	17.89	2.79	10.04	3.5	49.43
Cossuridae	23	2.77	6.2	3.47	52.91
Owenidae	11	2.43	6.81	3.05	55.96
Yoldiidae	15.33	2.38	5.63	2.99	58.95
Mesodesmatidae	8.56	2.28	9.31	2.86	61.8
Phoxocephalidae	9.89	2.18	4.15	2.74	64.54
Scalibregmatidae	6.78	2.11	6.8	2.64	67.18
Caprellid	3.78	1.93	11.61	2.43	69.61
Cardiidae	8.11	1.9	6.78	2.38	71.99
Halacaridae	10.67	1.84	1.71	2.31	74.3
Opheliidae	9.44	1.78	1.77	2.23	76.53
Terebellidae	8.33	1.77	1.81	2.22	78.75
Dorvilleidae	5.67	1.56	1.81	1.96	80.71
Nereidae	2.67	1.33	1.8	1.67	82.39
Goniadidae	2.78	1.31	1.79	1.64	84.03
Sigalionidae	2.22	1.26	1.8	1.59	85.62
Flabelligeridae	1.11	1.16	1.83	1.45	87.07
Cuspidaridae	2.78	1.09	1.14	1.37	88.44
Sipunculidea	2.11	0.94	1.13	1.18	89.62
Ophiactidae	2.11	0.94	1.14	1.18	90.81

Table B4. 6-Yr Closed Sites Infauna: SIMPER Analysis of Similarity between stations for infaunal assemblages at 6-yr closed sites.

Av. Sim.: 78.40					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Sabellidae	351.11	5.57	10.04	7.11	7.11
Syllidae	161.89	4.69	19.13	5.98	13.08
Ampharetidae	163.22	4.61	8.69	5.89	18.97
Cirratulidae	177.67	4.45	5	5.68	24.65
Maldanidae	54	3.5	9.4	4.46	29.11
Astartidae	46.89	3.39	14.51	4.32	33.43
Paraonidae	54.67	3.37	10.06	4.29	37.72
Cossuridae	33.56	2.93	6.81	3.74	41.46
Tanaidacea	23.22	2.85	14.36	3.63	45.09
Phoxocephalidae	17.89	2.63	9.98	3.35	48.45
Yoldiidae	15.89	2.53	16.28	3.23	51.68
Lumbrineridae	15.56	2.5	6.62	3.19	54.87
Spionidae	35.78	2.16	4.71	2.76	57.63
Cardiidae	10.56	2.16	10.92	2.75	60.38
Halacaridae	14.67	2.04	5.23	2.6	62.98
Sipunculidea	6.33	1.82	6.38	2.32	65.3
Terebellidae	4.89	1.78	4.89	2.27	67.58
Nereidae	3.56	1.75	6.65	2.24	69.82
Scalibregmatidae	4.78	1.7	5.88	2.17	71.99
Arcidae	3	1.69	12.01	2.15	74.14
Goniadidae	2.78	1.63	7.69	2.08	76.22
Owenidae	13	1.59	1.73	2.02	78.25
Flabelligeridae	2.56	1.54	8.01	1.96	80.2
Caprellid	7.44	1.49	1.72	1.9	82.1
Dorvilleidae	5.11	1.43	1.63	1.82	83.92
Opheliidae	3.67	1.1	1.16	1.4	85.33
Ampeliscidae	2.89	1	1.13	1.28	86.61
Janiridae	1.89	0.92	1.16	1.17	87.77
Chaetodermomorpha	1.78	0.9	1.14	1.15	88.92
Capitellidae	1.67	0.83	1.16	1.06	89.98
Ophiactidae	2.22	0.82	1.16	1.04	91.02

EPIFAUNAL TAXA

Table B5. Open 2003 Epifauna: SIMPER Analysis of Similarity between stations for epifaunal assemblages at Open 2003 sites.

Av. Sim.: 58.96					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Molgula sp.	193.25	27.23	1.43	46.19	46.19
Pandulus borealis	90.73	24.39	2.34	41.38	87.56
Bolocera tuediae	26.47	5.55	2	9.42	96.98

Table B6. Open 2004 Epifauna: SIMPER Analysis of Similarity between stations for epifaunal assemblages at Open 2004 sites.

Av. Sim.: 54.40					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Molgula sp.	314.98	25.29	2.03	46.48	46.48
Pandulus borealis	107.58	18.31	1.59	33.65	80.13
Bolocera tuediae	45.12	7.61	1.36	13.98	94.12

Table B7. 2-Yr Closed Sites Epifauna: SIMPER Analysis of Similarity between stations for epifaunal assemblages at 2-yr closed sites.

Av. Sim.: 60.43					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Molgula sp.	197.84	44.8	2.87	74.13	74.13
Pandulus borealis	38.24	7.91	0.97	13.09	87.22
Cerianthis borealis	19.05	4.3	1.69	7.11	94.33

Table B8. 4-Yr Closed Sites Epifauna: SIMPER Analysis of Similarity between stations for epifaunal assemblages at 4-yr closed sites.

Av. Sim.: 57.32					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Molgula sp.	394.11	43.98	1.85	76.72	76.72
Cerianthis borealis	50.34	4.68	2.04	8.16	84.88
Pandulus borealis	54.71	4.27	0.82	7.45	92.33

Table B9. 6-Yr Closed Sites Epifauna: SIMPER Analysis of Similarity between stations for epifaunal assemblages at 6-yr closed sites.

Av. Sim.: 63.19					
Taxa	Av. Ab.	Av. Sim.	Sim/SD	Contrib%	Cum%
Molgula sp.	879.7	40.92	3.4	64.76	64.76
Porifera	444.55	16.5	1.61	26.12	90.88

APPENDIX C

SIMPER ANALYSIS OF DISSIMILARITY

SIMPER analysis of dissimilarity showing the taxa responsible for 90% of the difference between treatments for infaunal and epifaunal assemblages at all sites. Columns in each table list the average abundance per station (Av. Ab.), the average dissimilarity between all pairs of inter-group stations (Av. Diss.), a measure of how consistently individual taxa contribute to the overall dissimilarity (Diss/SD), the percentage each individual taxa contributes to the total dissimilarity (Contrib%), and the cumulative percentages down the table (Cum%).

INFAUNAL TAXA

Table C1. Open 2003 vs. Open 2004 Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal assemblages at Open 2003 and Open 2004.

Av. Diss.: 23.77	Open '03		Open '04			
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Isaeidae	0	6.25	1.25	5.51	5.24	5.24
Oligochaete	28.89	1.25	1.22	1.73	5.12	10.36
Caprellidea	0	2.38	0.87	2.38	3.64	14
Mesodesmatidae	0	3.75	0.86	1.56	3.62	17.62
Owenidae	13	5.63	0.75	1.2	3.14	20.76
Stenothoidae	0.33	2.25	0.74	1.66	3.11	23.87
Dorvilleidae	4.22	9.38	0.66	1.13	2.76	26.64
Diastylidae	2.11	6.88	0.62	1.27	2.61	29.25
Opheliidae	4	2.5	0.62	1.23	2.59	31.84
Unciolidae	1	0	0.61	1.38	2.57	34.41
Ischyroceridae	2.33	0.75	0.58	1.3	2.45	36.86
Sipunculida	0.22	1.5	0.56	1.19	2.36	39.22
Scalibregmatidae	2.22	4.75	0.56	1.11	2.34	41.57
Ampeliscidae	0.22	1.38	0.55	1.2	2.33	43.89
Halacaridae	42.89	92.75	0.55	1.46	2.32	46.21
Leuconidae	4.44	4.5	0.51	1.04	2.14	48.35
Capitellidae	5.56	3.25	0.48	1.07	2.01	50.36
Ophiolepidae	0.67	0	0.48	1.1	2	52.36
Flabelligeridae	0.78	0.75	0.47	1.07	1.99	54.34
Yoldiidae	3.56	6.38	0.46	1.01	1.95	56.29
Chaetodermomorpha	0.22	0.88	0.46	1.02	1.92	58.21
Sigalionidae	0.67	2.13	0.46	1.07	1.92	60.13
Munnidae	2.33	5	0.46	1.04	1.91	62.05
Cardiidae	1.78	2.75	0.45	1.16	1.9	63.95
Phyllodocidae	0.44	0.63	0.44	1.03	1.87	65.82
Ophiactidae	0.33	1	0.43	0.89	1.82	67.64
Terebellidae	1.33	0.25	0.41	0.87	1.72	69.35
Paraonidae	111.11	55	0.41	1.11	1.71	71.06
Rissoidae	0.22	0.88	0.39	0.87	1.66	72.72

Table C1. continued:

Janiridae	0.22	1.13	0.39	0.78	1.62	74.34
Pleustidae	0.44	1.13	0.38	0.76	1.61	75.95
Myidae	0.56	0	0.37	0.88	1.54	77.49
Ampharetidae	197	192.13	0.35	1.56	1.46	78.95
Cirratulidae	106.11	146.88	0.34	1.34	1.43	80.38
Nannastacidae	0.33	0.5	0.33	0.76	1.38	81.76
Nephtyidae	3.78	3.25	0.3	0.89	1.26	83.02
Syllidae	73.11	57.63	0.3	1.5	1.24	84.26
Cossuridae	24.22	34.88	0.29	1.54	1.2	85.47
Sabellidae	82.33	64.5	0.28	1.09	1.17	86.64
Spionidae	297.89	247.5	0.27	1.42	1.12	87.75
Eurycopidae	0.44	0.13	0.25	0.65	1.07	88.83
Lysianassidae	0	0.63	0.25	0.57	1.04	89.86
Goniadidae	0.22	0.13	0.24	0.63	1.02	90.88

Table C2. Open 2003 vs. 4-Yr Closed Sites Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal assemblages at Open 2003 and 4-Yr Closed Sites.

Av. Diss.: 30.69	Open '03	4 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Mesodesmatidae	0	8.56	1.33	7.53	4.34	4.34
Oligochaete	28.89	0.44	1.21	2.03	3.95	8.29
Caprellid	0	3.78	1.1	8.81	3.59	11.89
Spionidae	297.89	70.33	1.05	2.63	3.43	15.31
Terebellidae	1.33	8.33	0.96	1.69	3.14	18.45
Leuconidae	4.44	0.11	0.95	2.2	3.09	21.53
Sabellidae	82.33	260.33	0.9	2.17	2.92	24.46
Cuspidaridae	0	2.78	0.85	1.76	2.76	27.22
Goniadidae	0.22	2.78	0.76	1.74	2.48	29.69
Halacaridae	42.89	10.67	0.74	1.4	2.42	32.12
Munnidae	2.33	0.22	0.69	1.54	2.26	34.38
Capitellidae	5.56	0.78	0.69	1.38	2.25	36.62
Ophiactidae	0.33	2.11	0.67	1.46	2.19	38.82
Sipunculidea	0.22	2.11	0.67	1.43	2.19	41.01
Yoldiidae	3.56	15.33	0.66	1.27	2.14	43.15
Arcidae	0	1	0.65	1.78	2.13	45.27
Syllidae	73.11	181.56	0.65	1.87	2.11	47.38
Scalibregmatidae	2.22	6.78	0.62	1.2	2.02	49.4
Opheliidae	4	9.44	0.61	1.16	1.98	51.38
Nannastacidae	0.33	1.56	0.6	1.25	1.95	53.33
Dorvilleidae	4.22	5.67	0.6	1.13	1.94	55.27
Unciolidae	1	0.22	0.57	1.33	1.87	57.14
Janiridae	0.22	1.11	0.57	1.42	1.86	59
Ischyroceridae	2.33	0.78	0.56	1.11	1.83	60.83
Rissoidae	0.22	1.11	0.52	1.2	1.68	62.51

Table C2. continued:

Flabelligeridae	0.78	1.11	0.51	1.26	1.66	64.17
Featherduster	0.11	1.78	0.49	0.9	1.59	65.76
Nephtyidae	3.78	2	0.48	1.09	1.57	67.33
Ophiolepidae	0.67	0.56	0.46	1.1	1.5	68.83
Paraonidae	111.11	48.44	0.45	1.15	1.48	70.31
Tanaidacea	6.22	18.56	0.45	1.96	1.47	71.78
Sigalionidae	0.67	2.22	0.45	1.09	1.46	73.25
Cardiidae	1.78	8.11	0.44	1.06	1.44	74.69
Lumbrineridae	43.78	17.89	0.43	1.73	1.42	76.11
Diastylidae	2.11	1	0.43	1.03	1.39	77.5
Ampharetidae	197	155.22	0.4	1.34	1.31	78.81
Chaetodermomorpha	0.22	0.56	0.39	0.94	1.28	80.09
Phyllodocidae	0.44	0.33	0.36	0.91	1.19	81.28
Isaeidae	0	0.56	0.36	0.88	1.18	82.45
Myidae	0.56	0	0.36	0.88	1.17	83.62
Ampeliscidae	0.22	0.56	0.36	0.83	1.16	84.78
Pleustidae	0.44	0.89	0.35	0.74	1.14	85.93
Podoceridae	0	1	0.32	0.68	1.05	86.97
Cossuridae	24.22	23	0.31	1.32	1.03	88
Lilljeborgidae	0	0.56	0.3	0.7	0.98	88.98
Cirratulidae	106.11	74.89	0.29	1.38	0.95	89.92
Eunicidae	0	0.56	0.29	0.69	0.94	90.86

Table C3. 4-Yr Closed Sites vs. Open 2004 Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal assemblages at 4-yr closed sites and Open 2004.

Av. Diss.: 27.88	4 yr cl	Open '04				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Halacaridae	10.67	92.75	1.13	2.23	4.06	4.06
Terebellidae	8.33	0.25	0.99	2.13	3.55	7.61
Munnidae	0.22	5	0.92	2.34	3.3	10.92
Spionidae	70.33	247.5	0.89	2.48	3.19	14.11
Sabellidae	260.33	64.5	0.86	2.65	3.1	17.21
Leuconidae	0.11	4.5	0.83	1.61	2.98	20.19
Isaeidae	0.56	6.25	0.82	1.78	2.95	23.14
Stenothoidae	0	2.25	0.82	2.38	2.93	26.06
Cuspidaridae	2.78	0	0.81	1.77	2.89	28.95
Goniadidae	2.78	0.13	0.78	2.01	2.79	31.74
Syllidae	181.56	57.63	0.71	3.1	2.54	34.28
Opheliidae	9.44	2.5	0.7	1.36	2.51	36.79
Owenidae	11	5.63	0.67	1.17	2.41	39.2
Diastylidae	1	6.88	0.6	1.48	2.16	41.36
Janiridae	1.11	1.13	0.6	1.64	2.14	43.51
Capitellidae	0.78	3.25	0.59	1.36	2.11	45.62
Ophiactidae	2.11	1	0.58	1.31	2.09	47.71

Table C3. continued:

Nannastacidae	1.56	0.5	0.57	1.25	2.04	49.75
Arcidae	1	0.13	0.57	1.53	2.03	51.78
Mesodesmatidae	8.56	3.75	0.54	1.15	1.92	53.7
Cardiidae	8.11	2.75	0.51	1.16	1.83	55.53
Ampeliscidae	0.56	1.38	0.51	1.17	1.82	57.35
Rissoidae	1.11	0.88	0.49	1.2	1.75	59.11
Sipunculidea	2.11	1.5	0.49	1.16	1.75	60.86
Nephtyidae	2	3.25	0.48	1.08	1.72	62.58
Lumbrineridae	17.89	49.13	0.48	2.22	1.71	64.29
Featherduster	1.78	0.13	0.46	0.91	1.67	65.96
Oligochaete	0.44	1.25	0.46	1.08	1.65	67.6
Ischyroceridae	0.78	0.75	0.44	1.12	1.59	69.19
Flabelligeridae	1.11	0.75	0.44	1.14	1.57	70.76
Chaetoderomomorpha	0.56	0.88	0.44	1.08	1.57	72.33
Cirratulidae	74.89	146.88	0.41	1.68	1.46	73.79
Phyllodocidae	0.33	0.63	0.4	1.01	1.45	75.24
Pleustidae	0.89	1.13	0.38	0.77	1.37	76.61
Dorvilleidae	5.67	9.38	0.38	1	1.37	77.98
Yoldiidae	15.33	6.38	0.37	1.45	1.34	79.32
Lysianassidae	1.11	0.63	0.37	0.77	1.34	80.66
Tanaidacea	18.56	7.88	0.35	1.74	1.24	81.9
Podoceridae	1	0.13	0.34	0.76	1.22	83.12
Nereidae	2.67	5.88	0.34	1.06	1.22	84.33
Cossuridae	23	34.88	0.34	1.44	1.2	85.54
Sigalionidae	2.22	2.13	0.32	0.93	1.16	86.69
Caprellid	3.78	2.38	0.31	1.02	1.11	87.8
Ampharetidae	155.22	192.13	0.31	1.1	1.1	88.9
Lilljeborgidae	0.56	0	0.29	0.7	1.02	89.92
Ophiolepidae	0.56	0	0.28	0.7	0.99	90.92

Table C4. Open 2003 vs. 6-Yr Closed Sites Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal assemblages at Open 2003 and 6-yr closed sites.

Av. Diss.: 31.99	Open '03	6 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Spionidae	297.89	35.78	1.61	2.4	5.03	5.03
Sabellidae	82.33	351.11	1.09	2.34	3.41	8.44
Caprellid	0	7.44	1.09	2.43	3.4	11.84
Arcidae	0	3	1	6.94	3.12	14.96
Sipunculidea	0.22	6.33	0.99	2.46	3.1	18.06
Oligochaete	28.89	3.67	0.97	1.39	3.03	21.1
Leuconidae	4.44	0.33	0.89	2.04	2.78	23.87
Terebellidae	1.33	4.89	0.84	1.79	2.63	26.5
Mesodesmatidae	0	8.56	0.83	1.07	2.61	29.11
Goniadidae	0.22	2.78	0.8	2.27	2.51	31.62

Table C4. continued:

Ampeliscidae	0.22	2.89	0.72	1.54	2.24	33.86
Ischyroceridae	2.33	5.78	0.67	1.23	2.1	35.96
Yoldiidae	3.56	15.89	0.66	1.32	2.06	38.02
Chaetodermomorpha	0.22	1.78	0.63	1.47	1.98	40
Janiridae	0.22	1.89	0.63	1.52	1.98	41.98
Ophiactidae	0.33	2.22	0.62	1.37	1.93	43.9
Flabelligeridae	0.78	2.56	0.61	1.39	1.9	45.8
Halacaridae	42.89	14.67	0.6	1.46	1.87	47.67
Dorvilleidae	4.22	5.11	0.58	1.21	1.82	49.49
Mytilidae	0.22	3.78	0.57	0.92	1.78	51.27
Unciolidae	1	0.33	0.56	1.35	1.75	53.02
Cardiidae	1.78	10.56	0.55	1.44	1.71	54.72
Diastylidae	2.11	0.67	0.55	1.22	1.71	56.43
Syllidae	73.11	161.89	0.54	1.64	1.69	58.12
Rissoidae	0.22	1	0.53	1.4	1.67	59.79
Anthuridae	0	0.78	0.53	1.39	1.66	61.45
Scalibregmatidae	2.22	4.78	0.53	1.18	1.65	63.1
Munnidae	2.33	0.89	0.53	1.27	1.65	64.75
Tanaidacea	6.22	23.22	0.52	2.23	1.61	66.36
Opheliidae	4	3.67	0.51	1.11	1.61	67.97
Cirratulidae	106.11	177.67	0.49	1.44	1.52	69.49
Owenidae	13	13	0.47	1.22	1.48	70.98
Capitellidae	5.56	1.67	0.47	1.13	1.48	72.45
Phyllodocidae	0.44	0.89	0.47	1.17	1.47	73.92
Nephtyidae	3.78	1.78	0.46	1.07	1.45	75.37
Lumbrineridae	43.78	15.56	0.46	2.03	1.43	76.8
Paraonidae	111.11	54.67	0.44	1.21	1.38	78.17
Ophiolepidae	0.67	0.78	0.42	1.06	1.31	79.48
Sigalionidae	0.67	0.89	0.42	1.07	1.3	80.78
Cuspidaridae	0	1.11	0.41	0.85	1.29	82.08
Gnathiidae	0	1.22	0.41	0.85	1.27	83.35
Ampharetidae	197	163.22	0.35	1.46	1.11	84.46
Myidae	0.56	0	0.34	0.88	1.08	85.54
Maldanidae	26.78	54	0.34	1.54	1.07	86.61
Nannastacidae	0.33	0.33	0.33	0.84	1.02	87.63
Cossuridae	24.22	33.56	0.3	1.31	0.93	88.56
Astartidae	24.78	46.89	0.29	1.34	0.92	89.48
Pleustidae	0.44	0.22	0.29	0.73	0.89	90.37

Table C5. 6-Yr Closed Sites vs. Open 2004 Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal assemblages at 6-yr closed sites and Open 2004.

Av. Diss.: 29.62	6 yr cl	Open '04				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Spionidae	35.78	247.5	1.43	2.28	4.82	4.82
Sabellidae	351.11	64.5	1.07	3.16	3.62	8.44
Isaeidae	0.33	6.25	1.02	2.94	3.44	11.88
Halacaridae	14.67	92.75	0.95	2.16	3.2	15.08
Terebellidae	4.89	0.25	0.87	2.29	2.94	18.02
Arcidae	3	0.13	0.86	3.14	2.89	20.91
Goniadidae	2.78	0.13	0.83	3.04	2.82	23.73
Leuconidae	0.33	4.5	0.78	1.53	2.64	26.37
Diastylidae	0.67	6.88	0.76	1.59	2.57	28.94
Stenothoidae	0.11	2.25	0.73	1.98	2.45	31.39
Mesodesmatidae	8.56	3.75	0.71	1.41	2.38	33.77
Owenidae	13	5.63	0.7	1.28	2.37	36.15
Munnidae	0.89	5	0.62	1.41	2.09	38.24
Janiridae	1.89	1.13	0.62	1.49	2.09	40.32
Oligochaete	3.67	1.25	0.6	1.16	2.01	42.33
Sipunculidea	6.33	1.5	0.6	1.33	2.01	44.34
Syllidae	161.89	57.63	0.59	2.46	2	46.34
Ophiactidae	2.22	1	0.55	1.34	1.87	48.21
Cardiidae	10.56	2.75	0.55	1.18	1.85	50.06
Opheliidae	3.67	2.5	0.54	1.22	1.84	51.9
Ischyroceridae	5.78	0.75	0.54	1.09	1.81	53.71
Mytilidae	3.78	0	0.53	0.88	1.8	55.51
Flabelligeridae	2.56	0.75	0.52	1.29	1.77	57.28
Anthuridae	0.78	0	0.51	1.39	1.71	58.99
Ampeliscaidae	2.89	1.38	0.5	1.15	1.7	60.69
Lumbrineridae	15.56	49.13	0.5	2.76	1.69	62.38
Chaetodermomorpha	1.78	0.88	0.49	1.19	1.64	64.01
Rissoidae	1	0.88	0.48	1.32	1.63	65.65
Caprellid	7.44	2.38	0.48	1.31	1.62	67.27
Sigalionidae	0.89	2.13	0.48	1.16	1.62	68.88
Capitellidae	1.67	3.25	0.48	1.25	1.6	70.49
Nephtyidae	1.78	3.25	0.46	1.08	1.55	72.04
Ophiolepidae	0.78	0	0.43	1.1	1.46	73.5
Tanaidacea	23.22	7.88	0.41	2.02	1.38	74.88
Phyllodocidae	0.89	0.63	0.41	1.08	1.37	76.25
Gnathiidae	1.22	0.13	0.4	0.91	1.35	77.59
Cuspidaridae	1.11	0	0.4	0.86	1.33	78.93
Cirratulidae	177.67	146.88	0.38	1.54	1.28	80.21
Lysianassidae	0.33	0.63	0.35	0.89	1.19	81.4
Dorvilleidae	5.11	9.38	0.35	0.94	1.17	82.57
Yoldiidae	15.89	6.38	0.34	1.41	1.16	83.72
Nannastacidae	0.33	0.5	0.33	0.86	1.12	84.84

Table C5. continued:

Pleustidae	0.22	1.13	0.32	0.75	1.09	85.93
Maldanidae	54	33.75	0.31	1.53	1.03	86.96
Ampharetidae	163.22	192.13	0.26	1.32	0.89	87.85
Paraonidae	54.67	55	0.26	1.55	0.88	88.73
Cossuridae	33.56	34.88	0.25	1.82	0.84	89.57
Eunicidae	0.33	0	0.24	0.7	0.8	90.37

Table C6. 4-Yr Closed Sites vs. 6-Yr Closed Sites Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal assemblages at 4- and 6-yr closed sites.

Av. Diss.: 22.83	4 yr cl	6 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Spionidae	70.33	35.78	0.74	1.66	3.23	3.23
Mesodesmatidae	8.56	8.56	0.68	1.48	2.97	6.2
Ampeliscidae	0.56	2.89	0.62	1.4	2.72	8.92
Ischyroceridae	0.78	5.78	0.58	1.13	2.52	11.45
Oligochaete	0.44	3.67	0.57	1.29	2.49	13.94
Cuspidaridae	2.78	1.11	0.57	1.28	2.48	16.42
Cirratulidae	74.89	177.67	0.54	1.59	2.34	18.76
Mytilidae	0	3.78	0.52	0.88	2.3	21.06
Opheliidae	9.44	3.67	0.52	1.13	2.26	23.32
Nannastacidae	1.56	0.33	0.51	1.26	2.23	25.55
Chaetodermomorpha	0.56	1.78	0.5	1.26	2.17	27.72
Sigalionidae	2.22	0.89	0.47	1.18	2.07	29.79
Anthuridae	0.11	0.78	0.47	1.3	2.07	31.86
Nephtyidae	2	1.78	0.46	1.09	2.03	33.9
Sipunculidea	2.11	6.33	0.45	1.15	1.98	35.88
Halacaridae	10.67	14.67	0.45	1.22	1.96	37.84
Featherduster	1.78	0.22	0.44	0.9	1.94	39.78
Owenidae	11	13	0.44	1.27	1.93	41.7
Capitellidae	0.78	1.67	0.43	1.13	1.89	43.6
Phyllodocidae	0.33	0.89	0.43	1.15	1.89	45.48
Diastylidae	1	0.67	0.43	1.16	1.88	47.37
Ophiactidae	2.11	2.22	0.43	1.12	1.87	49.24
Ophiolepidae	0.56	0.78	0.42	1.11	1.85	51.08
Munnidae	0.22	0.89	0.41	1.07	1.81	52.89
Dorvilleidae	5.67	5.11	0.4	1.08	1.76	54.65
Gnathiidae	0.11	1.22	0.39	0.9	1.71	56.37
Sabellidae	260.33	351.11	0.39	1.42	1.71	58.07
Lysianassidae	1.11	0.33	0.37	0.89	1.61	59.69
Janiridae	1.11	1.89	0.36	1	1.59	61.27
Rissoidae	1.11	1	0.36	0.98	1.58	62.86
Arcidae	1	3	0.36	1.08	1.58	64.44
Astartidae	22.89	46.89	0.36	1.48	1.57	66.01
Isaeidae	0.56	0.33	0.36	0.94	1.57	67.57

Table C6. continued:

Eunicidae	0.56	0.33	0.34	0.92	1.51	69.08
Caprellid	3.78	7.44	0.34	1.24	1.5	70.58
Podoceridae	1	0.33	0.33	0.77	1.47	72.05
Cossuridae	23	33.56	0.33	1.31	1.46	73.51
Terebellidae	8.33	4.89	0.33	0.99	1.46	74.97
Cardiidae	8.11	10.56	0.32	1.48	1.4	76.37
Phoxocephalidae	9.89	17.89	0.31	1.23	1.34	77.71
Pleustidae	0.89	0.22	0.3	0.74	1.31	79.02
Ampharetidae	155.22	163.22	0.3	1.17	1.3	80.32
Lilljeborgidae	0.56	0.11	0.29	0.76	1.29	81.61
Yoldiidae	15.33	15.89	0.28	1.38	1.21	82.82
Paraonidae	48.44	54.67	0.27	1.44	1.2	84.02
Nereidae	2.67	3.56	0.25	0.92	1.09	85.11
Oedicerotidae	0.22	0.22	0.25	0.72	1.08	86.19
Goniadidae	2.78	2.78	0.24	0.99	1.07	87.26
Maldanidae	43.67	54	0.24	1.36	1.06	88.33
Flabelligeridae	1.11	2.56	0.24	0.85	1.03	89.36
Scalibregmatidae	6.78	4.78	0.23	1.36	1.02	90.38

Table C7. Open 2003 vs. Open 2004 Functional Feeding Groups Infauna: SIMPER
Analysis of Dissimilarity between treatments for infaunal functional feeding groups at Open 2003 and Open 2004 sites.

- (S): Selective
- (N): Non-selective

Av. Diss.: 5.40	Open '03	Open '04				
Feeding Groups	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
(S) Deposit feeders	51.67	115.38	2.32	1.58	43.02	43.02
(N) Deposit feeders	820.89	732.5	1.26	1.25	23.24	66.27
Suspension feeders	120.44	119.13	1.1	1.17	20.35	86.61
Carnivores	142.33	140.13	0.72	1.46	13.39	100

Table C8. Open 2003 vs. 4-Yr Closed Sites Functional Feeding Groups Infauna:
SIMPER Analysis of Dissimilarity between treatments for infaunal functional feeding groups at Open 2003 and 4-yr closed sites.

Av. Diss.: 8.56	Open '03	4 yr cl				
Feeding Groups	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Suspension feeders	120.44	324.11	3.36	1.95	39.25	39.25
(N) Deposit feeders	820.89	459.11	2.36	1.3	27.6	66.86
Carnivores	142.33	225.22	1.54	1.73	17.99	84.84
(S) Deposit feeders	51.67	34.89	1.3	1.36	15.16	100

Table C9. 4-Yr Closed Sites vs. Open 2004 Functional Feeding Groups Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal functional feeding groups at 4-yr closed sites and Open 2004.

Av. Diss.: 9.09	4 yr cl		Open '04			
Feeding Groups	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Suspension feeders	324.11	119.13	2.93	1.91	32.23	32.23
(S) Deposit feeders	34.89	115.38	2.75	2.28	30.2	62.43
(N) Deposit feeders	459.11	732.5	2.01	1.63	22.1	84.53
Carnivores	225.22	140.13	1.41	1.86	15.47	100

Table C10. Open 2003 vs. 6-Yr Closed Sites Functional Feeding Groups Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal functional feeding groups at Open 2003 and 6-yr closed sites.

Av. Diss.: 8.68	Open '03		6 yr cl			
Feeding Groups	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Suspension feeders	120.44	445.44	4.4	2.54	50.72	50.72
(N) Deposit feeders	820.89	565.56	1.65	1.23	18.97	69.69
Carnivores	142.33	209.89	1.32	1.65	15.25	84.94
(S) Deposit feeders	51.67	48.44	1.31	1.23	15.06	100

Table C11. 6-Yr Closed Sites vs. Open 2004 Functional Feeding Groups Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal functional feeding groups at 6-yr closed sites and Open 2004 sites.

Av. Diss.: 8.57	6 yr cl		Open '04			
Feeding Groups	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Suspension feeders	445.44	119.13	4.08	3.2	47.63	47.63
(S) Deposit feeders	48.44	115.38	2.18	1.64	25.49	73.13
Carnivores	209.89	140.13	1.17	1.69	13.7	86.83
(N) Deposit feeders	565.56	732.5	1.13	1.48	13.17	100

Table C12. 4-Yr Closed Sites vs. 6-Yr Closed Sites Functional Feeding Groups Infauna: SIMPER Analysis of Dissimilarity between treatments for infaunal functional feeding groups at 4- and 6-yr closed sites.

Av. Diss.: 4.90	4 yr cl	6 yr cl				
Feeding Groups	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Suspension feeders	324.11	445.44	1.81	1.47	36.96	36.96
(N) Deposit feeders	459.11	565.56	1.21	1.17	24.62	61.58
(S) Deposit feeders	34.89	48.44	1.15	1.63	23.55	85.12
Carnivores	225.22	209.89	0.73	1.44	14.88	100

EPIFAUNAL TAXA

Table C13. Open 2003 vs. Open 2004 Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at Open 2003 and Open 2004 sites.

Av. Diss.: 42.20	Open '03	Open '04				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	193.25	314.98	24.06	1.35	57.01	57.01
Pandulus borealis	90.73	107.58	6.86	1.05	16.26	73.27
Porifera	20.24	42.76	4.29	1.05	10.16	83.43
Bolocera tuediae	26.47	45.12	3.88	3.88	9.2	92.63

Table C14. 2-Yr Closed Sites vs. Open 2003 Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 2-yr closed and Open 2003 sites.

Av. Diss.: 45.21	2 yr cl	Open '03				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	197.84	193.25	22.81	1.4	50.45	50.45
Pandulus borealis	38.24	90.73	9.43	1.25	20.86	71.31
Bolocera tuediae	5.33	26.47	3.59	1.25	7.93	79.24
Porifera	9.34	20.24	3.36	0.73	7.42	86.67
Cerianthis borealis	19.05	17.28	3.13	1.38	6.91	93.58

Table C15. 2-Yr Closed Sites vs. Open 2004 Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 2-yr closed and Open 2004 sites.

Av. Diss.: 48.07	2 yr cl	Open '04				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	197.84	314.98	23.47	1.35	47.08	47.08
Pandulus borealis	38.24	107.58	11.22	1.22	22.5	69.59
Bolocera tuediae	5.33	45.12	5.9	1.44	11.83	81.42
Porifera	9.34	42.76	4.05	0.98	8.13	89.56
Cerianthis borealis	19.05	13.97	2.22	1.33	4.45	94.01

Table C16. Open 2003 vs. 4-Yr Closed Sites Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at Open 2003 and 4-yr closed sites.

Av. Diss.: 52.02	Open '03	4 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	193.25	394.11	27.04	1.34	51.99	51.99
Porifera	20.24	153.54	13.11	0.65	25.21	77.19
Pandulus borealis	90.73	54.71	5.58	1.18	10.72	87.92
Cerianthis borealis	17.28	50.34	4.04	1.43	7.76	95.68

Table C17. 4-Yr Closed Sites vs. Open 2004 Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 4-yr closed and Open 2004 sites.

Av. Diss.: 64.18	4 yr cl	Open '04				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	394.11	314.98	28.12	1.68	51.04	51.04
Porifera	153.54	42.76	12.44	0.68	22.57	73.61
Pandulus borealis	54.71	107.58	6.84	1.12	12.42	86.03
Cerianthis borealis	50.34	13.97	3.63	1.35	6.58	92.61

Table C18. Open 2003 vs. 6-Yr Closed Sites Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at Open 2003 and 6-yr closed sites.

Av. Diss.: 66.95	Open '03	6 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	193.25	879.7	36.04	2.16	55.83	53.83
Porifera	20.24	444.55	21.46	1.91	32.06	85.88
Pandulus borealis	90.73	46.67	3.19	1.03	4.77	90.65

Table C19. 6-Yr Closed Sites vs. Open 2004 Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 6-yr closed and Open 2004 sites.

Av. Diss.: 64.18	6 yr cl	Open '04				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	879.7	314.98	33.69	2.06	52.49	52.49
Porifera	444.55	42.76	19.45	1.73	30.3	82.79
Pandulus borealis	46.67	107.58	4.27	0.98	6.65	89.44
Cerianthis borealis	54.44	13.97	2.19	1.13	3.41	92.85

Table C20. 2-Yr Closed Sites vs. 4-Yr Closed Sites Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 2- and 4-yr closed sites.

Av. Diss.: 50.53	2 yr cl	4 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	197.84	394.11	26.01	1.53	51.48	51.48
Porifera	9.34	153.54	13.3	0.63	26.32	77.8
Pandulus borealis	38.24	54.71	4.96	1.44	9.82	87.62
Cerianthis borealis	19.05	50.34	3.5	1.4	6.92	94.55

Table C21. 2-Yr Closed Sites vs. 6-Yr Closed Sites Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 2- and 6-yr closed sites.

Av. Diss.: 66.86	2 yr cl	6 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	197.84	879.7	35.95	2.38	53.77	53.77
Porifera	9.34	444.55	22.41	2.02	33.52	87.29
Cerianthis borealis	19.05	54.44	2.13	1.06	3.18	90.47

Table C22. 4-Yr Closed Sites vs. 6-Yr Closed Sites Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal assemblages at 4- and 6-yr closed sites.

Av. Diss.: 48.07	4 yr cl	6 yr cl				
Taxa	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Molgula sp.	394.11	879.7	22.71	1.67	47.24	47.24
Porifera	153.54	444.55	18.07	1.64	37.58	84.82
Pandulus borealis	54.71	46.67	2.31	1.24	4.8	89.62
Cerianthis borealis	50.34	54.44	2.15	1.21	4.47	94.09

Table C23. Open 2003 vs. Open 2004 Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at Open 2003 and Open 2004 sites.

Av. Diss.: 37.17	Open '03	Open '04				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	259.58	426.94	30.29	1.28	81.49	81.49
Mobile	91.19	108.92	6.88	1.05	18.51	100

Table C24. 2-Yr Closed Sites vs. Open 2003 Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 2-yr closed and Open 2003 sites.

Av. Diss.: 34.14	2 yr cl	Open '03				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	232.21	259.58	26.51	1.37	77.63	77.63
Mobile	52.49	91.19	7.64	1	22.37	100

Table C25. 2-Yr Closed Sites vs. Open 2004 Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 2-yr closed and Open 2004 sites.

Av. Diss.: 35.20	2 yr cl	Open '04				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	232.21	426.94	25.26	1.11	71.76	71.76
Mobile	52.49	108.92	9.94	1.11	28.24	100

Table C26. Open 2003 vs. 4-Yr Closed Sites Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at Open 2003 vs. 4-yr closed sites.

Av. Diss.: 44.69	Open '03	4 yr cl				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	259.58	612.46	39.23	1.68	87.79	87.79
Mobile	91.19	56.73	5.46	1.19	12.21	100

Table C27. 4-Yr Closed Sites vs. Open 2004 Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 4-yr closed and Open 2004 sites.

Av. Diss.: 44.67	4 yr cl	Open '04				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	612.46	426.94	37.9	2.19	84.84	84.84
Mobile	56.73	108.92	6.77	1.13	15.16	100

Table C28. Open 2003 vs. 6-Yr Closed Sites Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at Open 2003 and 6-yr closed sites.

Av. Diss.: 64.51	Open '03	6 yr cl				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	259.58	1479.8	61.5	2.68	95.34	95.34

Table C29. 6-Yr Closed Sites vs. Open 2004 Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 6-yr closed and Open 2004 sites.

Av. Diss.: 59.18	6 yr cl	Open '04				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	1479.8	426.94	55.04	2.26	93	93

Table C30. 2-Yr Closed Sites vs. 4-Yr Closed Sites Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 2- and 4-yr closed sites.

Av. Diss.: 43.59	2 yr cl	4 yr cl				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	232.21	612.46	38.61	2.05	88.59	88.59
Mobile	52.49	56.73	4.98	1.31	11.41	100

Table C31. 2-Yr Closed Sites vs. 6-Yr Closed Sites Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 2- and 6-yr closed sites.

Av. Diss.: 65.65	2 yr cl	6 yr cl				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	232.21	1479.8	63.39	3.24	96.56	96.56

Table C32. 4-Yr Closed Sites vs. 6-Yr Closed Sites Mobility Epifauna: SIMPER Analysis of Dissimilarity between treatments for epifaunal mobility groups at 4- and 6-yr closed sites.

Av. Diss.: 41.13	4 yr cl	6 yr cl				
Mobility	Av. Ab.	Av. Ab.	Av. Diss.	Diss/SD	Contrib%	Cum%
Sessile	612.46	1479.8	38.88	1.94	94.53	94.53

APPENDIX D

DIVERSITY MEASURES

List of taxonomic richness (S), abundance (N), dominance (d), evenness (J'), and Shannon-Weiner diversity H'(loge) for all treatments levels of infaunal and epifaunal assemblages.

INFAUNAL TAXA

Table D1. Open 2003 Infauna Diversity

Site/station	S	N	d	J'	H'(loge)
S14/s1	30	1362	4.018	0.6707	2.281
S14/s2	39	2196	4.939	0.6627	2.428
S14/s3	30	808	4.332	0.6745	2.294
S15/s1	34	1284	4.61	0.6595	2.326
S15/s2	27	787	3.899	0.765	2.521
S15/s3	28	750	4.079	0.7241	2.413
S16/s1	32	1068	4.445	0.6939	2.405
S16/s2	33	1070	4.588	0.6707	2.345
S16/s3	25	936	3.508	0.706	2.272
Averages	30.89	1140.1	4.27	0.69	2.37

Table D2. Open 2004 Infauna Diversity

Site/station	S	N	d	J'	H'(loge)
S25/s1	33	1033	4.611	0.6563	2.295
S25/s2	31	1015	4.334	0.7507	2.578
S25/s3	36	1287	4.888	0.6972	2.498
S26/s1	37	1005	5.208	0.7122	2.572
S26/s2	34	1091	4.718	0.6779	2.391
S26/s3	33	1155	4.538	0.7313	2.557
S27/s1	32	958	4.516	0.7244	2.511
S27/s2	40	1345	5.414	0.7028	2.592
Averages	34.5	1111.1	4.78	0.71	2.49

Table D3. 4-Yr Closed Sites Infauna Diversity

Site/station	S	N	d	J'	H'(loge)
S19/s1	33	1150	4.541	0.7258	2.538
S19/s2	38	938	5.406	0.6763	2.46
S19/s3	35	705	5.184	0.6733	2.394
S20/s1	40	991	5.653	0.6801	2.509
S20/s2	38	995	5.36	0.6918	2.516
S20/s3	38	820	5.515	0.6842	2.489
S21/s1	43	1181	5.937	0.5715	2.149
S21/s2	43	1419	5.787	0.6654	2.503
S21/s3	36	1248	4.909	0.6815	2.442
Averages	38.22	1049.7	5.37	0.67	2.44

Table D4. 6-Yr Closed Sites Infauna Diversity

Site/station	S	N	d	J'	H'(loge)
S22/s1	45	1205	6.202	0.7034	2.678
S22/s2	46	1675	6.062	0.607	2.324
S22/s3	42	1016	5.922	0.7327	2.739
S23/s1	45	1157	6.238	0.6349	2.417
S23/s2	38	1377	5.119	0.5898	2.145
S23/s3	40	1131	5.547	0.6325	2.333
S24/s1	37	1438	4.951	0.6384	2.305
S24/s2	40	1375	5.397	0.686	2.53
S24/s3	35	1156	4.821	0.643	2.286
Averages	40.89	1281.1	5.58	0.65	2.42

EPIFAUNAL TAXA

Table D5. Open 2003 Epifauna Diversity

Site/station	S	N	d	J'	H'(loge)
S14/s2	8	583	1.099	0.545	1.133
S14/s3	8	300	1.228	0.5528	1.15
S15/s1	5	300	0.7013	0.6184	0.9952
S15/s2	4	208	0.5621	0.7889	1.094
S15/s3	4	339	0.515	0.6925	0.96
S16/s3	7	676	0.9208	0.5979	1.163
S17/s1	2	80	0.2282	0.5436	0.3768
S17/s2	5	323	0.6924	0.6719	1.081
Averages	5.38	351.13	0.74	0.63	0.99

Table D6. Open 2004 Epifauna Diversity

Site/station	S	N	d	J'	H'(loge)
S25/s1	7	503	0.9645	0.5613	1.092
S25/s2	6	312	0.8706	0.6883	1.233
S25/s3	7	232	1.102	0.7273	1.415
S26/s1	6	315	0.8691	0.6494	1.164
S26/s2	4	455	0.4903	0.6864	0.9516
S26/s3	7	256	1.082	0.6019	1.171
S27/s1	7	894	0.8829	0.5786	1.126
S27/s2	9	1656	1.079	0.3856	0.8472
S27/s3	6	205	0.9397	0.7202	1.291
Averages	6.56	536.44	0.92	0.62	1.14

Table D7. 2-Yr Closed Sites Epifauna Diversity

Site/station	S	N	d	J'	H'(loge)
S3/s2	7	398	1.002	0.3389	0.6596
S3/s3	8	388	1.174	0.3773	0.7845
S3/s4	7	272	1.07	0.551	1.072
S5/s1	8	188	1.337	0.7394	1.538
S6/s1	7	232	1.102	0.6346	1.235
S6/s2	5	355	0.6813	0.4671	0.7518
S7/s1	4	159	0.5916	0.6573	0.9111
Averages	6.57	284.57	0.99	0.54	0.99

Table D8. 4-Yr Closed Sites Epifauna Diversity

Site/station	S	N	d	J'	H'(loge)
S19/s1	7	538	0.9543	0.3595	0.6995
S19/s2	7	311	1.046	0.6614	1.287
S19/s3	7	1024	0.8656	0.513	0.9982
S20/s1	6	545	0.7934	0.4186	0.75
S20/s2	5	768	0.602	0.4391	0.7066
S20/s3	7	503	0.9645	0.3904	0.7596
S21/s1	7	894	0.8829	0.4023	0.7828
S21/s2	5	823	0.5959	0.3973	0.6395
S21/s3	4	614	0.4673	0.5407	0.7496
Averages	6.11	668.89	0.8	0.46	0.82

Table D9. 6-Yr Closed Sites Epifauna Diversity

Site/station	S	N	d	J'	H'(loge)
S22/s1	6	345	0.8885	0.6321	1.133
S22/s2	7	1355	0.832	0.5882	1.145
S22/s3	7	1865	0.7967	0.552	1.074
S22/s4	8	1926	0.9255	0.4617	0.9601
S22/s5	8	2759	0.8835	0.4266	0.887
S23/s1	7	885	0.8842	0.7163	1.394
S23/s2	6	867	0.7391	0.5768	1.033
S23/s3	9	667	1.23	0.3578	0.7861
S23/s4	8	1835	0.9315	0.3675	0.7641
S23/s5	9	1988	1.053	0.4538	0.9971
S24/s1	10	692	1.376	0.3436	0.7911
S24/s2	9	1161	1.134	0.5108	1.122
S24/s3	10	1992	1.185	0.5129	1.181
S24/s4	8	2239	0.9074	0.395	0.8213
S24/s5	7	1779	0.8017	0.6361	1.238
Averages	7.93	1490.3	0.97	0.5	1.02

APPENDIX E

GRAIN SIZE ANALYSIS

Grain Size analysis of Open 2004 and 6-yr closed sites.

Table E1. Grain Size Percentages: percentage breakdown of each grain size class.

TRT	Site/station	%Gravel	%Sand	%Silt	%Clay
6 yr cl	S22/s1	1.965	71.193	11.575	15.267
6 yr cl	S22/s2	33.142	50.891	5.153	10.814
6 yr cl	S22/s3	30.241	55.634	6.01	8.115
6 yr cl	S23/s1	50.015	28.27	10.919	10.796
6 yr cl	S23/s2	24.69	48.069	10.769	16.472
6 yr cl	S23/s3	7.916	47.597	19.756	24.731
6 yr cl	S24/s1	16.872	43.628	17.877	21.623
6 yr cl	S24/s2	15.558	55.042	3.883	25.517
6 yr cl	S24/s3	25.002	28.049	21.492	25.457
Open '04	S25/s1	19.986	35.687	21.837	22.49
Open '04	S25/s2	7.819	31.164	31.335	29.682
Open '04	S25/s3	7.296	16.123	62.548	14.033
Open '04	S26/s1	5.941	34.408	29.302	30.349
Open '04	S26/s3	1.067	7.14	85.668	6.125
Open '04	S27/s1	10.558	34.693	27	27.749
Open '04	S27/s2	6.931	59.151	11.008	22.91

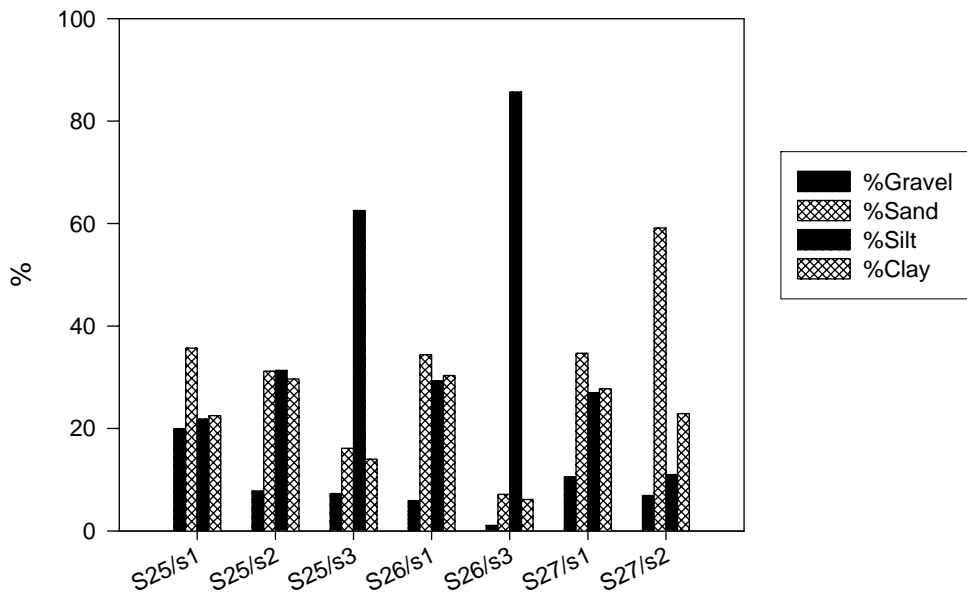


Figure E1. Open 2004 Grain Size: average percentage of gravel, sand, silt and clay at Open '04 sites.

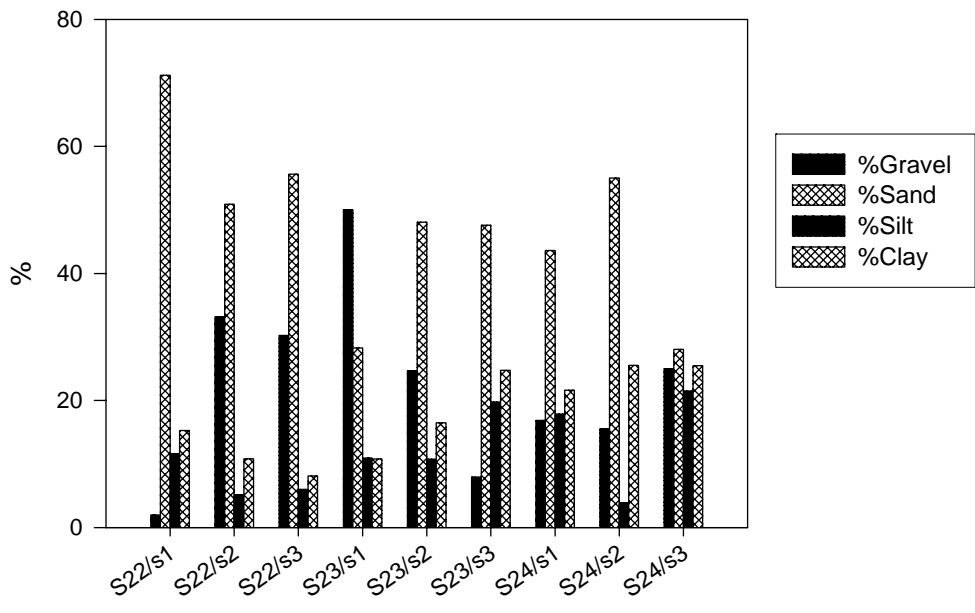


Figure E2. 6-Yr Closed Grain Size: average percentage of gravel, sand, silt and clay at 6-yr closed sites.

BIOGRAPHY OF THE AUTHOR

Emily Patricia Knight was born in Baltimore, Maryland on October 7, 1978. She was raised in Catonsville, Maryland and graduated from Catonsville Public High School in 1996. She attended Salve Regina University in Newport, RI on a Dean's Scholarship where she majored in Biology with a minor in Psychology. While at Salve, she was awarded the Regina Scholarship in the fall of 1997. In the summer of 1999 she attended Sea Education Association in Woods Hole, Massachusetts where she spent a month at sea in the N. Atlantic as a student of Nautical Science, Maritime History, and Oceanography aboard the brigantine *Corwith Cramer*. In May 2000, Emily received her B.S. in Biology and was also awarded the Environmental Science Award by her department. Upon graduation, Emily went to work for South St. Seaport Museum in New York City as the education coordinator for the 19th century schooner *Pioneer*. She later began graduate work at the University of Maine in September 2002.

After receiving her degree, Emily will be moving to Washington D.C. to work on Capitol Hill in the legislature as a Knauss Fellow in Marine Policy. Emily is currently a candidate for the Master of Science degree in Oceanography from the University of Maine in December 2005.