Dynamics of Hard Substratum Communities Inside and Outside of a Fisheries Habitat Closed Area in Stellwagen Bank National Marine Sanctuary (Gulf of Maine, NW Atlantic)

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Dynamics of Hard Substratum Communities Inside and Outside of a Fisheries Habitat Closed Area in Stellwagen Bank National Marine Sanctuary (Gulf of Maine, NW Atlantic)

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Cover

A diversity of organisms live on hard substratum surfaces in the deep waters of Stellwagen Bank National Marine Sanctuary.

Suggested Citation

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Abstract

The dynamics of gravel and boulder reef invertebrate community structure in areas inside and outside a closed fisheries habitat that overlaps Stellwagen Bank National Marine Sanctuary were analyzed based on time-series photographic transects from 1998-2005. The effectiveness of this protected area was evaluated based on three common predictions that emerge from previous studies of fishing impacts and the performance of temperate marine protected areas. We determined if: (1) gravel and boulder habitats have similar community composition, (2) community structure diverged between fished and unfished sites attributable to chronic fishing impacts, (3) structure forming invertebrates increased in abundance within the protected area, and (4) diversity increased within the protected area. Overall our results demonstrate that community structure over the seven years since closure in 1998 has been dynamic across both habitat types as well as within and outside the Western Gulf of Maine Closure (WGOMC) despite a high degree of similarity between paired habitat stations at the time of closure. Comparisons of each habitat type inside and outside the closure across years in regards to community structure, populations of component taxa, and patterns of diversity all demonstrated a response to the closure but not in ways that are normally predicted from previous closed areas studies. Despite the presence of hard substratum resources in both boulder and gravel habitats, community structure was different between habitat types across all years. Community structure changed across time both inside and outside the WGOMC suggesting, at least to-date, recovery without resilience. While community composition tended to be more similar within each station than between each year, the pattern of similarity from 2005 transects suggest a greater degree of difference in composition between replicates from inside gravel and boulder stations than those paired stations outside. This pattern suggests the dominance of local processes, such as predation and competition, may be driving community composition inside the closed areas (i.e., contributing to greater variation in the distributions of taxa within stations). This is in contrast to larger spatial scale disturbance processes, produced either by natural events or by fishing activities that dominate at outside stations. Species populations and community structure within the closed area have yet to reach any stable configuration. Interestingly, structural guilds and population trajectories of component taxa changed over time in unpredictable ways. We predicted that structure forming invertebrates would increase in abundance over time within the protected area due to elimination of fishing gear disturbance and a recovery of erect and emergent fauna. However, only encrusting forms at the boulder stations outside the closed area increased significantly from 1998 to 2005. Finally, the expected increase in species diversity at stations within the WGOMC was not observed by the end of the study period at either gravel or boulder stations. Overall the findings indicate that the WGOMC is having a significant impact on invertebrate community structure and that the community inside the closure area on both boulder and gravel habitats is recovering from chronic fishing gear impacts. However, community structure is dynamic and that "recovery" of the seafloor community does not necessarily lead to a climax community.

Key Words

Marine protected area, resilience, recovery, disturbance, benthic, fishing, photography

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Introduction

The National Marine Sanctuary Act (NMSA) requires that marine sanctuaries are managed to allow multiple uses (e.g., fishing), assuming that those activities are compatible with the primary goal, which is resource protection. However, there are no clear metrics and reference points to trigger management actions (Samhouri et al. 2010) and information to guide decision-making is often fragmented and incomplete. The need to balance human uses of the marine environment with the conservation of biological diversity requires knowledge of how particular activities affect diverse populations and communities within particular habitats (Barr 1995). Further, the reauthorization of the Magnuson Fishery Conservation and Management Act in 1996 mandated the identification and protection of Essential Fish Habitat (EFH) defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity" (Schmitten 1999), but like the NMSA, there are no clear reference points for action. One management strategy to conserve EFH and biological diversity overall is the use of year-round closed areas (National Research Council 2002). Such areas have been used off the northeast United States, both as ad hoc areas of habitat protection when regions were closed to reduce fishing mortality on selected species as well as areas closed specifically for habitat management (Link et al. 2005, Murawski et al 2005). Gravel and boulder habitats are of particular concern as attributes of habitat complexity have been linked to survivorship of species of economic importance (Auster et al. 1996, Auster 1998, Lindholm et al. 1999, 2001).

Bottom contact fishing gears have been found to have significant effects on seafloor communities and habitats (e.g., Watling and Norse 1998, Auster and Langton 1999, National Research Council 2002, Kaiser et al. 2006). In particular, use of mobile gear can reduce habitat complexity by removing and damaging emergent fauna, smoothing seafloor features (e.g., small patches of piled boulders and sand waves), and removing structure producing taxa (e.g., crabs and fish that produce depressions and burrows; Auster 1998, Auster et al. 1996, Collie et al. 1997, Collie et al. 2005,). Long-term studies to evaluate recovery rates under a variety of conditions, both in terms of gear type and community settings, are rare (Auster and Langton 1999, Kaiser et al. 2006). Two meta-analyses of results from available gear impact studies around the globe, across a range of gear types and from multiple habitats, suggest recovery times of hard substrate communities in temperate ecosystems on the order of 8-10 or more years (Collie et al. 2000, Kaiser et al. 2006). Empirical studies of gravel habitat communities on the Northeast Peak of Georges Bank, subject to strong tidal currents and a well-mixed water column, have recovery times in excess of ten years based on time-series monitoring (Collie et al. 2005). Such patterns are consistent with our understanding of the life histories of many large habitat-forming epifaunal species (e.g., sponges, corals, calcareous worms, bryozoa) that tend to be long-lived and ill-adapted to frequent disturbance (Auster et al. 1996, Watling and Norse 1998). In this region undisturbed deep-water gravel habitats were found to have increased biomass, species richness, and species abundance relative to comparable gravel sites in fished areas (Collie et al 2005).

The results of these previous studies indicate that hard-substratum epifaunal communities are not likely resilient to disturbances by fishing gear but can recover. The resilience of a community can be evaluated by determining if the community: 1) can be disturbed and recover to its prior state; 2) is able to resist the disturbance (i.e., remains essentially unchanged following a disturbance event); or 3) shifts to another state following a disturbance event (Palumbi et al. 2008). Communities that exhibit resilience to disturbance will either rapidly return to the pre-disturbed state (recovery) or remain fundamentally unchanged following a disturbance (resilient). Communities that are not resilient to disturbance will recover to an altered community state (Auster and Langton 1999). Prior studies indicate that hard-substrate habitats may exhibit some level of resilience to disturbance by reaching a state of "recovery" within a particular time period. Alternatively, recovery may indicate the community is not resilient to disturbance, and instead shifts to an alternative community state.

There are two generally accepted models of community dynamics (see Auster and Langton 1999 and references therein). The first is the traditional linear successional model where a disturbed community recruits "pioneer" species that alter the local environment to a state favorable to recruitment of sequential "intermediate" species, that then further modify an environment to be suitable for recruitment and development of a sustained "climax" community. The second model is a lottery-based model where shifts in the community structure result from competition among species or disturbance events that alter the environment to one that favors a different community composition. In such a model, the shifts in the community structure are not predictable and do not follow a sequential successional pattern. Communities that fit either model may be resilient to disturbances. In the successional model, resilient communities that are subjected to disturbance may: 1) remain unchanged (i.e., resilient), or 2) revert back to a prior state or may "skip" a step in the linear progression to the climax community, but will always return to the climax community state over time (i.e., recovery). In the lottery-based model, disturbed communities may remain unchanged following disturbance (i.e., resilient); or 2) shift to another stable community state (i.e., recovery without resilience). To evaluate the model that applies in a community subjected to disturbance a stable state must be reached and maintained.

Stellwagen Bank National Marine Sanctuary (SBNMS) is a multiple use marine protected area located in the western Gulf of Maine. The sanctuary contains Stellwagen Bank as well as many other high relief topographic features composed of a range of coarse substratum (Battista et al. 2006). The eastern side of Stellwagen Bank is isolated from sediment sources while sands that drape a gravel pavement on the top of the bank are eroding over time. Tidal currents are weak and reach maximum speeds of 20–30 cm s^{-1}. However, the bank lies in the path of strong northeasterly storms and currents generated by storm waves in the deep waters of the Gulf of Maine modify the seabed as they pass over the bank to depths of 50 – 80 m (Valentine & Schmuck 1995). Internal waves impinge on the bank and affect rates of food delivery and invertebrate larvae for recruitment at the seafloor (Battista et al. 2006, Haury et al. 1983, Witman et al. 1993).

The Western Gulf of Maine Closure (WGOMC), a fisheries closure implemented in 1998

(Murawski et al. 2005), encompasses approximately 21% of SBNMS and includes gravel pavement and boulder reef habitats. Originally the closure prohibited the use of mobile fishing gear capable of catching groundfish species such as cod and haddock. In 2004, the closure was redesignated as a habitat closure and all mobile, bottom-tending fishing gear was prohibited. However, lobster traps, recreational hook-and-line, and mid-water trawls are still allowed in the closure area.

Here we report on the dynamics of gravel and boulder reef invertebrate community structure inside and outside the WGOMC within SBNMS from 1998 - 2005. Further, we evaluate the effectiveness of this marine protected area based on four common issues that emerge from previous studies of fishing impacts and the effectiveness of temperate marine protected areas (e.g., Auster and Shackell 2000, Auster and Langton 1999, Link et al. 2005). In particular, we determine if: (1) gravel and boulder habitats have similar community composition, (2) community structure diverges between fished and unfished sites attributable to chronic fishing impacts, (3) structure forming invertebrates increase in abundance within the protected area, and (4) diversity increases within the protected area. Based on the results of these comparisons, we address issues of resilence and their fit to models of community dynamics. While time series data will continue to be collected at these stations, the results in this report have implications for management of biological diversity within SBNMS as well as management of EFH across the Gulf of Maine region.

Materials and Methods

Sample Collection

Monitoring of seafloor communities on a near annual basis was performed inside and outside the WGOMC in Stellwagen Bank National Marine Sanctuary using underwater still and video imaging (Appendix 1, Table 1). Replicate transects at each habitat (i.e., gravel and boulder) by fishing treatment (inside and outside the closed area) were conducted over a seven year time period from 1998 to 2005. Paired stations for each habitat type were chosen at the time of closure (i.e., 1998) based on knowledge of seafloor geology from a continuous coverage multibeam sonar map (Valentine et al. 2003) as well as direct observations made from underwater video of the seafloor . Station selection was constrained by minimizing differences in depth and distance to the greatest extent possible between stations within each habitat treatment (Figure 1). A minimum of three transects composed of twenty photographs each (one photo per minute for the duration of a twenty minute transect) were conducted at each station during each year. Three different vehicle platforms were used to capture seafloor images over the time series (i.e., two different ROVs and a camera sled) but all acquired data in the same manner. Photographs were obtained using a down-looking 35mm film camera with an electronic flash unit for illumination. Two lasers mounted in parallel (20 cm spacing) were used to calibrate images and to maintain camera height at 0.75 m. Area of each photograph was nominally 0.39 m^2. The three transect lines were offset by approximately 50 m at each station in order to ensure no areas of overlap and independence of photographs between transects. Transects were conducted by drift or

active motoring depending on the support vessel. While there was year-to-year variation in the exact location of transects, all were conducted within an approximate 0.50 km
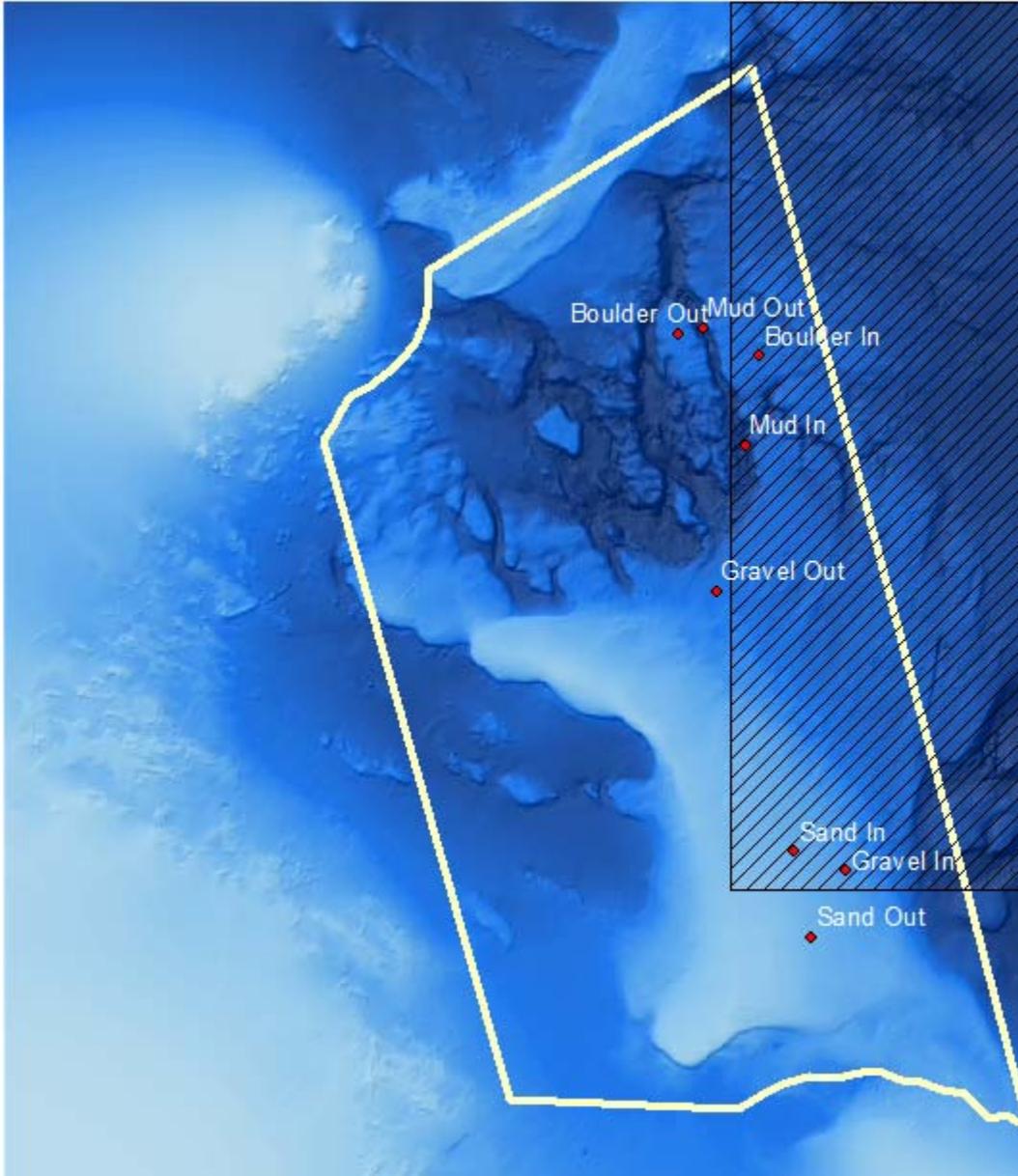
Figure 1. Location of sampling stations in the Stellwagen Bank National Marine Sanctuary. Hatched area is Western Gulf of Maine Closure (WGOMC). Boundary in white is Stellwagen Bank National Marine Sanctuary. Sampling stations are noted by substrate type. Sand and mud stations were evaluated using different methods and will be reported elsewhere.

radius of the sample station. Invertebrate fauna recorded in the photographs were identified to the lowest possible taxonomic level and enumerated as either total counts or, if highly abundant, extrapolated by sub-sampling. A digital still camera was used during 2003 and 2004 and subsequent analysis revealed that images did not resolve some important taxa as well as 35 mm film. Therefore, these years were excluded from this analysis. Analyses presented here include data from 1998, 2001, 2002, and 2005.

In order to reduce bias from stations where additional transects were performed in a particular year, only photographs obtained from the first three transects were used for analysis. Photographs containing greater than 20% shadow, where it was not possible to identify organisms, were excluded. Imagery obtained during 1998 and 2001 was analyzed by a previous observer (Douglas McNaught, Brown University) while we analyzed photographs obtained during the 2002 and 2005 sampling years. In order to minimize bias in the data produced by two sequential observers we selected and analyzed photographs from 1998 and 2001 to comport species identifications. This exercise resulted in aggregating some species into higher taxonomic groupings (see Appendix 1, Table 2 for a list of taxa used in this study).

Analysis

Multivariate approaches utilized the PRIMER version 5.2.9 software and were used to compare community composition and patterns of diversity between habitats, years, and closure status (Clarke and Warwick 2001). Similarity matrices, based on the Bray-Curtis similarity coefficient, were produced using mean taxon counts per transect for each year. Mean abundance of each taxon per transect was used to account for occasional differences in transect sample size (e.g., early termination of transects due to weather or other logistical constraints). Similarity matrices were produced for gravel and boulder habitats separately as well as a global similarity matrix that included both habitat types. Non-metric multidimensional scaling (MDS) was used to visualize and evaluate the similarity in species composition between treatments. The relative similarity of the community structure for each sample site (i.e., each transect, each year at both gravel and boulder stations) was plotted in a non-metric space to evaluate the relative similarity of each sample location to each other sample site. Analysis of similarities (ANOSIM) tests were performed on similarity matrices for each habitat type to evaluate differences in contributions of each taxon between habitat type, years sampled and closure status. For each ANOSIM test where a significant difference ($p<0.05$) was identified between treatments, similarity percentage - species contributions (SIMPER) analyses were performed to identify the top 10 taxa most responsible for the dissimilarity between the groups. Standardized un-transformed means for each taxon were used for all SIMPER analyses.

Analysis of variance (ANOVA) using the general linear model was performed to elucidate patterns at the level of individual taxa. A global model including three main effects (habitat type, year, and closure status) and four interactions terms was used to test all taxa for significant differences. Taxa identified in the SIMPER analyses were also separated by habitat type where the model included two main effects (year and closure status) and one interaction term to test for significant differences. Additional ANOVAs were performed using the same global model on structural groups. Species abundance data were aggregated *a priori* into three structural groups in order to generalize the role of invertebrate species as structural components of fish habitat: 1) encrusting forms (e.g. *Didemnum* species, encrusting sponges and bryozoans), 2) erect-emergent forms (e.g. *Terebratulina septentrionalis, Tubularia indivisa*, sabellid worms, cerianthid anemones),

and 3) mobile species (e.g., crustaceans, echinoderms).

ANOVAs conducted for individual taxa and structural groups were performed using square-root transformed mean abundance per transect data to satisfy homogeneity of variance (HOV) requirements. Homogeneity of variance was determined for each taxon using either Bartlett's or Levene's test statistic depending on violation of the normality assumption. As the ANOVA is fairly robust to violations of normality, when the normality assumption was not met, Levene's test statistic for HOV was used (Dytham 1999, Sokal and Rohlf 2001).

Species diversity measures (i.e., species richness, Shannon-Weiner, and Simpson) were calculated for each transect for comparison by univariate ANOVA, again using the general linear model. The Shannon-Weiner diversity index responds to changes in the number of rare species in a sample while the Simpson diversity index is sensitive to the number and abundance of dominant species. Diversity indices were compared based on habitat, year, and closure status. Shannon-Weiner and Simpson indices were transformed to satisfy HOV requirements (Shannon index was cubed, Simpson index was squared).

K-dominance curves were produced using mean abundance values for each taxa.   All taxa were ranked by abundance and the percentage of each taxon contributing to the the total number of individuals in each year was plotted cumulatively against taxon rank. Abundance data was plotted for individual habitat types by year and closure status, for all years by closure status, and for closure status by year in order to evaluate changes in the relative dominance of the most abundant taxa over time and between habitats within and outside the WGOMC.

Results

A total of 928 photographic images were analyzed in which 41,690 individuals or colonies were counted and assigned to 78 taxonomic categories (species and species groups) and 3 structural groups (Appendix 1, Table 2). Based on the structural group classification, 11 (14.1%) taxa were encrusting, 39 (50.0%) erect-emergent, and 28 (35.9%) were mobile.

The results of two-dimensional non-metric MDS revealed differences in community structure based on habitat type, year and closure status (Figure 2). Separate MDS procedures for each habitat type by year and closure status illustrate the shifts in community structure through time and by closure status (Figure 3a and b). Both gravel and boulder stations outside and inside the closure area changed over time from relatively similar community structures at the time of closure in 1998. Both the gravel inside and outside stations changed through time, but the outside station exhibited less change from the initial community state based on relative distances in the MDS plot. The boulder stations exhibited the same general type of pattern as the gravel stations.

A two-way ANOSIM revealed significant differences in community structure between years in gravel habitats (R=0.897, p=0.001) and between inside and outside stations

(R=0.880, p=0.001). There were also significant differences in pairwise comparisons of all years (p=0.01 for all comparisons; Table 1). Similar results were obtained for boulder habitats. There were significant differences between years (R=0.730, p=0.001) and between stations inside versus outside the closed area (R=0.759, p=0.001). There were also significant differences in invertebrate community composition for all years based on pairwise comparisons (p=0.01 for all comparisons; Table 1). A one-way ANOSIM comparing taxon composition between gravel and boulder habitats revealed significant differences in taxon abundances (R=0.421, p=0.01).

Of the top ten taxa identified by SIMPER, analysis comparing community composition and abundance of individual taxa between gravel and boulder habitats, four taxa were more abundant at gravel stations while six taxa were more abundant at boulder stations (Table 2). Seven of the 10 taxa contributing to nearly 67% of the dissimilarity between boulder and gravel habitats were structure forming invertebrates classified as erect-emergent. Analysis of the community composition of gravel habitats based on closure status identified a total of four taxa in greater abundance inside the closure and six were more abundant outside (Table 3). Here, seven of the taxa contributing to the dissimilarity were erect-emergent forms. However, while the erect *Iophon* spp. and erect bryozoa were most abundant inside the closed area *Terebratulina septentrionalis*, serpulid spp., and *Cerianthus borealis* were most abundant outside. Pairwise comparisons of both gravel stations between years using SIMPER revealed differences in taxon abundance patterns that did not produce clear directionality in terms of increases in dominant taxa (Table 4).

Similarly, of the top ten taxa contributing to the dissimilarity between boulder stations inside and outside the closure area identified by SIMPER analysis three taxa were more abundant at stations inside while seven taxa were more abundant outside the closed area (Table 5). Seven taxa, contributing to nearly 79% of the dissimilarity between stations, were erect-emergent forms. The ascidian *Molgula* spp. was more than twice as abundant at the inside station while the brachiopod *Terebratulina septentrionalis* was more than six times as abundant at the outside station. Two species or forms of *Iophon* were also more abundant outside. Pairwise comparisons of both boulder stations between years using SIMPER most strikingly reveal this pattern (Table 6).

K-dominance curves of gravel communities did not reveal any clear shifts in the patterns of dominance of taxa by year or closure status (Figures 4 a, b). However, patterns in the curves of boulder communities illustrate a marked increase in the cumulative percent dominance of the highest ranked taxa beginning in 2002 at stations inside the closure area (Figure 4c). The shape of the dominance curves at the boulder stations outside the WGOMC display a slight but consistent increase in abundance of top ranked taxa over time (Figure 4d).

The global ANOVA revealed a total of 20 taxa that differed significantly (p<0.05) in abundance based on closure status (Table 7a). Overall, 68 of 79 taxa exhibited one or more statistically significant differences based on comparisons of habitat type, year, and closure status. Of these a total of 21 taxa were identified to contribute to the

dissimilarity between stations by the previous SIMPER analyses. ANOVAs for each habitat type revealed all but five of the 21 taxa had significant differences in abundance based on closure status (Table 7b). Changes over time in the mean abundance for the 21 taxa at each station are summarized in Figure 5. Pairwise comparisons by closure status and year for each habitat type identified significant changes in the mean abundance of 20 taxa (Table 8). Pairwise comparisons also revealed differences in taxon abundance patterns that did not produce clear directionality in terms of increases or decreases in abundance over time based on closure status at gravel stations. At boulder stations, pairwise comparisons revealed significantly higher abundances of *T. septentrionalis* and associatied encrusting species *P. sulfurous* at stations outside the closure and significantly higher abundances of Asteroidea species at outside stations beginning in 2002 (see Appendix 2 for pairwise comparisons across all years).

Results of the global ANOVA based on structural group designations demonstrated that all groups differed significantly in abundance based on habitat type, year, and the habitat type by year interaction term (Table 7c). At gravel stations, all structural groups differed significantly in abundance by year but only the erect-emergent fauna differed significantly (p=0.062) based on closure status (Table 7d). Additionally, both the erect-emergent structural group and mobile fauna differed significantly in the year by closure status interaction term (Table 7d). At boulder stations, all structural groups differed significantly across years and only encrusting fauna differed significantly based on closure status (Table 7e). Pairwise comparisons by closure status and across years for each habitat type also revealed differences in the abundance of structural groups that did not produce clear trends over time (Table 9 and Appendix 2).

In general, species diversity differed significantly based on habitat types, years, and closure status (Figures 6 and 7). The global analysis of the Shannon-Wiener index revealed significant differences by year, habitat, and all interaction terms, including interaction terms with closure status (ANOVA, all p<0.05), but not closure status alone (Table 10). Separate analyses based on habitat type revealed a significant difference in the year by closure status interaction term at boulder stations but not at gravel stations. Finally, there were significant differences by year for both habitat types.

The global analysis of the Simpson diversity index revealed significant differences (ANOVA, p<0.05) in species diversity for all main effects and interaction terms except habitat type (Table 10). Separate analyses based on habitat type revealed significant differences (p < 0.01) in diversity across years at gravel habitats, but there were no significant differences in closure status, or the interaction of year and closure status (Table 10). For boulder habitats, there were significant differences (p < 0.01) by year, closure status, and the interaction between year and closure status (Table 10). For each habitat type, both the Shannon-Wiener and Simpson index values fluctuated over time and were higher at stations located outside the WGOMC with the exception of the boulder stations in 2001 (Table 9). At gravel stations, species richness was not significantly different based on closure status or the interaction term of year by closure status, but was significantly different across years (ANOVA, p < 0.05; Table 10). Species richness at gravel stations varied over time, but exhibited an overall decline from

1998 to 2005. At the boulder stations, species richness differed significantly based on the year by closure status interaction term (ANOVA, p< 0.05), but there was no significant difference between years or closure status (Table 10). Species richness was relatively stable across years and among stations, but in 2001 there was a decrease in richness at the boulder station outside the closure area (Figure 7c).
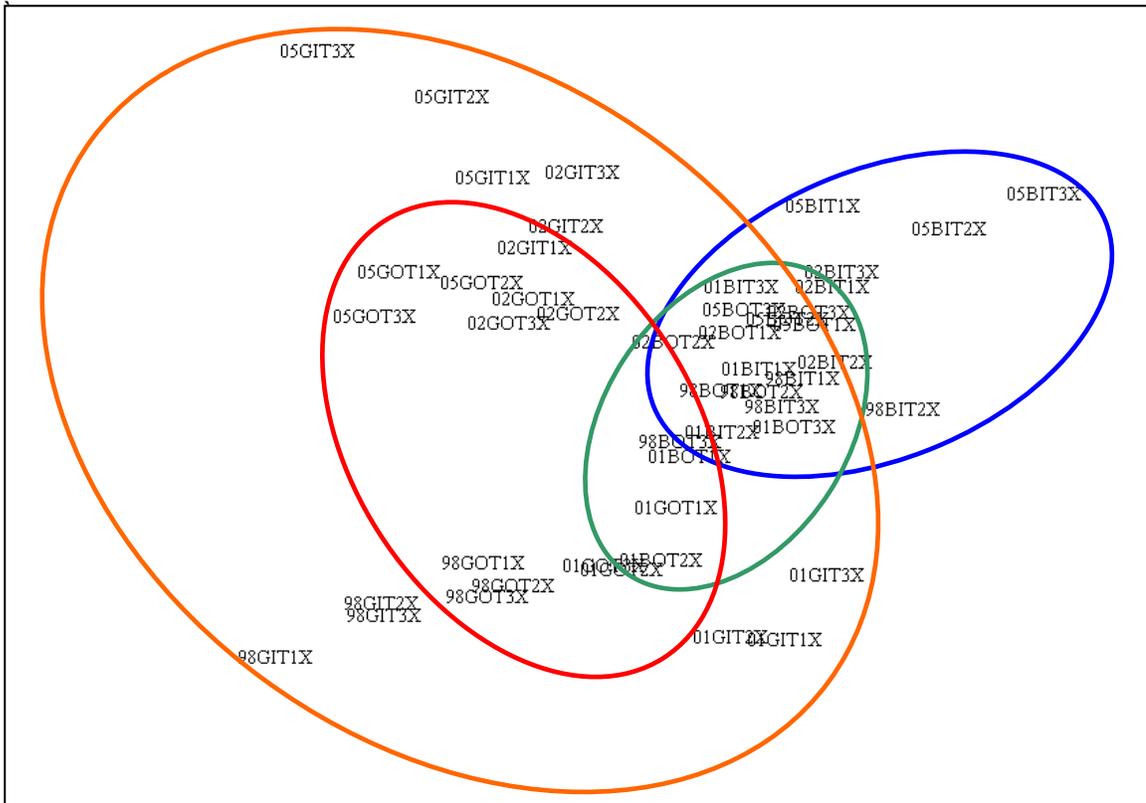
Figure 2. MDS of gravel and boulder habitat community composition. Non-metric multidimensional scaling (MDS) ordination for community composition at gravel and boulder stations (based on a Bray-Curtis similarity matrix). The naming convention of the stations is 98GIT1, where the first two numbers indicate the year, the first letter indicates the habitat type, the second the closure status, and the third letter and last number indicate the transect number. The letter X denotes the location of the station on the plot. The codes are as follows: G = gravel, B = boulder, I = inside the closed area, and O = outside the closed area. The grouping of each substrate type by closure status is encircled by solid lines.

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Figure 3. Non-metric multidimensional scaling plot illustrating community dynamics by habitat type over time; a. gravel habitats, b. boulder habitats. Refer to Figure 2 for label code. The grouping of stations by closure status and sampling years is encircled by solid lines.

Table 1. Analysis of similarities (ANOSIM) between habitat types; and within each habitat type between closure status and sample years. Significant p-values (p<0.100) indicate the analyzed terms are signigicantly different from eachother.

	Gravel					Boulder			
	1998	**2001**	**2002**	**2005**		**1998**	**2001**	**2002**	**2005**
1998		p = 0.01	p = 0.01	p = 0.01	**1998**		p = 0.01	p = 0.01	p = 0.01
2001			p = 0.01	p = 0.01	**2001**			p = 0.01	p = 0.01
2002				p = 0.01	**2002**				p = 0.01
2005					**2005**				
	Closure Status **p = 0.001**					Closure Status **p = 0.001**			
	Habitat Type **p= 0.001**								

Table 2. SIMPER analysis of data by habitat type. Taxa contributing to the dissimilarity (D), based on mean abundance (M.A.), between gravel and boulder habitats (average dissimilarity of the mean abundance of taxa = 70.49).

Species	Gravel M.A.	Boulder M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	0.56	25.72	12.21	1.24	17.33	17.33
Erect *Iophon* spp.	2.36	2.14	6.39	1.07	9.06	26.39
Terebratulina septentrionalis	1.72	8.40	5.10	1.31	7.24	33.63
Serpulid spp.	1.89	1.56	3.90	0.83	5.54	39.16
Cerianthus borealis	1.35	0.68	3.73	1.04	5.29	44.45
Erect bryozoan spp.	1.33	5.46	3.47	1.36	4.93	49.38
Encrusting red sponge spp.	2.02	3.93	3.19	1.19	4.52	53.90
Iophon pattersoni	0.93	4.98	3.13	1.08	4.45	58.35
Encrusting *Iophon* spp.	1.67	3.20	3.03	1.25	4.30	62.65
Encrusting yellow sponge spp.	1.12	0.82	2.77	0.64	3.93	66.57

Table 3. SIMPER analysis of data for gravel habitats by closure status. Taxa contributing to the dissimilarity (D), based on mean abundance (M.A.), at gravel habitats inside and outside the WGOMC (average dissimilarity of the mean abundance of taxa = 72.69).

Taxa	Inside M.A.	Outside M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Erect *Iophon* spp.	2.63	2.08	7.12	1.18	9.80	9.80
Terebratulina septentrionalis	0.09	3.35	6.53	1.35	8.98	18.78
Serpulid spp.	1.37	2.41	5.37	0.98	7.39	26.17
Erect bryozoan spp.	2.58	0.08	5.06	1.70	6.96	33.13
Cerianthus borealis	0.80	1.90	4.92	1.57	6.76	39.89
Encrusting red sponge spp.	2.47	1.56	4.36	1.21	6.00	45.89
Encrusting yellow sponge spp.	1.08	1.16	4.14	0.81	5.70	51.59
Encrusting *Iophon* spp.	1.53	1.81	3.79	1.20	5.21	56.81
Iophon pattersoni	0.01	1.84	3.55	1.22	4.88	61.68
Holothurian spp.	0.56	0.50	2.71	0.86	3.72	65.41

Table 4. SIMPER analysis of data for gravel stations between years. Taxa contributing to the dissimilarity (D), based on mean abundance (M.A.), between years at gravel habitats.

a. Gravel Years 1998 and 2001 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 65.73)

Taxa	1998 M.A.	2001 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Erect *Iophon* spp.	1.96	4.82	8.96	1.74	13.63	13.63
Cerianthus borealis	2.55	0.58	8.25	3.82	12.55	26.18
Holothurian spp.	1.78	0.00	6.71	4.88	10.21	36.39
Terebratulina septentrionalis	0.76	3.48	6.41	1.10	9.75	46.14
Asterias vulgaris	0.98	0.30	3.95	1.11	6.00	52.14
Iophon pattersoni	0.31	1.81	3.37	1.00	5.13	57.27
Filograna implexa	0.03	1.03	3.24	1.16	4.93	62.21
Erect bryozoan spp.	0.38	0.85	2.93	1.18	4.45	66.66
Molgula spp.	0.01	0.91	2.69	1.14	4.09	70.75
Encrusting bryozoan spp. (pink)	0.66	0.41	2.57	1.10	3.92	74.67
Encrusting red sponge spp.	0.23	0.19	0.84	1.22	1.28	

b. Gravel Years 1998 and 2002 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 76.22)

Taxa	1998 M.A.	2002 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Encrusting red sponge spp.	0.23	6.38	8.55	3.13	11.21	11.21
Cerianthus borealis	2.55	1.12	8.14	5.45	10.68	21.89
Encrusting *Iophon* spp.	0.06	4.34	6.92	2.66	9.08	30.97
Holothurian spp.	1.78	0.31	6.24	4.38	8.19	39.16
Serpulid spp.	0.00	3.23	5.01	5.02	6.57	45.72
Erect *Iophon* spp.	1.96	2.23	4.59	1.76	6.02	51.75
Erect bryozoan spp.	0.38	3.48	4.38	1.13	5.75	57.49
Asterias vulgaris	0.98	0.03	4.04	0.95	5.30	62.79
Terebratulina septentrionalis	0.76	1.98	3.62	1.18	4.74	67.54
Encrusting bryozoan spp. (pink)	0.66	0.07	2.50	0.89	3.29	70.82

c. Gravel Years 1998 and 2005 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 80.84)

Taxa	1998 M.A.	2005 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Serpulid spp.	0.00	4.32	10.63	1.79	13.15	13.15
Encrusting yellow sponge spp.	0.00	3.13	8.69	1.47	10.75	23.90
Cerianthus borealis	2.55	1.14	7.56	2.75	9.35	33.25
Holothurian spp.	1.78	0.02	6.68	4.85	8.26	41.51
Erect *Iophon* spp.	1.96	0.43	6.67	2.44	8.25	49.76
Encrusting *Iophon* spp.	0.06	1.88	4.62	1.52	5.71	55.47
Asterias vulgaris	0.98	0.03	4.05	0.95	5.01	60.48
Caridean shrimp	0.28	0.43	3.14	0.64	3.89	64.36
Pagurus spp.	0.04	0.10	2.70	0.50	3.34	67.70
Encrusting bryozoan spp. (pink)	0.66	0.00	2.56	0.90	3.17	70.87

Table 4. Continued.

d. Gravel Years 2001 and 2002 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 72.49)

Taxa	2001 M.A.	2002 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Erect *Iophon* spp.	4.82	2.23	12.29	1.97	16.95	16.95
Encrusting red sponge spp.	0.19	6.38	9.19	3.48	12.68	29.63
Terebratulina septentrionalis	3.48	1.98	6.59	1.14	9.09	38.72
Encrusting *Iophon* spp.	0.39	4.34	6.19	2.27	8.54	47.27
Serpulid spp.	0.02	3.23	4.96	4.96	6.85	54.11
Erect bryozoan spp.	0.85	3.48	4.49	1.21	6.19	60.31
Iophon pattersoni	1.81	1.31	3.66	1.11	5.06	65.36
Filograna implexa	1.03	0.42	2.91	1.08	4.02	69.38
Encrusting yellow sponge spp.	0.02	1.33	2.06	2.32	2.85	72.23
Molgula spp.	0.91	1.18	1.95	1.04	2.69	74.92

e. Gravel Years 2001 and 2005 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 82.59)

Taxa	2001 M.A.	2005 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Erect *Iophon* spp.	4.82	0.43	14.54	2.33	17.61	17.61
Serpulid spp.	0.02	4.32	10.59	1.78	12.82	30.43
Encrusting yellow sponge spp.	0.02	3.13	8.66	1.47	10.49	40.91
Terebratulina septentrionalis	3.48	0.65	6.38	1.00	7.72	48.63
Encrusting *Iophon* spp.	0.39	1.88	3.98	1.32	4.82	53.46
Caridean shrimp	0.03	0.43	3.66	0.71	4.43	57.88
Iophon pattersoni	1.81	0.28	3.35	0.94	4.06	61.95
Filograna implexa	1.03	0.39	3.02	1.27	3.66	65.61
Erect bryozoan spp.	0.85	0.63	2.91	1.24	3.53	69.14
Encrusting red sponge spp.	0.19	1.27	2.80	1.66	3.39	72.52

f. Gravel Years 2002 and 2005 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 58.96)

Taxa	2002 M.A.	2005 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Encrusting yellow sponge spp.	1.33	3.13	7.29	1.43	12.36	12.36
Encrusting red sponge spp.	6.38	1.27	6.58	2.13	11.15	23.51
Serpulid spp.	3.23	4.32	5.99	1.06	10.16	33.67
Erect bryozoan spp.	3.48	0.63	4.35	1.18	7.38	41.05
Encrusting *Iophon* spp.	4.34	1.88	3.76	1.43	6.37	47.43
Caridean shrimp	0.45	0.43	3.33	0.67	5.64	53.07
Terebratulina septentrionalis	1.98	0.65	3.28	1.04	5.56	58.63
Pagurus spp.	0.00	0.10	2.67	0.48	4.52	63.15
Cerianthus borealis	1.12	1.14	2.50	1.57	4.24	67.39
Erect Iophon spp.	2.23	0.43	2.31	1.47	3.92	71.31

Table 5. SIMPER analysis of data for boulder habitats based on closure status. Taxa contributing to the dissimilarity (D), based on mean abundance (M.A.), at boulder habitats inside and outside the WGOMC (average dissimilarity of the mean abundance of taxa = 51.75).

Taxa	Inside M.A.	Outside M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	36.40	15.05	11.44	1.08	22.10	22.10
Terebratulina septentrionalis	2.25	14.56	6.44	2.17	12.44	34.54
Iophon pattersoni	0.42	9.54	4.94	1.91	9.56	44.09
Erect Iophon spp.	1.53	2.75	3.81	0.89	7.37	51.46
Myxicola infundibulum	2.10	1.27	3.21	1.02	6.21	57.67
Erect bryozoan spp.	5.00	5.93	2.99	1.34	5.78	63.45
Ophiopholis aculeata	1.55	2.16	2.65	0.88	5.13	68.58
Pseudosuberites sulfureus	1.70	4.59	1.94	1.59	3.75	72.33
Encrusting Iophon spp.	2.71	3.69	1.65	1.18	3.19	75.52
Asteroidea unidentifiable	1.95	1.18	1.54	1.35	2.97	78.49

Table 6. SIMPER analysis of data for boulder stations between years. Taxa contributing to the dissimilarity (D), based on mean abundance (M.A.), between years at boulder stations.

a. Boulder Years 1998 and 2001 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 45.92)

Taxa	1998 M.A.	2001 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Erect *Iophon* spp.	1.86	2.82	5.60	1.08	12.18	12.18
Ophiopholis aculeata	6.76	0.52	4.79	1.69	10.43	22.61
Myxicola infundibulum	2.63	2.39	4.42	1.21	9.62	32.23
Erect bryozoan spp.	7.07	1.41	3.91	1.61	8.52	40.75
Terebratulina septentrionalis	7.26	1.89	3.28	1.82	7.13	47.88
Molgula spp.	9.01	2.94	3.27	1.13	7.13	55.01
Asteroidea unidentifiable	1.36	1.57	2.35	4.38	5.11	60.12
Pseudosuberites sulfureus	3.60	0.91	1.92	1.39	4.19	64.30
Iophon pattersoni	2.40	0.70	1.84	1.37	4.01	68.32
Encrusting *Iophon* spp.	1.84	1.10	1.47	1.44	3.19	71.51

b. Boulder Years 1998 and 2002 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 49.26)

Taxa	1998 M.A.	2002 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	9.01	19.13	8.41	1.69	17.07	17.07
Ophiopholis aculeata	6.76	0.01	5.99	2.30	12.17	29.24
Terebratulina septentrionalis	7.26	8.11	4.69	1.56	9.53	38.77
Erect bryozoan spp.	7.07	2.83	4.15	1.65	8.42	47.18
Iophon pattersoni	2.40	5.93	3.83	1.39	7.77	54.95
Erect *Iophon* spp.	1.86	3.28	2.58	1.15	5.23	60.18
Encrusting *Iophon* spp.	1.84	4.69	2.27	1.16	4.62	64.80
Myxicola infundibulum	2.63	1.29	2.22	1.14	4.50	69.30
Pseudosuberites sulfureus	3.60	2.06	2.07	1.35	4.20	73.51
Filograna implexa	0.46	2.08	1.52	1.12	3.09	76.60

c. Boulder Years 1998 and 2005 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 53.12)

Taxa	1998 M.A.	2005 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	9.01	71.82	15.38	1.21	28.96	28.96
Ophiopholis aculeata	6.76	0.13	5.93	2.28	11.17	40.13
Terebratulina septentrionalis	7.26	16.36	5.15	1.64	9.70	49.83
Iophon pattersoni	2.40	10.90	3.75	1.39	7.06	56.88
Erect bryozoan spp.	7.07	10.54	3.27	1.35	6.16	63.05
Myxicola infundibulum	2.63	0.43	2.35	1.00	4.42	67.47
Pseudosuberites sulfureus	3.60	6.01	2.13	1.35	4.01	71.48
Erect *Iophon* spp.	1.86	0.61	1.46	0.89	2.75	74.23
Polymastia hispida	1.71	0.00	1.43	1.06	2.70	76.93
Serpulid spp.	0.09	3.93	1.39	1.90	2.62	79.55

Table 6. Continued.

d. Boulder Years 2001 and 2002 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 48.25)

Taxa	2001 M.A.	2002 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	2.94	19.13	9.52	1.68	19.72	19.72
Erect *Iophon* spp.	2.82	3.28	5.59	1.24	11.59	31.32
Terebratulina septentrionalis	1.89	8.11	4.54	2.20	9.41	40.72
Myxicola infundibulum	2.39	1.29	4.42	1.04	9.16	49.88
Iophon pattersoni	0.70	5.93	3.86	1.33	7.99	57.87
Erect bryozoan spp.	1.41	2.83	2.37	1.26	4.90	62.78
Encrusting *Iophon* spp.	1.10	4.69	1.89	1.13	3.92	66.70
Asteroidea unidentifiable	1.57	2.32	1.60	1.55	3.32	70.02
Filograna implexa	0.74	2.08	1.46	1.39	3.02	73.04
Pseudosuberites sulfureus	0.91	2.06	1.28	1.42	2.65	75.69

e. Boulder Years 2001 and 2005 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 58.87)

Taxa	2001 M.A.	2005 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	2.94	71.82	16.69	1.29	28.36	28.36
Erect *Iophon* spp.	2.82	0.61	5.83	0.99	9.91	38.27
Terebratulina septentrionalis	1.89	16.36	5.14	2.86	8.73	47.00
Myxicola infundibulum	2.39	0.43	5.13	1.18	8.72	55.72
Iophon pattersoni	0.70	10.90	3.78	1.36	6.41	62.13
Asteroidea unidentifiable	1.57	1.01	3.19	6.38	5.41	67.54
Erect bryozoan spp.	1.41	10.54	2.64	1.43	4.49	72.03
Pseudosuberites sulfureus	0.91	6.01	1.66	1.54	2.81	74.85
Encrusting red sponge spp.	1.25	7.46	1.41	1.31	2.40	77.25
Encrusting *Iophon* spp.	1.10	5.17	1.38	1.46	2.34	79.58

f. Boulder Years 2002 and 2005 Dissimilarity (Average dissimilarity of the mean abundance of taxa: 41.05)

Taxa	2002 M.A.	2005 M.A.	Mean D	St. Dev.	Contributing %	Cumulative %
Molgula spp.	19.13	71.82	12.70	1.28	30.93	30.93
Terebratulina septentrionalis	8.11	16.36	5.24	1.15	12.77	43.70
Iophon pattersoni	5.93	10.90	4.03	1.15	9.83	53.52
Erect *Iophon* spp.	3.28	0.61	2.76	1.09	6.73	60.25
Erect bryozoan spp.	2.83	10.54	2.23	1.48	5.42	65.68
Encrusting *Iophon* spp.	4.69	5.17	2.02	1.15	4.93	70.61
Pseudosuberites sulfureus	2.06	6.01	1.61	1.47	3.91	74.52
Asteroidea unidentifiable	2.32	1.01	1.60	1.62	3.89	78.41
Filograna implexa	2.08	1.67	1.49	1.20	3.62	82.03
Myxicola infundibulum	1.29	0.43	1.04	0.97	2.53	84.56
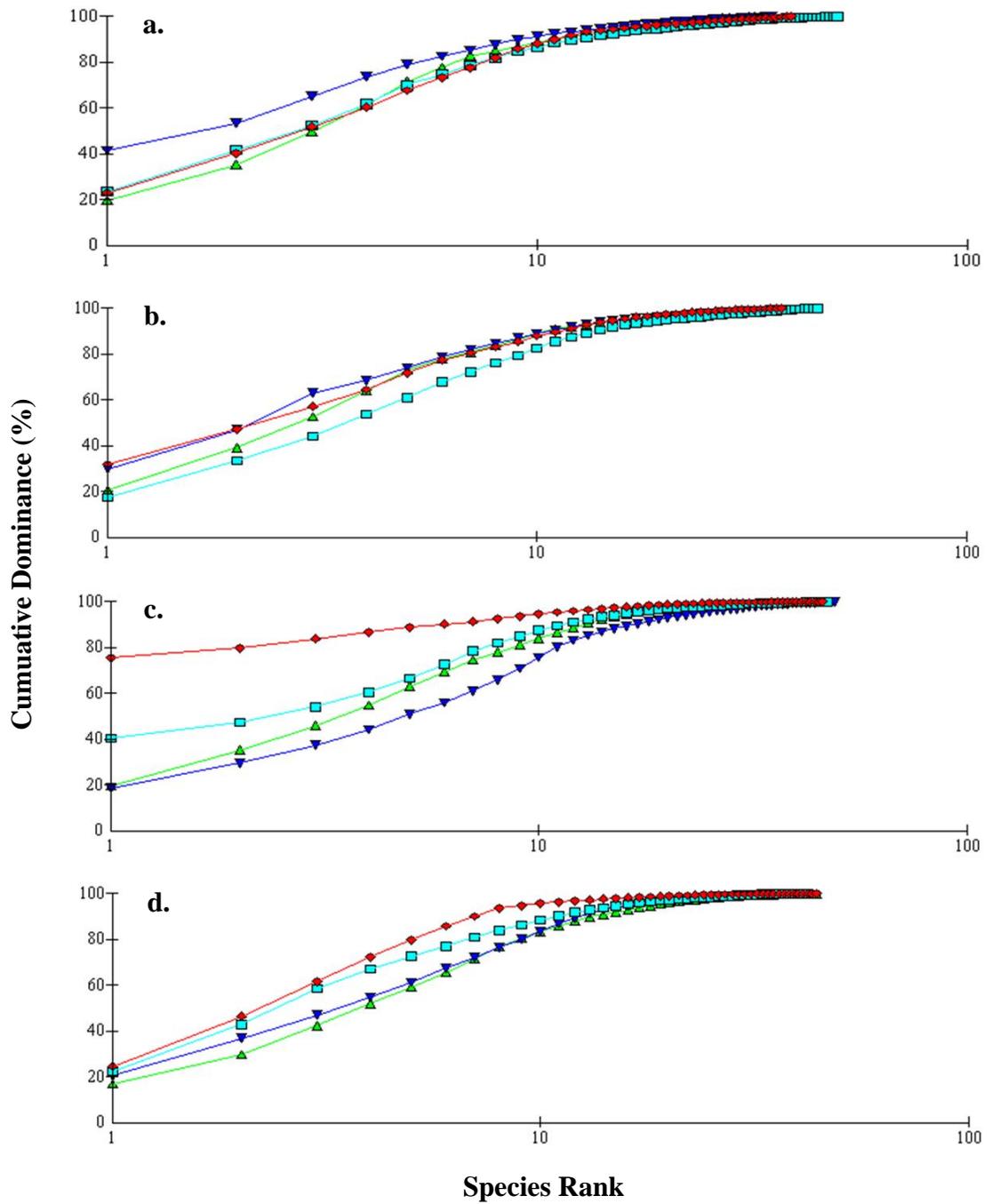
Figure 4. K dominance curves for gravel and boulder habitats by year and closure status. Taxon rank plotted against the cumulative dominance based on percent representation for gravel (a and b) and boulder (c and d) stations located inside (a and c) and outside (b and d) the WGOMC by year. Legend : △ = 1998, ▽ = 2001, □ = 2002, and ◇ = 2005.

Table 7. Analysis of Variance for individual taxa and structural groups. Results of ANOVAs for: a. all taxa; b. 21 taxa identified by SIMPER analysis; c. structural groups (global model); d. structural groups in gravel habitats; and e. structural groups in boulder habitats. P-values are given for the terms that are significant (p<0.10); n.s. = p > 0.10. The terms are: habitat type (H), year (Y), and closure status (CS).

a.

Taxa	H	Y	CS	H*Y	H*CS	Y*CS	H*Y*CS
Aplysilla spp.	0.009	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Encrusting yellow sponge spp.	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Haliclona oculata	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Haliclona urceola	<0.001	0.019	0.035	n.s.	0.012	0.038	n.s.
Leuconia spp.	n.s.	<0.001	0.001	n.s.	n.s.	<0.001	n.s.
Hymedesmia sp. 1	n.s.	0.010	n.s.	n.s.	n.s.	n.s.	n.s.
Hymedesmia sp. 2	n.s.	0.014	n.s.	n.s.	n.s.	n.s.	0.017
Encrusting red sponge spp.	<0.001	<0.001	n.s.	<0.001	n.s.	0.007	n.s.
Encrusting Iophon spp.	<0.001	<0.001	n.s.	0.033	n.s.	n.s.	n.s.
Erect *Iophon* spp.	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Iophon pattersoni	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Pseudosuberites sulfurous	<0.001	0.037	<0.001	<0.001	n.s.	0.006	0.015
Isodictya palmate	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mycale spp.	n.s.	<0.001	n.s.	n.s.	n.s.	0.017	<0.001
Suberites spp.	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Plocambionida ambigua	0.005	0.008	n.s.	0.001	n.s.	<0.001	<0.001
Polymastia hispida	0.007	0.001	n.s.	0.001	n.s.	n.s.	n.s.
Polymastia spp.	<0.001	n.s.	0.029	0.014	n.s.	n.s.	n.s.
Sycon ciliate	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Phakellia ventilabrum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Alcyonium digitatum	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Closed Anemone	0.042	0.010	n.s.	0.010	n.s.	n.s.	n.s.
Bolocera tuediae	n.s.	n.s.	n.s.	n.s.	n.s.	0.007	0.008
Cerianthus borealis	0.001	<0.001	<0.001	0.012	<0.001	<0.001	n.s.
Cerianthiopsis americanus	n.s.	<0.001	n.s.	n.s.	0.038	0.022	n.s.
Tubularia indivisa	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Urticina feline	0.028	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Urticina spp.	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Erect bryozoan spp.	<0.001	0.001	0.001	<0.001	0.001	<0.001	n.s.
Tubilopora sp. 1	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Encrusting Bryozoan spp. pink	<0.001	<0.001	<0.001	<0.001	0.002	0.007	0.024
Encrusting Bryozoan spp. white	0.004	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Terebratulina septentrionalis	<0.001	0.033	<0.001	<0.001	0.028	0.002	<0.001
Amphiporus angulatus	n.s.	0.025	n.s.	n.s.	n.s.	n.s.	n.s.
Nereis sp.	0.054	0.016	n.s.	0.016	n.s.	0.016	0.016
Filograna implexa	<0.001	0.003	<0.001	0.012	n.s.	n.s.	n.s.
Myxicola infundibulum	<0.001	0.001	n.s.	n.s.	<0.001	0.007	0.001
Serpulid spp.	n.s.	<0.001	n.s.	0.002	n.s.	<0.001	0.011
Sabelid spp. white	0.027	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Sabelid spp. red	0.035	n.s.	0.014	n.s.	n.s.	n.s.	n.s.
Calliostoma spp.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Colus spp.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Epitonium spp.	0.005	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Neptunea lyrata decemcostata	n.s.	n.s.	0.008	0.038	n.s.	n.s.	n.s.

Table 7. Continued.

a. Continued.

Taxa	H	Y	CS	H*Y	H*CS	Y*CS	H*Y*CS
Astarte **spp.**	n.s.	0.004	n.s.	0.025	n.s.	n.s.	n.s.
Cyclocardia borealis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Modiolus modiolus	0.002	0.032	n.s.	n.s.	0.029	n.s.	n.s.
Nudibranch	n.s.	0.001	0.022	n.s.	0.022	n.s.	n.s.
Hyas **spp.**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Pagurus **spp.**	<0.001	0.044	<0.001	0.013	0.030	n.s.	0.015
Caridean Shrimp	0.023	<0.001	n.s.	<0.001	0.014	n.s.	n.s.
Balanus balanus	0.001	n.s.	0.026	n.s.	n.s.	n.s.	0.032
Asterias vulgaris	0.046	<0.001	0.002	<0.001	<0.001	<0.001	0.002
Crossaster papposus	0.002	n.s.	n.s.	0.036	0.010	n.s.	n.s.
Henricia sanguinolenta	<0.001	<0.001	n.s.	0.003	n.s.	n.s.	n.s.
Hippasteria phrygiana	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Porania insignis	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Solaster endeca	n.s.	0.025	0.043	0.022	n.s.	n.s.	n.s.
Stephanasterias albula	0.054	0.016	n.s.	0.016	n.s.	n.s.	n.s.
Asteroidea unidentifiable	<0.001	n.s.	n.s.	0.006	<0.001	0.019	n.s.
Pteraster militaria	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ophiopholis aculeate	<0.001	<0.001	n.s.	<0.001	n.s.	n.s.	n.s.
Echinarachnius parma	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hathrometra **spp.**	0.008	<0.001	n.s.	<0.001	n.s.	n.s.	n.s.
Cucumaria frondosa	n.s.	n.s.	n.s.	0.010	n.s.	n.s.	n.s.
Psolus **spp.**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Holothurian spp.	<0.001	<0.001	n.s.	0.001	n.s.	n.s.	n.s.
Strongylocentrotus droebachiensis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ascidia callosa	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
Boltenia echinata	0.066	<0.001	n.s.	0.023	n.s.	n.s.	0.043
Boltenia ovifera	0.004	n.s.	n.s.	n.s.	0.025	n.s.	n.s.
Ciona intestinalis	<0.001	n.s.	0.007	0.004	n.s.	n.s.	0.023
Didemnum albidum	n.s.	n.s.	n.s.	0.013	n.s.	n.s.	n.s.
Didemnum **sp.1**	<0.001	<0.001	0.002	0.009	n.s.	0.021	n.s.
Halocynthia pyriformis	0.037	0.002	n.s.	n.s.	0.005	n.s.	n.s.
Trididemnum solidum	0.035	0.082	n.s.	n.s.	n.s.	0.023	0.023
Molugula **spp.**	<0.001	<0.001	0.021	<0.001	0.030	n.s.	n.s.
Synocium pulmonaria	n.s.	0.001	n.s.	n.s.	n.s.	n.s.	n.s.

Table 7. Continued.

b.

Taxa Identified by SIMPER	Gravel			Boulder		
	Y	CS	Y*CS	Y	CS	Y*CS
Encrusting yellow sponge	<0.001	n.s.	n.s.	<0.001	n.s.	n.s.
Encrusting red sponge	<0.001	n.s.	0.008	<0.001	0.04	n.s.
Encrusting *Iophon* spp.	<0.001	n.s.	n.s.	<0.001	n.s.	n.s.
Iophon pattersoni	n.s.	<0.001	n.s.	<0.001	<0.001	<0.001
Pseudosuberites sulfureus	n.s.	<0.001	n.s.	0.004	0.002	0.009
Erect *Iophon* spp.	<0.001	n.s.	0.013	n.s.	n.s.	n.s.
Polymastia hispida	NA	NA	NA	0.003	n.s.	n.s.
Cerianthus borealis	<0.001	<0.001	0.002	0.001	n.s.	0.056
Erect bryozan spp.	0.01	<0.001	0.006	<0.001	n.s.	0.009
Encrusting bryozoan spp. (pink)	n.s.	0.016	n.s.	0.035	0.073	0.035
Terebratulina septentrionalis	0.088	<0.001	n.s.	<0.001	<0.001	<0.001
Filograna implexa	0.002	0.001	n.s.	0.041	0.044	0.092
Myxicola infundibulum	0.029	<0.001	0.02	0.026	0.046	0.005
Serpulid spp.	<0.001	0.032	<0.001	<0.001	n.s.	0.055
Pagurus spp.	0.008	0.001	0.017	n.s.	n.s.	n.s.
Caridean shrimp	<0.001	0.003	0.011	0.004	n.s.	n.s.
Asterias vulgaris	<0.001	<0.001	<0.001	0.039	n.s.	n.s.
Asteroidea unidentifiable	<0.001	<0.001	<0.001	<0.001	<0.001	0.009
Ophiopholis aculeata	0.001	n.s.	0.025	<0.001	n.s.	n.s.
Holothurian spp.	<0.001	n.s.	n.s.	<0.001	n.s.	n.s.
Molgula spp.	<0.001	n.s.	n.s.	<0.001	0.03	n.s.

c.

Structural Group	H	Y	CS	H*Y	H*CS	Y*CS	H*Y*CS
Encrusting	<0.001	<0.001	n.s.	0.001	n.s.	n.s.	n.s.
Erect-emergent	<0.001	<0.001	n.s.	<0.001	n.s.	n.s.	n.s.
Mobile	<0.001	<0.001	n.s.	<0.001	n.s.	n.s.	0.015

d.

Gravel

Structural Group	Y	CS	Y*CS
Encrusting	<0.001	n.s.	n.s.
Erect-emergent	0.012	0.062	0.094
Mobile	<0.001	n.s.	0.023

e.

Boulder

Structural Group	Y	CS	Y*CS
Encrusting	<0.001	0.064	n.s.
Erect-emergent	<0.001	n.s.	n.s.
Mobile	<0.001	n.s.	n.s.
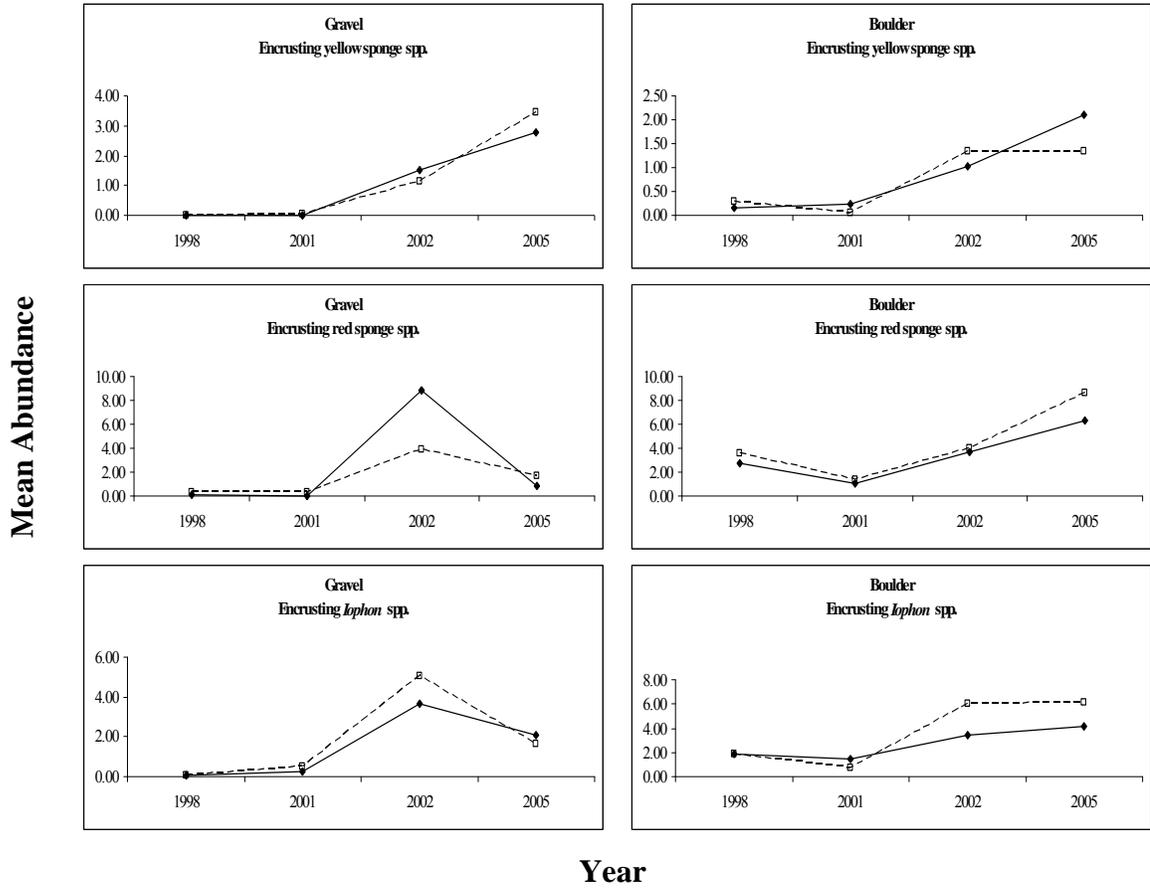
Figure 5. Mean abundance of selected taxa over time based on habitat type and closure status. The mean abundance of the 21 taxa identified by SIMPER analysis are plotted by year and habitat type. Stations inside the WGOMC are plotted as solid lines and outside stations are plotted as dotted lines.
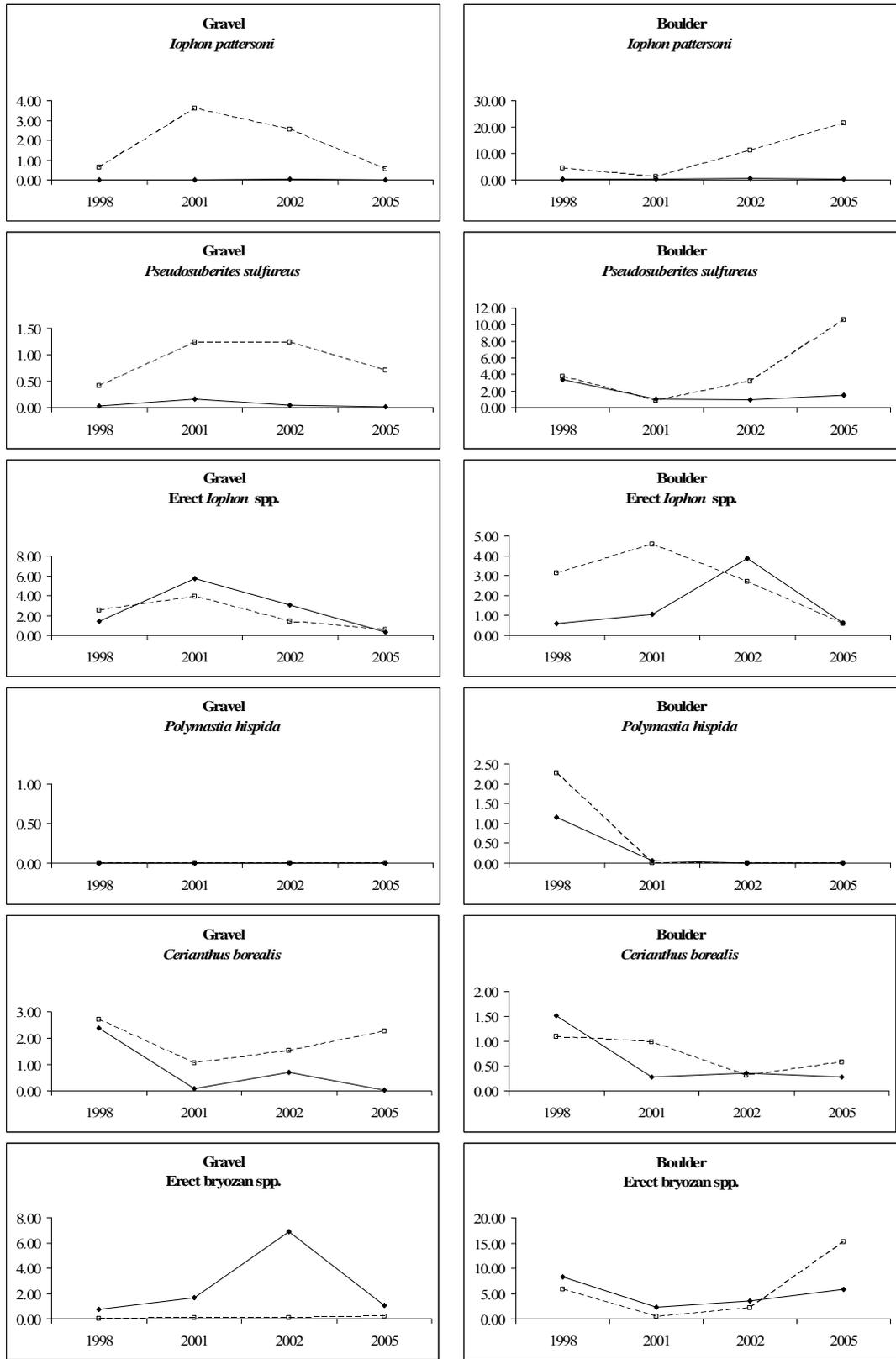
21

Mean Abundance

Year

Figure 5. Continued.

22

Mean Abundance

Year

Figure 5. Continued.

23

Mean Abundance (y-axis label)

Year (x-axis label)

Figure 5. Continued.

24
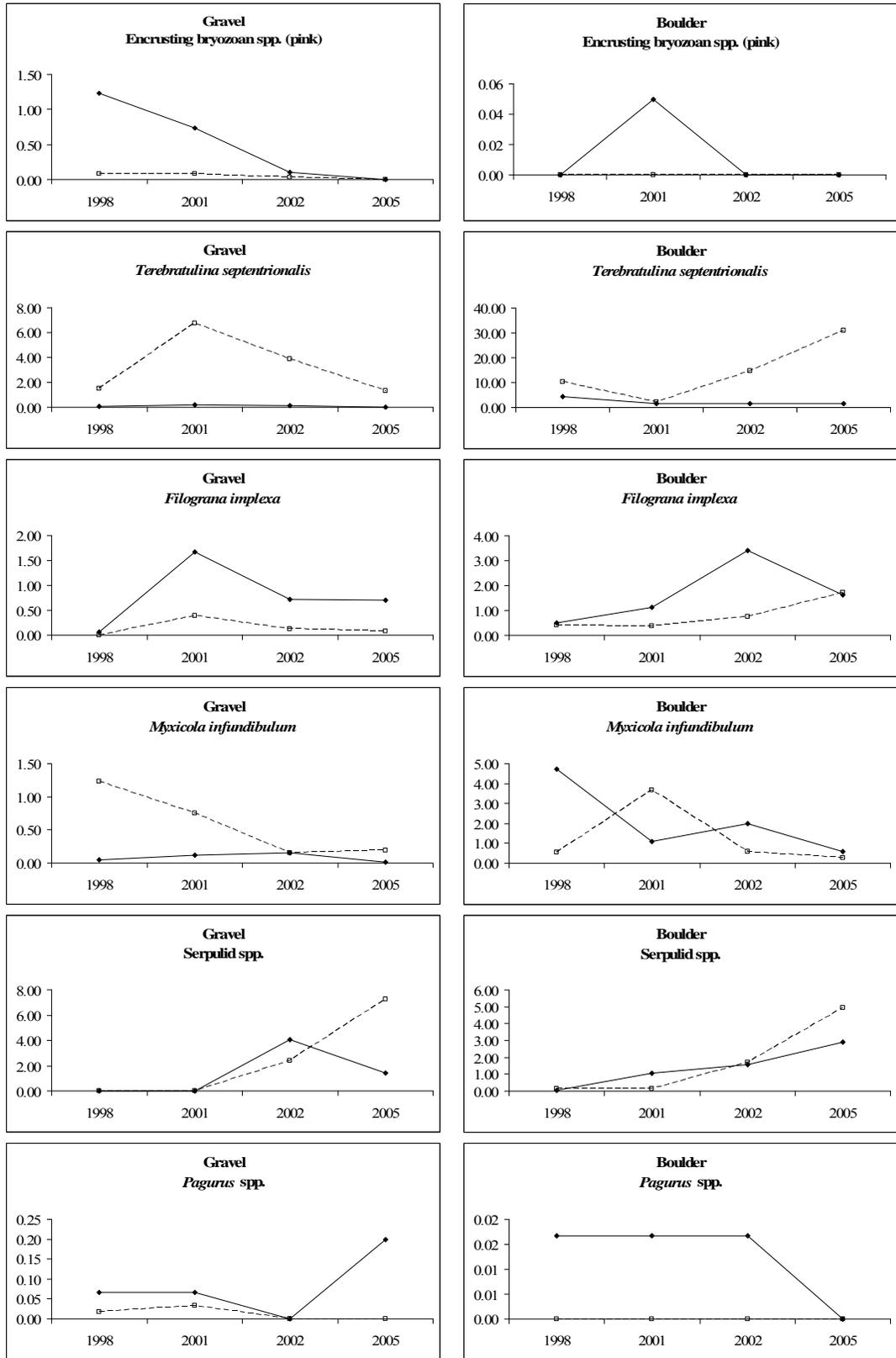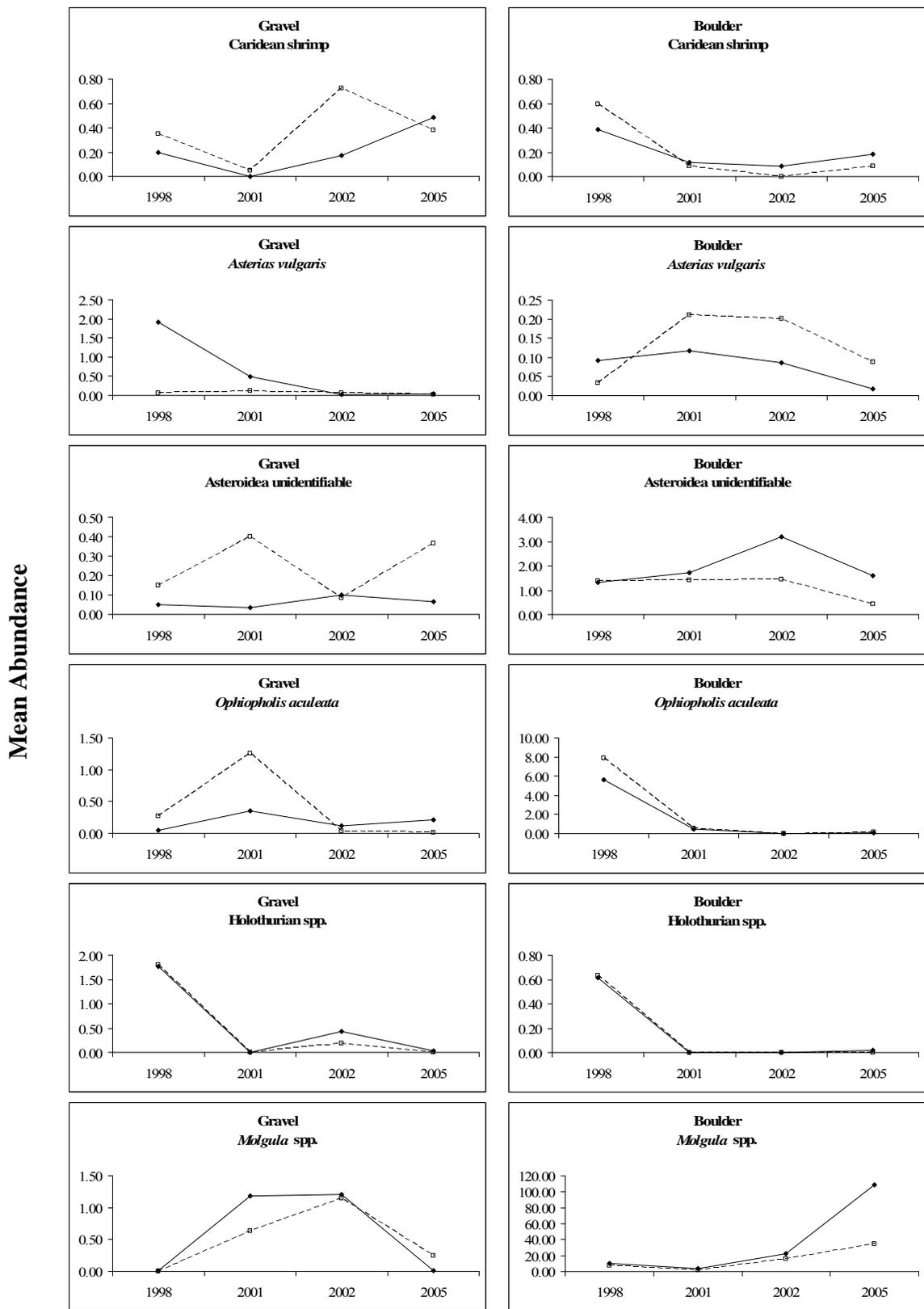
Table 8. Pairwise comparisons for taxonomic categories in gravel and boulder habitat. Cell values indicate the percent of the 21 taxa identified by SIMPER analysis. For comparisons between years (a thru d), the first value represents the percent of taxa that had higher abundance in the earlier year. The second value represents the percent of taxa that had higher abundance in the later year. For comparisons based on closure status (e and d), the first value represents the percent of taxa that had higher abundance inside the closed area. The second value represents the percent of taxa that had higher abundance outside the closed area.

a. Gravel In

	1998	2001	2002	2005
1998				
2001	14%, 19%			
2002	19%, 33%	19%, 33%		
2005	24%, 5%	19%, 5%	14%, 0%	

b. Boulder In

	1998	2001	2002	2005
1998				
2001	33%, 10%			
2002	14%, 14%	5%, 19%		
2005	19%, 14%	5%, 14%	5%, 0%	

c. Gravel Out

	1998	2001	2002	2005
1998				
2001	5%, 0%			
2002	5%, 24%	0%, 24%		
2005	14%, 14%	0%, 24%	19%, 10%	

d. Boulder Out

	1998	2001	2002	2005
1998				
2001	24%, 0%			
2002	10%, 24%	5%, 38%		
2005	10%, 38%	5%, 43%	5%, 24%	

e. Gravel In versus Gravel Out

	1998	2001	2002	2005
1998	14%, 14%			
2001		19%, 5%		
2002			19%, 14%	
2005				0%, 24%

f. Boulder In versus Boulder Out

	1998	2001	2002	2005
1998	5%, 5%			
2001		5%, 5%		
2002			5%, 14%	
2005				5%, 24%

Table 9. Pairwise comparisons for structural group categories in gravel and boulder habitat. Cell values indicate the percent of the 3 structural groups exhibiting significant differences between years. For comparisons between years (a thru d), the first value represents the percent of taxa that had higher abundance in the earlier year. The second value represents the percent of taxa that had higher abundance in the later year. For comparisons based on closure status (e and d), the first value represents the percent of taxa that had higher abundance inside the closed area. The second value represents the percent of taxa that had higher abundance outside the closed area.

a. Gravel In

	1998	2001	2002	2005
1998				
2001	33%, 33%			
2002	33%, 66%	0%, 66%		
2005	0%, 33%	0%, 0%	33%, 0%	

b. Boulder In

	1998	2001	2002	2005
1998				
2001	66%, 0%			
2002	33%, 0%	0%, 100%		
2005	33%, 66%	0%, 66%	0%, 66%	

c. Gravel Out

	1998	2001	2002	2005
1998				
2001	0%, 0%			
2002	0%, 33%	0%, 33%		
2005	33%, 33%	33%, 33%	33%, 0%	

d. Boulder Out

	1998	2001	2002	2005
1998				
2001	100%, 0%			
2002	33%, 33%	0%, 66%		
2005	33%, 66%	33%, 66%	0%, 100%	

e. Gravel In versus Gravel Out

	1998	2001	2002	2005
1998	0%, 0%			
2001		0%, 33%		
2002			33%, 0%	
2005				0%, 33%

f. Boulder In versus Boulder Out

|	1998	2001	2002	2005
1998	0% , 0%			
2001		0%, 0%		
2002			33%, 33%	
2005				33%, 0%
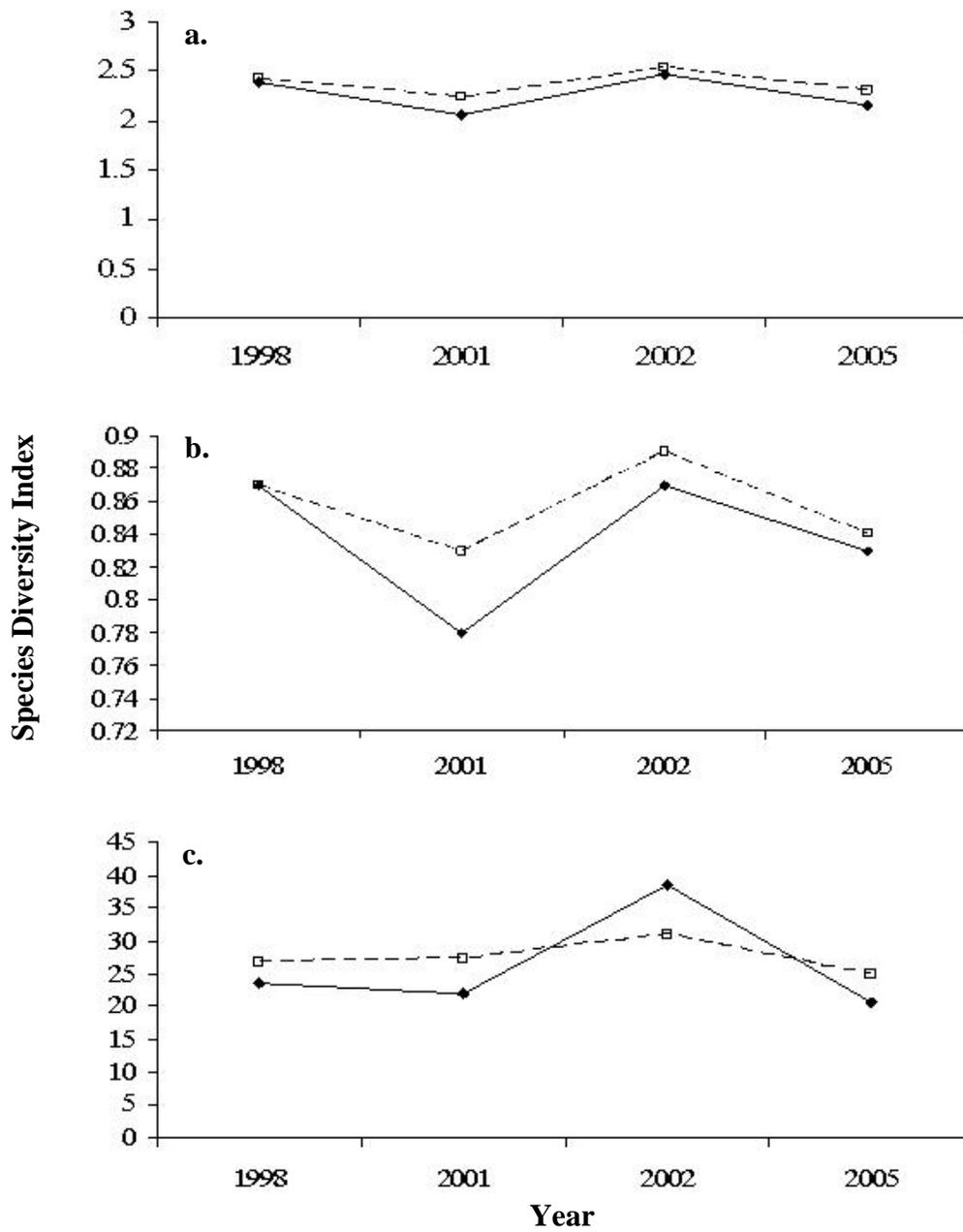
Figure 6. Species diversity indices for gravel habitats by year. a. Shannon-Weinner Index; b. Simpson Index; c. Species Richness. Legend: ——◆—— = inside, - -□- - · = outside.
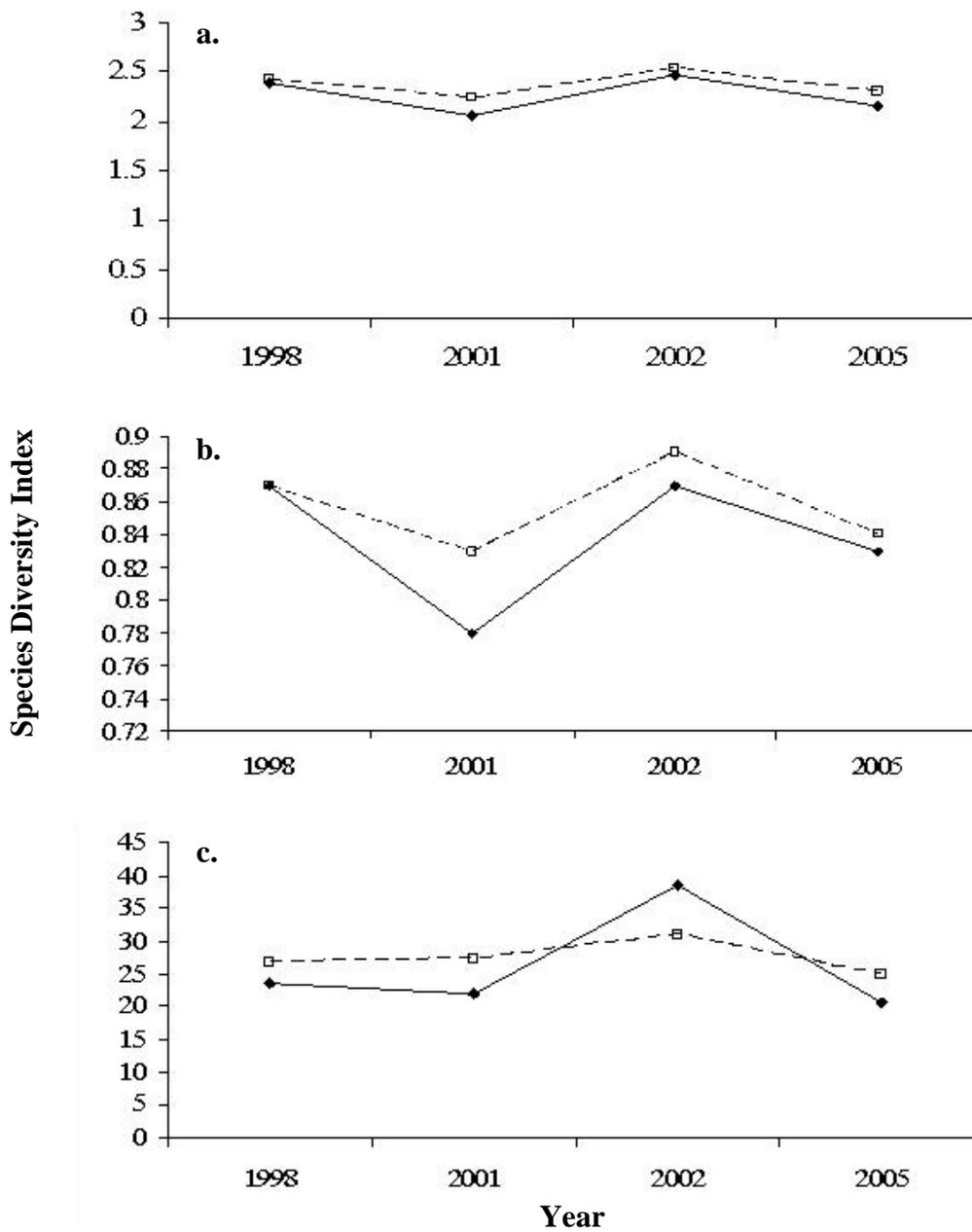
Figure 7. Species diversity indices for boulder habitats by year. a. Shannon-Weinner Index; b. Simpson Index; c. Species Richness. Legend: ◆ = inside, - - □ - · = outside.

Table 10. Analysis of variance for species diversity indices. Results of ANOVAs for: a. global model; and b. gravel and boulder habitats separately. P-values are given for the terms that are significant (p<0.10); n.s. = p > 0.10. The terms are: habitat type (H), year (Y), and closure status (CS).

a.

Diversity Index	H	Y	CS	H*Y	H*CS	Y*CS	H*Y*CS
Shannon-Wiener	0.006	< 0.001	n.s	< 0.001	n.s	0.014	0.006
Simpson	n.s	< 0.001	0.001	< 0.001	0.048	0.003	< 0.001
Species Richness	< 0.001	0.004	n.s	0.032	n.s	n.s	0.058

b.

	Gravel			Boulder		
Diversity Index	Y	CS	Y*CS	Y	CS	Y*CS
Shannon-Wiener	0.002	n.s	n.s	< 0.001	n.s	0.003
Simpson	< 0.001	n.s	n.s	< 0.001	0.007	0.002
Richness	0.017	n.s	n.s	n.s	n.s	0.021

Discussion

Overall these results demonstrate that community structure over the seven years since closure has been dynamic across both habitat types, as well as within and outside the WGOMC, despite a high degree of similarity between paired habitat stations at the time of closure. Multivariate and univariate comparisons of community structure, populations of component taxa, and patterns of diversity between habitat types inside and outside the closed area across years all demonstrate a response to the closure, but not in ways that are normally predicted from previous closed area studies.

Despite hard substratum resources in both boulder and gravel habitats, community structure was different between habitat types across all years. The effects of variations in: 1) flow regime, 2) growth and competition of suspension feeders, and 3) shelter resources from predators can contribute to such differences (Denny 1988, Lesser et al. 1995). We infer that boulder habitats have a much higher degree of variation in flow fields over hard substratum due to wide variation in size and density of boulders whereas gravel habitats have lower flow field variation because they are generally planar and with cobble-pebble distributed as a flat pavement (based on interpretation of maps; Valentine et al. 2003).

Community structure changed across time both inside and outside the WGOMC suggesting recovery without resilience at both habitat types (Paine et al. 1998, Gunderson 2000). In gravel and boulder habitats, the community structure changed significantly across the time series at sites outside the WGOMC indicating the communities are not resilient to disturbance effects (Palumbi et al. 2008, Levin and Lubchenco 2008). The significant differences between gravel stations inside and outside the closure based on multiple analyses suggest recovery is occurring inside the closure but, to date, there is no clearly definable stable community structure. In contrast, at boulder stations there was a clear shift in community composition inside the closure area over time that we infer was due to local processes (i.e., competitive interactions).

Most taxa at the gravel station inside the closed area did not exhibit clear trajectories in abundance, and both increased and decreased over the time series. Only caridean shrimp exhibited a significant overall increase in abundance inside the WGOMC (see Appendix 2 for details on individual taxa). In contrast, encrusting red sponges, *Molgula* spp., *Suberites* spp., and Serpulid spp. significantly increased in abundance at boulder stations inside the closed area. It is difficult to ascribe drivers to the patterns of abundance for most taxa. However, the significantly greater abundance of *T. septentrionalis* at boulder stations outside the closed area and the distinct shift in dominance to *Molgula* spp. inside the closed area may be attributed to competitive interactions. Brachiopod species worldwide have exhibited declining trends in abundance when productivity of local ecosystems increased. Due to the slower metabolisms and filtration rates of brachiopods, modern suspension-feeders (i.e., mollusks, asidians) gain a competitive advantage where local processes drive species interactions (Thayer, 1986; Bambach 1993; Rhodes and Thompson, 1993; McKinney and Hageman, 2006; Clapham and Bottjer 2007). Here we conclude that disturbance by fishing outside the closed area is the dominant driver of the

community structure allowing brachiopods to dominate space resources, whereas inside the closed area competitive interactions are favoring *Molgul*a spp. and other modern suspension-feeders reducing the dominant role of *T. septentrionalis*. Interestingly, there were no clear shifts in dominance or clear directionality in the abundance of particular taxa at gravel stations, although pairwise comparisons revealed *T. septentrionalis* was significantly higher in abundance outside the closed area in 2005. The pattern with *T. septentrionalis* suggests local processes are driving the changes in the epifaunal community structure between stations inside and outside the closure area. *Terebratulina septentrionalis* may be a good indicator species for chronic disturbance in the western Gulf of Maine.

Community structure within the closed area has yet to reach any stable composition. Further, community structure outside the closed area has not remained in what might be considered a consistent impacted state. While community composition tended to be more similar within each station than between each year, the pattern of similarity from 2005 data suggest a greater degree of difference in composition between replicates from gravel and boulder stations inside the closed area than paired stations outside the closed area. This pattern also suggests the community-level processes, such as predation and competition, may be driving species composition inside the closed area (i.e., contributing to greater variation in species distributions within stations). This is in contrast to broader spatial scale disturbance processes, produced either by natural events or by fishing activities that dominate at stations outside the closed area.

This study is predicated on the fact that the human disturbance regime (largely in the form of bottom trawl and sink gillnet fishing gear) has greatly diminished inside the closure while continuing at a higher level immediately outside the closure. However, it is important to note that the fishing pressure outside the closed area has not been constant over time and has varied with changes in both the regulatory regime and fishing economics (Murawski et al. 2005). For example, the outside gravel station at the time of closure was impacted primarily by trawl gear. Due to the implementation of seasonal closures and other fishing sector interactions, the site is now primarily impacted by fixed gillnets. Further, over the course of time the level of overall fishing effort has decreased regionally as well as locally (Murawski et al. 2005). The effect of such variation in fishing effort and gear types on the dynamics of community structure reported here is unknown.

Interestingly, structural guilds and population trajectories of component taxa changed over time in unpredictable ways. We predicted that erect-emergent (structure forming) invertebrates would increase in abundance over time within the protected area due to elimination of fishing gear disturbance. At the gravel stations the erect-emergent fauna was significantly different based on closure status, but abundance was generally greater at the outside station over the time series (with the exception of 2002). Whereas there was no significant difference in the erect-emergent fauna based on closure status at boulder stations over time, there was a significant difference in the abundance of encrusting forms, with greater numbers found outside the closure area (with the exception of 2001). No significant differences were identified in mobile fauna based on closure

status for either habitat type. Perhaps most importantly, at the initiation of the time series the sites outside the closure area of both habitats had greater abundances of the erect-emergent and encrusting structural groups and this pattern remained essentially unchanged over time.

The expected increase in species diversity at stations within the WGOMC was not observed by the end of the study at either the gravel or boulder stations. The K-dominance curves for gravel habitat illustrate little difference in patterns of dominance over the seven years. In contrast to the results of prior studies (Collie et al. 1997, Collie et al. 2005), the gravel stations outside the WGOMC had higher diversity than the gravel stations inside, although this relationship varied between years. Initially species diversity decreased from 1998 to 2001, then increased from 2001 to 2002, and then decreased again from 2002 to 2005. The same patterns where observed in species richness. The difference in diversity over years may be due either to competitive interactions between species within each station or the recruitment of new species which require habitats with reduced levels of disturbance.

Species diversity also differed significantly at boulder stations across years and by closure status. At the station inside the closure area diversity increased from 1998 to 2001 and subsequently decreased through 2005 when calculated using Shannon-Wiener's diversity index. This increase likely indicates an increase in abundance of rare species (e.g., not detected in earlier surveys) or an initial recruitment event post-closure. The subsequent decline in diversity indicates recruitment leveled off and competitive interactions or predation, or both, dominated thereby decreasing the abundance of rare species. Except for a slight increase in 2001, diversity declined inside the closure area across the time series based upon Simpson's diversity index. This decline reflects the observed changes in patterns of dominance. The K-dominance curves illustrate these changes in species diversity over time. The marked upward shift of the K-dominance curve at the inside station over time is due to the large increase in abundance of *Molgula* spp.. This shift in the contribution of dominant species would result in a reduction in evenness of the community and reduce diversity as calculated by Simpson's index. At the station outside the closure area, there was a continual, minor decline in diversity when calculated by both Shannon-Wiener and Simpson's diversity indices. There was also a marked decrease in species richness in 2001. The observed declines in species diversity outside the closure area are likely linked to the decrease in species richness in 2001 which subsequently increased to near the 1998 level in 2002 and 2005.

These observations neither support nor reject the assumption that cessation or reduction of fishing will allow populations and communities to recover to a climax community state. As of 2005, a successional end point of the communities at gravel and boulder stations remains unclear. These findings do indicate that the WGOMC is having a significant impact on invertebrate community structure, and that the community inside the closure area on both boulder and gravel habitats is recovering from chronic fishing gear impacts. The lack of stability suggests that community structure under protected and impacted regimes is dynamic and that "recovery" of the seafloor community has not, and perhaps will not, reach a stable climax state. At this time it is not possible to match the

dynamics of communities at SBNMS to either of the two general models of community dynamics. Neither gravel nor boulder stations inside the closed area have reached a stable community state. Only the results of continued monitoring will enable us to define the type of community model that operates in this region of the Gulf of Maine.

While identifying the type of community model driving the changes we have documented in the community structure remains elusive, the changes we have identified indicate the WGOMC is conserving biodiversity in both gravel and boulder habitats. Because the essential elements of Essential Fish Habitat have yet to be defined for all stages of managed fish species (e.g., Lindolm et al 1999, Gotceitas and Brown 1993), the conservation of biodiversity through the use of MPAs across a broad spectrum of habitats remains a valuable management tool (Alcala et al 2005, Hart 2006, Auster 2001). Further studies are necessary to evaluate which attributes of invertebrate community structure are important to maintain and enhance the productivity of managed fish species across a wide variety of habitat types.

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Appendix 1: Sampling and Data Collection Details

Table 1. Sampling cruise schedule from 1998 through 2005. Unless otherwise noted gravel and boulder habitats were sampled on the same cruise.

Year	Sampling Begin	Sampling End
1998	July 5	July 8
2001	August 7	August 13
2002	April 30 (gravel), June 6 (boulder)	May 1 (gravel), June 6 (boulder)
2003	June 18	June 20
2004	July 17	July 20
2005	June 11	June 13

Table 2. Taxonomic categories (species and species groups*) and structural groups identified in image analysis.

Phylum	Taxon Groups	Structural Group	Comment
Porifera	*Aplysilla* sp.	Encrusting	
	Encrusting yellow sponge spp.	Encrusting	Halichondria sp. 1 + Iophon yellow encrusting + Leptosia yellow
	Haliclona oculata	Erect-emergent	
	Haliclona urceola	Erect-emergent	
	Leuconia spp.	Erect-emergent	
	Hymedesmia sp. 1	Encrusting	blue
	Hymedesmia sp. 2	Encrusting	orange
	Encrusting red sponge spp.	Encrusting	Hymedesmia sp. 3 (red) + Myxilla fimbriata + Leptosia pink
	Encrusting *Iophon* spp.	Encrusting	Iophon white encrusting + Porifera sp. 1 and sp. 2 + Porifera gray
	Erect *Iophon* spp.	Erect-emergent	
	Iophon pattersoni	Erect-emergent	
	Pseudosuberites sulfurous	Erect-emergent	
	Isodictya palmate	Erect-emergent	
	Mycale spp.	Erect-emergent	Mycale lingua + Mycale placoides + Porifer yellow smooth
	Suberites spp.	Erect-emergent	Mycale lobata + Suberites spp.
	Plocamionida ambigua	Erect-emergent	
	Polymastia hispida	Erect-emergent	
	Polymastia spp.	Erect-emergent	Polymastia infrapilosa + Polymastia sp. 1
	Sycon ciliate	Erect-emergent	
	Phakellia ventilabrum	Erect-emergent	
	Alcyonium digitatum	Erect-emergent	
Cnidaria	Closed anemone	Erect-emergent	
	Bolocera tuediae	Erect-emergent	
	Cerianthus borealis	Erect-emergent	
	Ceriantheoposis americanus	Erect-emergent	
	Tubularia indivisa	Erect-emergent	
	Urticina feline	Erect-emergent	
	Urticina spp.	Erect-emergent	

Table 2. Continued.

Phylum	Taxon Groups	Structural Group	Comment
Bryozoa	Erect bryozoan spp.	Erect-emergent	Caberea ellisii + Idmidronea atlantica
	Tubulipora sp. 1	Erect-emergent	
	Encrusting bryozoan spp.	Encrusting	pink
	Encrusting bryozoan spp.	Encrusting	white
Brachiopoda	*Terebratulina septentrionalis*	Erect-emergent	
Nermertea	*Amphiporus angulatus*	Mobile	
	Nereis sp.	Mobile	
Annelida	*Filograna implexa*	Erect-emergent	
	Myxicola infundibulum	Erect-emergent	
	Serpulid spp.	Erect-emergent	
	Sabellid spp. (white)	Erect-emergent	
	Sabellid spp. (red)	Erect-emergent	
Mollusca	*Calliostoma* spp.	Mobile	
	Colus spp.	Mobile	
	Epitonium spp.	Mobile	
	Neptunea lyrata decemcostata	Mobile	
	Astarte spp.	Mobile	
	Cyclocardia borealis	Mobile	
	Modiolus modiolus	Erect-emergent	
	Nudibranch	Mobile	
Crustacea	*Hyas* spp.	Mobile	
	Pagurus spp.	Mobile	
	Caridean shrimp	Mobile	
	Balanus balanus	Erect-emergent	
Echinodermata	*Asterias vulgaris*	Mobile	
	Crossaster papposus	Mobile	
	Henricia sanguinolenta	Mobile	
	Hippasteria phrygiana	Mobile	
	Porania insignis	Mobile	
	Solaster endeca	Mobile	
	Stephanasterias albula	Mobile	
	Asteroidea unidentifiable	Mobile	Asteroidea spp. + Leptasterias spp.
	Pteraster militaria	Mobile	
	Ophiopholis aculeate	Mobile	
	Echinarachnius parma	Mobile	
	Hathrometra spp.	Mobile	
	Cucumaria frondosa	Mobile	

Table 2. Continued.

Phylum	Taxon Groups	Structural Group	Comment
Echinodermata continued	*Psolus* spp.	Mobile	
	Holothurian spp.	Mobile	
	Strongylocentrotus droebachiensis	Mobile	
Urochordata	*Ascidia callosa*	Erect-emergent	
	Boltenia echinata	Erect-emergent	
	Boltenia ovifera	Erect-emergent	
	Ciona intestinalis	Erect-emergent	
	Didemnum albidum	Encrusting	
	Didemnum sp. 1	Encrusting	
	Halocynthia pyriformis	Erect-emergent	
	Trididemnum solidum	Encrusting	
	Molgula spp.	Erect-emergent	Molgula spp. + Gray and silt-covered individuals*
	Synoicum pulmonaria	Erect-emergent	

*Silt covered tunicates were counted as individuals for 1998 and 2001 data, and counted as blocks for 2002 and 2005 data. The following conversion was used to convert block counts to individual counts: Silt-covered individual = individual count; Silt-covered blocks low density (1-3 individuals per block) = total number of blocks multiplied by 1; Silt-covered blocks medium density (4-10 individuals per block) = total number of blocks multiplied by 4; and Silt-covered blocks high density (>10 individuals per block) = total number of blocks multiplied by 11. The sum of the block conversions was then entered as the total number of individuals for the taxa.

Appendix 2: Details of Pairwise Comparisons

Table 1. Results of pairwise comparisons of data for taxonomic categories in gravel habitat. a. comparison of 1998 and 2001; b. comparisons of 1998 and 2002; c. comparisons of 1998 and 2005; d. comparisons of 2001 and 2002; e. comparisons of 2001 and 2005; and f. comparisons of 2002 and 2005.

a.

SPECIES	GI v. GO 2001	GI 1998 v. GI 2001	GO 1998 v. GO 2001
Encrusting yellow sponge	NS	NS	NS
Encrusting red sponge	NS	NS	NS
Encrusting *Iophon* spp.	NS	NS	NS
Iophon pattersoni	NS	NS	NS
Pseudosuberites sulfureus	GO=Higher, p=0.051	NS	NS
Erect *Iophon* spp.	NS	2001=Higher, p=0.005	NS
Polymastia hispida	NS	NS	NS
Cerianthus borealis	GI=Higher, p=0.019	1998=Higher, p=0.001	NS
Erect bryozan spp.	GI=Higher, p=0.021	NS	NS
Encrusting bryozoan (pink)	NS	NS	NS
Terebratulina septentrionalis	NS	NS	NS
Filograna implexa	NS	2001=Higher, p=0.005	NS
Myxicola infundibulum	NS	NS	NS
Serpulid spp.	NS	NS	NS
Pagurus spp.	NS	NS	NS
Caridean shrimp	NS	NS	1998=Higher, p=0.01
Asterias vulgaris	GI=Higher, p=0.005	1998=Higher, p=0.015	NS
Asteroidea unidentifiable	NS	NS	NS
Ophiopholis aculeata	NS	2001=Higher, p=0.01	NS
Holothurian tentacles	GI=Higher, p=0.002	1998=Higher, p=0.002	NS
Molgula spp.	NS	2001=Higher, p=0.03	NS

Table 1. Continued.

b.

TAXA	GI v. GO 2002	GI 1998 v. GI 2002	GO 1998 v. GO 2002
Encrusting yellow sponge	NS	2002=Higher, p<0.001	2002=Higher, p=0.036
Encrusting red sponge	GI=Higher, p=0.016	2002=Higher, p=0.002	2002=Higher, p=0.001
Encrusting *Iophon* spp.	NS	2002=Higher, p=0.01	2002=Higher, p<0.001
Iophon pattersoni	GO=Higher, p=.115	NS	NS
Pseudosuberites sulfureus	GO=Higher, p=0.046	NS	NS
Erect *Iophon* spp.	GI=Higher, p=0.028	2002=Higher, p=0.05	NS
Polymastia hispida	NS	NS	NS
Cerianthus borealis	NS	1998=Higher, p=0.011	NS
Erect bryozan spp.	GI=Higher, p=0.047	NS	NS
Encrusting bryozoan (pink)	NS	NS	NS
Terebratulina septentrionalis	NS	NS	NS
Filograna implexa	NS	2002=Higher, p=0.041	NS
Myxicola infundibulum	NS	NS	1998=Higher, p=0.043
Serpulid spp.	GI=Higher, p<0.001	2002=Higher, p<0.001	2002=Higher, p<0.001
Pagurus spp.	NS	1998=Higher, p=0.016	NS
Caridean shrimp	GO=Higher, p=0.019	NS	2002=Higher, p=0.035
Asterias vulgaris	NS	1998=Higher, p=0.005	NS
Asteroidea unidentifiable	NS	NS	NS
Ophiopholis aculeata	NS	NS	NS
Holothurian tentacles	NS	1998=Higher, p=0.001	NS
Molgula spp.	NS	2002=Higher, p=0.01	NS

c.

TAXA	GI v. GO 1998	GI v. GO 2005	GI 1998 v. GI 2005	GO 1998 v. GO 2005
Encrusting yellow sponge	NS	NS	NS	2005 Higher, p=0.009
Encrusting red sponge	GO Higher, p=0.039	NS	NS	2005 Higher, p=0.052
Encrusting *Iophon* spp.	GI Higher, p=0.047	NS	NS	NS
Iophon pattersoni	NS	NS	NS	NS
Pseudosuberites sulfureus	NS	GO Higher, p=0.017	NS	NS
Erect *Iophon* spp.	NS	NS	1998 Higher, p=0.057	1998 Higher, p=0.047
Polymastia hispida	NS	NS	NS	NS
Cerianthus borealis	NS	GO Higher, p=0.008	1998 Higher, p=0.001	NS
Erect bryozan spp.	NS	NS	NS	NS
Encrusting bryozoan (pink)	NS	NS	1998 Higher, p=0.055	NS
Terebratulina septentrionalis	NS	GO Higher, p=0.005	NS	NS
Filograna implexa	GI Higher, p=0.016	NS	NS	NS
Myxicola infundibulum	GO Higher, p=0.031	NS	NS	1998 Higher, p=0.048
Serpulid spp.	NS	GO Higher, p=0.023	NS	2005 Higher, p=0.004
Pagurus spp.	NS	NS	NS	NS
Caridean shrimp	GO Higher, p=0.06	NS	2005 Higher, p=0.009	NS
Asterias vulgaris	GI Higher, p=0.006	NS	1998 Higher, p=0.006	NS
Asteroidea unidentifiable	NS	GO Higher, p=0.053	NS	NS
Ophiopholis aculeata	NS	NS	NS	NS
Holothurian tentacles	NS	NS	1998 Higher, p=0.001	1998 Higher, p=0.058
Molgula spp.	NS	NS	NS	NS

Table 1. Continued.

d.

TAXA	GI 2001 v. GI 2002	GO 2001 v. GO 2002
Encrusting yellow sponge	2002=Higher, p<0.001	2002=Higher, p=0.039
Encrusting red sponge	2002=Higher, p=0.002	2002=Higher, p=0.001
Encrusting *Iophon* spp.	2002=Higher, p=0.01	2002=Higher, p<0.001
Iophon pattersoni	NS	NS
Pseudosuberites sulfureus	NS	NS
Erect *Iophon* spp.	2002=Higher, p=0.05	NS
Polymastia hispida	NS	NS
Cerianthus borealis	2001=Higher, p=0.011	NS
Erect bryozan spp.	NS	NS
Encrusting bryozoan (pink)	NS	NS
Terebratulina septentrionalis	NS	NS
Filograna implexa	2002=Higher, p=.041	NS
Myxicola infundibulum	NS	NS
Serpulid spp.	2002=Higher, p<0.001	2002=Higher, p<0.001
Pagurus spp.	2001=Higher, p=0.016	NS
Caridean shrimp	NS	2002=Higher, p=0.003
Asterias vulgaris	2001=Higher, p<0.001	NS
Asteroidea unidentifiable	NS	NS
Ophiopholis aculeata	NS	NS
Holothurian tentacles	2001=Higher,p=0.011	NS
Molgula spp.	2002=Higher, p=0.01	NS

e.

TAXA	GI 2001 v. GI 2005	GO 2001 v. GO 2005
Encrusting yellow sponge	NS	2005=Higher, p=0.009
Encrusting red sponge	NS	2005=Higher, p=0.053
Encrusting *Iophon* spp.	NS	NS
Iophon pattersoni	NS	NS
Pseudosuberites sulfureus	NS	NS
Erect *Iophon* spp.	NS	NS
Polymastia hispida	NS	NS
Cerianthus borealis	2001=Higher, p=0.001	2005=Higher, p=0.051
Erect bryozan spp.	NS	NS
Encrusting bryozoan (pink)	2001=Higher, p=0.047	NS
Terebratulina septentrionalis	NS	NS
Filograna implexa	NS	NS
Myxicola infundibulum	NS	NS
Serpulid spp.	NS	2005=Higher, p=0.005
Pagurus spp.	NS	NS
Caridean shrimp	2005=Higher, p=0.001	2005=Higher, p=0.001
Asterias vulgaris	2001=Higher, p=0.001	NS
Asteroidea unidentifiable	NS	NS
Ophiopholis aculeata	NS	NS
Holothurian tentacles	2001=Higher, p=0.002	NS
Molgula spp.	NS	NS

Table 1. Continued.

f.

TAXA	GI 2002 v. GI 2005	GO 2002 v. GO 2005
Encrusting yellow sponge	NS	2005=Higher, p=0.046
Encrusting red sponge	2002=Higher, p=0.004	2002=Higher, p=0.023
Encrusting *Iophon* spp.	NS	2002=Higher, p=0.011
Iophon pattersoni	NS	NS
Pseudosuberites sulfurous	NS	NS
Erect *Iophon* spp.	2002=Higher, p=0.007	2002=Higher, p=0.041
Polymastia hispida	NS	NS
Cerianthus borealis	NS	NS
Erect bryozan spp.	NS	NS
Encrusting bryozoan (pink)	NS	NS
Terebratulina septentrionalis	NS	NS
Filograna implexa	NS	NS
Myxicola infundibulum	NS	NS
Serpulid spp.	NS	2005=Higher, p=0.017
Pagurus spp.	NS	NS
Caridean shrimp	NS	2002=Higher, p=0.032
Asterias vulgaris	NS	NS
Asteroidea unidentifiable	NS	NS
Ophiopholis aculeate	NS	NS
Holothurian tentacles	NS	NS
Molgula spp.	2002=Higher, p=0.01	NS

Table 2. Results of pairwise comparisons of data for taxonomic categories in boulder habitat. a. comparison of 1998 and 2001; b. comparisons of 1998 and 2002; c. comparisons of 1998 and 2005; d. comparisons of 2001 and 2002; e. comparisons of 2001 and 2005; and f. comparisons of 2002 and 2005.

a.

TAXA	BI v. BO 2001	BI 1998 v. BI 2001	BO 1998 v. BO 2001
Encrusting yellow sponge	NS	NS	NS
Encrusting red sponge	NS	1998=Higher, p=0.016	1998=Higher, p=0.012
Encrusting *Iophon* spp.	NS	NS	NS
Iophon pattersoni	NS	NS	1998=Higher, p=0.011
Pseudosuberites sulfureus	NS	NS	NS
Erect *Iophon* spp.	NS	NS	NS
Polymastia hispida	NS	NS	NS
Cerianthus borealis	BO=Higher, p=0.027	1998=Higher, p=0.043	NS
Erect bryozan spp.	NS	1998=Higher, p=0.011	1998=Higher, p=0.009
Encrusting bryozoan (pink)	BI=Higher, p=0.016	2001=Higher, p=0.016	NS
Terebratulina septentrionalis	NS	NS	1998=Higher, p=0.007
Filograna implexa	NS	NS	NS
Myxicola infundibulum	NS	1998=Higher, p=0.044	NS
Serpulid spp.	NS	2001=Higher, p=0.029	NS
Pagurus spp.	NS	NS	NS
Caridean shrimp	NS	1998=Higher, p=0.031	NS
Asterias vulgaris	NS	NS	NS
Asteroidea unidentifiable	NS	NS	NS
Ophiopholis aculeata	NS	1998=Higher, p<0.001	1998=Higher, p=0.052
Holothurian tentacles	NS	1998=Higher, p=0.045	NS
Molgula spp.	NS	NS	NS

Table 2. Continued.

b.

TAXA	BI v. BO 2002	BI 1998 v. BI 2002	BO 1998 v. BO 2002
Encrusting yellow sponge	NS	2002=Higher, p=0.003	2002=Higher, p=0.007
Encrusting red sponge	NS	NS	NS
Encrusting *Iophon* spp.	NS	NS	2002=Higher, p=0.013
Iophon pattersoni	BO=Higher, p<0.001	NS	2002=Higher, p=0.001
Pseudosuberites sulfureus	BO=Higher, p=0.028	NS	NS
Erect *Iophon* spp.	NS	NS	NS
Polymastia hispida	NS	NS	NS
Cerianthus borealis	NS	NS	NS
Erect bryozan spp.	NS	NS	1998=Higher, p=0.039
Encrusting bryozoan (pink)	NS	NS	NS
Terebratulina septentrionalis	BO=Higher, p<0.001	NS	NS
Filograna implexa	NS	2002=Higher, p=0.04	NS
Myxicola infundibulum	NS	NS	NS
Serpulid spp.	NS	NS	2002=Higher, p=0.001
Pagurus spp.	NS	NS	NS
Caridean shrimp	NS	1998=Higher, p=0.031	NS
Asterias vulgaris	NS	NS	2002=Higher, p=0.035
Asteroidea unidentifiable	BI=Higher, p=0.027	2002=Higher, p=0.01	NS
Ophiopholis aculeata	NS	1998=Higher, p<0.001	1998=Higher, p=0.041
Holothurian tentacles	NS	1998=Higher, p=0.045	NS
Molgula spp.	NS	NS	NS

c.

TAXA	BI v. BO 1998	BI v. BO 2005	BI 1998 v. BI 2005	BO 1998 v. BO 2005
Encrusting yellow sponge	NS	NS	NS	2005 Higher, p=0.012
Encrusting red sponge	NS	BO Higher, p=0.037	2005 Higher, p=0.009	2005 Higher, p=0.003
Encrusting *Iophon* spp.	NS	NS	NS	2005 Higher, p=0.014
Iophon pattersoni	BO Higher, p=0.001	BO Higher, p<0.001	NS	2005 Higher, p<0.001
Pseudosuberites sulfureus	NS	BO Higher, p=0.006	NS	2005 Higher, p=0.033
Erect *Iophon* spp.	NS	NS	NS	NS
Polymastia hispida	NS	NS	NS	NS
Cerianthus borealis	NS	NS	1998 Higher, p=0.041	NS
Erect bryozan spp.	NS	BO Higher, p=0.057	NS	2005 Higher, p=0.018
Encrusting bryozoan (pink)	NS	NS	NS	NS
Terebratulina septentrionalis	NS	BO Higher, p<0.001	NS	2005 Higher, p=0.002
Filograna implexa	NS	NS	NS	NS
Myxicola infundibulum	BI Higher, p=0.026	NS	1998 Higher, p=0.025	NS
Serpulid spp.	NS	NS	2005 Higher, p=0.009	2005 Higher, p=0.024
Pagurus spp.	NS	NS	NS	NS
Caridean shrimp	NS	NS	NS	NS
Asterias vulgaris	NS	NS	NS	NS
Asteroidea unidentifiable	NS	BI Higher, p=0.045	NS	1998 Higher, p=0.003
Ophiopholis aculeata	NS	NS	1998 Higher, p<0.001	1998 Higher, 0.044
Holothurian tentacles	NS	NS	1998 Higher, p=0.049	NS
Molgula spp.	NS	NS	2005 Higher, p=0.003	NS

Table 2. Continued.

d.

TAXA	BI 2001 v. BI 2002	BO 2001 v. BO 2002
Encrusting yellow sponge	2002=Higher, p=0.005	2002=Higher, p=0.003
Encrusting red sponge	2002=Higher, p=0.023	2002=Higher, p=0.003
Encrusting *Iophon* spp.	NS	2002=Higher, p=0.004
Iophon pattersoni	NS	2002=Higher, p<0.001
Pseudosuberites sulfurous	NS	2002=Higher, p=0.029
Erect *Iophon* spp.	NS	NS
Polymastia hispida	NS	NS
Cerianthus borealis	NS	2001=Higher, p=0.011
Erect bryozoan spp.	NS	NS
Encrusting bryozoan (pink)	2001=Higher, p=0.016	NS
Terebratulina septentrionalis	NS	2002=Higher, p<0.001
Filograna implexa	2002=Higher, p=0.051	NS
Myxicola infundibulum	NS	NS
Serpulid spp.	NS	2002=Higher, p<0.001
Pagurus spp.	NS	NS
Caridean shrimp	NS	NS
Asterias vulgaris	NS	NS
Asteroidea unidentifiable	2002=Higher, p=0.023	NS
Ophiopholis aculeate	NS	NS
Holothurian tentacles	NS	NS
Molgula spp.	NS	2002=Higher, p=0.048

e.

TAXA	BI 2001 v. BI 2005	BO 2001 v. BO 2005
Encrusting yellow sponge	NS	2005=Higher, p=0.004
Encrusting red sponge	2005=Higher, p=0.001	2005=Higher, p=0.001
Encrusting *Iophon* spp.	2005=Higher, p=0.04	2005=Higher, p=0.003
Iophon pattersoni	NS	2005=Higher, p<0.001
Pseudosuberites sulfurous	NS	2005=Higher, p=0.004
Erect *Iophon* spp.	NS	NS
Polymastia hispida	NS	NS
Cerianthus borealis	NS	NS
Erect bryozoan spp.	NS	2005=Higher, p=0.002
Encrusting bryozoan (pink)	2001=Higher, p=0.016	NS
Terebratulina septentrionalis	NS	2005=Higher, p<0.001
Filograna implexa	NS	2005=Higher, p=0.05
Myxicola infundibulum	NS	NS
Serpulid spp.	2005=Higher, p=0.022	2005=Higher, p=0.023
Pagurus spp.	NS	NS
Caridean shrimp	NS	NS
Asterias vulgaris	NS	NS
Asteroidea unidentifiable	NS	2001=Higher, p=0.002
Ophiopholis aculeate	NS	NS
Holothurian tentacles	NS	NS
Molgula spp.	NS	NS

Table 2. Continued.

f.

TAXA	BI 2002 v. BI 2005	BO 2002 v. BO 2005
Encrusting yellow sponge	NS	NS
Encrusting red sponge	NS	2005=Higher, p=0.005
Encrusting *Iophon* spp.	NS	NS
Iophon pattersoni	NS	2005=Higher, p=0.001
Pseudosuberites sulfurous	NS	2005=Higher, p=0.012
Erect *Iophon* spp.	NS	NS
Polymastia hispida	NS	NS
Cerianthus borealis	NS	NS
Erect bryozan spp.	NS	2005=Higher, p=0.003
Encrusting bryozoan (pink)	NS	NS
Terebratulina septentrionalis	NS	2005=Higher, p=0.002
Filograna implexa	NS	NS
Myxicola infundibulum	NS	NS
Serpulid spp.	NS	NS
Pagurus spp.	NS	NS
Caridean shrimp	NS	NS
Asterias vulgaris	NS	NS
Asteroidea unidentifiable	2002=Higher, p=0.025	2002=Higher, p=0.024
Ophiopholis aculeate	NS	NS
Holothurian tentacles	NS	NS
Molgula spp.	NS	NS

Table 3. Results of pairwise comparisons of data for structural groups in gravel habitat. a. comparison of 1998 and 2001; b. comparisons of 1998 and 2002; c. comparisons of 1998 and 2005; d. comparisons of 2001 and 2002; e. comparisons of 2001 and 2005; and f. comparisons of 2002 and 2005.

a.

GROUP	GI v. GO 2001	GI 1998 v. GI 2001	GO 1998 v. GO 2001
Encrusting	NS	NS	NS
Erect-Emergent	NS	2001=Higher, p=0.006	NS
Mobile	GO = Higher, p=0.026	1998=Higher, p=0.001	NS

b.

GROUP	GI v. GO 2002	GI 1998 v. GI 2002	GO 1998 v. GO 2002
Encrusting	GI = Higher, p=0.058	2002=Higher, p=0.002	2002=Higher, p<0.001
Erect-Emergent	NS	2002=Higher, p=0.007	NS
Mobile	NS	1998=Higher, p=0.004	NS

c.

GROUP	GI v. GO 1998	GI v. GO 2005	GI 1998 v. GI 2005	GO 1998 v. GO 2005
Encrusting	NS	NS	NS	2005=Higher, p=0.002
Erect-Emergent	NS	GO = Higher, p=0.087	NS	NS
Mobile	NS	NS	2005=Higher, p=0.010	1998=Higher, p=0.047

d.

GROUP	GI 2001 v. GI 2002	GO 2001 v. GO 2002
Encrusting	2002=Higher, p=0.001	2002=Higher, p=0.003
Erect-Emergent	2002=Higher, p=0.057	NS
Mobile	NS	NS

e.

GROUP	GI 2001 v. GI 2005	GO 2001 v. GO 2005
Encrusting	NS	2005=Higher, p=0.019
Erect-Emergent	NS	NS
Mobile	NS	2001=Higher, p=0.008

f.

GROUP	GI 2002 v. GI 2005	GO 2002 v. GO 2005
Encrusting	NS	2002=Higher, p=0.042
Erect-Emergent	2002=Higher, p=0.045	NS
Mobile	NS	NS

Table 4. Results of pairwise comparisons of data for structural groups in boulder habitat. a. comparison of 1998 and 2001; b. comparisons of 1998 and 2002; c. comparisons of 1998 and 2005; d. comparisons of 2001 and 2002; e. comparisons of 2001 and 2005; and f. comparisons of 2002 and 2005.

a.

GROUP	BI v. BO 2001	BI 1998 v. BI 2001	BO 1998 v. BO 2001
Encrusting	NS	NS	1998 = Higher, p=0.011
Erect-Emergent	NS	1998 = Higher, p=0.002	1998 = Higher, p=0.006
Mobile	NS	1998 = Higher, p<0.001	1998 = Higher, p=0.013

b.

GROUP	BI v. BO 2002	BI 1998 v. BI 2002	BO 1998 v. BO 2002
Encrusting	BO=Higher, p=0.069	NS	2002=Higher, p=0.033
Erect-Emergent	NS	NS	NS
Mobile	BI=Higher, p=0.030	1998=Higher, p=0.001	1998=Higher, p=0.011

c.

GROUP	BI v. BO 1998	BI v. BO 2005	BI 1998 v. BI 2005	BO 1998 v. BO 2005
Encrusting	NS	NS	2005 = Higher, p=0.049	2005 = Higher, p=0.002
Erect-Emergent	NS	NS	2005 = Higher, p=0.095	2005 = Higher, p=0.001
Mobile	NS	BI=Higher, p=0.041	1998 = Higher, p<0.001	1998=Higher, p=0.006

d.

GROUP	BI 2001 v. BI 2002	BO 2001 v. BO 2002
Encrusting	2002=Higher, p=0.006	2002=Higher, p=0.001
Erect-Emergent	2002=Higher, p=0.004	2002=Higher, p=0.004
Mobile	2002=Higher, p=0.072	NS

e.

GROUP	BI 2001 v. BI 2005	BO 2001 v. BO 2005
Encrusting	2005=Higher, p=0.006	2005=Higher, F=751.19, p<0.001
Erect-Emergent	2005=Higher, p=0.033	2005=Higher, F=132.61, p<0.001
Mobile	NS	2001=Higher, F=7.52, p=0.052

f.

GROUP	BI 2002 v. BI 2005	BO 2002 v. BO 2005
Encrusting	2005=Higher, p=0.094	2005=Higher, p=0.029
Erect-Emergent	NS	2005=Higher, p=0.006
Mobile	2002=Higher, Fp=0.032	2002=Higher, p=0.028

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Survey report of NOAA Ship McArthur II cruises AR-04-04, AR-05-05 and AR-06-03: Habitat classification of side scan sonar imagery in support of deep-sea coral/sponge explorations at the Olympic Coast National Marine Sanctuary (NMSP-07-01)

2002 - 03 Florida Keys National Marine Sanctuary Science Report: An Ecosystem Report Card After Five Years of Marine Zoning (NMSP-06-12)

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M/V *WAVE WALKER* Coral Reef Restoration Baseline Monitoring Report - 2004 Florida Keys National Marine Sanctuary Monroe County, Florida (NMSP-06-08)

Olympic Coast National Marine Sanctuary Habitat Mapping: Survey report and classification of side scan sonar data from surveys HMPR-114-2004-02 and HMPR-116-2005-01 (NMSP-06-07)

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