Effects of Fishing on Gravel Habitats: Assessment and Recovery of Benthic Megafauna on Georges Bank

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Abstract

This study assessed the effects of disturbance to benthic communities and the rate of recovery in an area closed to bottom fishing. The study site was the gravel sediment habitat on the northern edge of Georges Bank, which is an important fishing ground and a nursery area for juvenile fish. On eight cruises to this area from 1994 to 2000, we collected dredge samples and photographs from sites of varying depths and with varying degrees of disturbance from otter trawling and scallop dredging. We assessed the megafaunal communities at two adjacent sites in Canadian waters, one heavily fished and the other only lightly trawled. The lightly trawled site (84 m water depth) had significantly higher numerical abundance and biomass of benthic megafauna than the heavily fished site. There were also marked differences in community composition between the two sites: the undisturbed site was characterized by fragile species—shrimps, polychaetes, and brittle stars—that live in the complex habitat provided by colonial epifauna, which is not present at the disturbed site (80 m). We also monitored the recovery of a previously disturbed shallow area (47 m) that was closed to bottom fishing in January 1995. In the closed area (Closed Area II), we observed significant increases in abundance (×4), biomass (×18), production (×4), and epifaunal cover, and significant shifts in species composition. Among the taxa that have increased are species of crabs, molluscs, polychaetes, and echinoderms. Species-dominance curves reversed following the closure, with species abundance progressively decreasing and species biomass progressively increasing, as large animals came to dominate the biomass. Results of this and prior studies have been used by the New England Fishery Management Council to designate and maintain a Habitat Area of Particular Concern for juvenile cod.

Introduction

The direct effects of fishing on benthic habitats are generally well understood (NRC 2002). The main effect is the physical disturbance of benthic communities by trawls and dredges. The resulting mortality includes organisms captured in fishing nets and those killed but not retained (Bergman and van Santbrink 2000). In particular, bottom fishing gear damages colonial epifaunal taxa (e.g. algae, sponges, corals, colonial tube worms, hydroids, bryozoa, among others) that provide a three-dimensional habitat for other animals (Jennings and Kaiser 1998; Hall 1999).

Second-order effects of fishing are also well documented but not well quantified. These indirect effects include nutrient resuspension, altered predator-prey dynamics, and loss of ecosystem engineers that burrow into and rework seabed materials (Coleman and Williams 2002). The mechanisms whereby bottom fishing affects fish survival are known through laboratory (Lindholm et al. 1999) and field studies (Tupper and Boutilier 1995), but it is difficult to extrapolate these results to the population level. Bottom fishing also reduces production of benthic infauna (Jennings et al. 2001) and megafauna (Hermsen et al. 2003) thereby reducing the energy available for fish production. Structural epifauna plays a dual role by providing a habitat for many of the small, fragile invertebrates that are important prey species (Collie et al. 1997) and also by providing juvenile fish protection from predators. Removal of this epifauna requires juvenile fish to forage for longer periods, thereby exposing them to higher levels of predation (Walters and Juanes 1993).

The response of benthic communities to fishing depends on the fishing gear, sediment type, and the sensitivity of particular taxa to physical disturbance (Collie et al. 2000b). Most of the data on fishing effects come from controlled fishing experiments with before-after and/or control-impact (BACI) designs. These experiments benefit from a controlled experimental design, but suffer by being of short duration. For reasons of practicality, the most common studies have been short-term experiments with otter trawls on sandy sediments in relatively shallow water—situations in which the size of the affected area is likely to be small (Collie et al. 2000b). More recently, trawl-impact studies are being conducted in deeper water and on more complex habitats (e.g. Freese et al. 1999). Even so, experimental fishing cannot emulate the spatial extent or intensity of commercial fishing operations. Collie et al. (2000b) found that chronic effects of bottom fishing exceeded acute effects. Only recently have there been studies to compare benthic communities over a gradient of fishing effort (e.g. Thrush et al. 1998; Bradshaw et al. 2000; Jennings et al. 2001)

Consideration of the chronic effects of bottom fishing requires understanding and measurement of recovery rates. Experimental trawl corridors often are surrounded by undisturbed populations that can quickly recolonize the disturbed areas. In contrast, on commercial fishing grounds there may be no adjacent undisturbed areas and recovery may need to come from remnant populations or rely on longer-range transport of larvae from remote sources. Unfortunately, relatively few trawl-impact studies have measured recovery rates (Collie et al. 2000b) and those that have, suffer by being of small spatial scale. Existing recovery data suggest that in some soft-sediment habitats (e.g. mud and sand), recovery can be complete in about one year, and it might occur more rapidly in mobile sand. However these studies did not include complex habitats with long-lived animals that may stabilize the sedimentary substrate. Trawl-caught specimens of cold-water and deep-sea corals have been aged at tens to thousands of years old (Hall-Spencer et al. 2002). When bottom fishing damages these epifaunally rich communities, the implied recovery times are decades to millennia.

In this paper, we present results of field work conducted on gravel habitats on the northern edge of Georges Bank in the northwest Atlantic Ocean. This gravel pavement is fished with scallop dredges and bottom trawls. The gravel is a substrate for the demersal eggs of Atlantic herring and a nursery area for juvenile cod and haddock (Lough et al. 1989; Valentine and Lough 1991). A portion of this habitat in U.S. waters inside Closed Area II has been designated a Habitat Area of Particular Concern (HAPC) for juvenile cod. In earlier papers, based on data from two cruises in 1994, we compared disturbed and undisturbed sites on the gravel pavement. Differences between sites were quantified from dredge samples (Collie et al. 1997) and bottom photographs (Collie et al. 2000a).

In January 1995 a large area (3,960 km^2) of the U.S. part of Georges Bank adjacent to the U.S.-Canada boundary was closed to all bottom fishing to reduce fishing mortality on demersal fish. The establishment of Closed Area II provided an excellent opportunity to measure the recovery rate of the benthic communities on gravel habitat. We have monitored the recovery with annual sampling inside and outside the closed areas and with sediment recolonization experiments. We also have compared the characteristics of benthic gravel communities over time in adjacent fished and unfished areas on the

Canadian part of the bank. In this paper we report on the time series of data collected at these sites since 1994.

Methods

Eight sampling cruises were conducted to northern Georges Bank, approximately once per year, between 1994 and 2000 (Table 1). The original sampling strategy was guided by side-scan sonar surveys conducted by the U.S. Geological Survey. Quadrants of the sea bottom, measuring approximately 5 km × 10 km, were selected for side-scan sonar surveys (Fig. 1). Trawl door marks, and particularly the parallel tracks of paired scallop dredges, are visible in the sonograms and were used to classify the sites as disturbed or undisturbed. Scallop fishing effort data up to 1993 were also used to classify the degree of disturbance (Collie et al. 1997). Based on this information, we chose disturbed and undisturbed sites at 80-90 m on the Canadian side of Georges Bank and a set of sites with different disturbance histories at 40-50 m depth on the U.S. side. Even though all the study sites are located on a shallow submarine bank, we grouped the sites as “deep” and “shallow” to distinguish them in this paper.

More recent data show the fishing patterns at these sites since 1993. Data on scallop dredging and bottom trawling in the Canadian zone were derived from logbook reports and are recorded to the closest minute of longitude and latitude. These data were extracted from the Zonal Interchange Format database (Jerry Black, Canada Department of Fisheries and Oceans, personal communication). Data on the locations of American fishing boats come from two different sources. Fishing locations of trawlers and scallop vessels were compiled from logbook and trip reports, with a spatial resolution of 10 minutes latitude and longitude (David Stevenson, National Marine Fisheries Service, personal communication). Scallop fishing locations were also obtained from the satellite vessel-monitoring program, which is mandatory on U.S. scallop fishing vessels. Scallop vessels are assumed to be in transit when speed is above 5 knots and fishing when speed is < 5 knots. Total fishing time in each 1 nm^2 cell was therefore estimated as the sum of vessel hours at speeds less than 5 knots (Rago and McSherry 2001).

In this study we contrast two adjacent sites, 13 (80 m) and 20 (84 m), on the Canadian side that have similar gravel sediments and similar depths (Table 1) but different fishing histories. We also compare three sites on the shallower U.S. side of the gravel pavement. Site 17 (47 m) was heavily disturbed prior to 1994 (Collie et al. 1997), but is located in the northern part of Closed Area II, which was closed to all bottom fishing in January 1995. Site 18 (45 m) is located outside the closed area. Prior to the closure, it was lightly disturbed but has attracted more fishing effort since the closure. In 1997, we initiated sampling at Site 17W (49 m), which is adjacent to the closed area and should be a good disturbed control for Site 17. All the sampling sites are located on the gravel pavement (predominantly large pebbles and small cobbles, Fig. 1), though there were subtle differences in sediment composition.

At each site, samples of the benthic megafauna (animals retained on a 5-mm screen) were collected with a 1-m wide Naturalists' dredge fitted with a ¼" mesh liner. We aimed for three replicate dredge samples at each site, though the number was sometimes more or less than three depending on sea condition and time constraints (Table 1). Once the site locations were established on the 1994 cruises, the same sites were resampled on subsequent cruises to establish time series.

Tow duration was kept short (30-60 s) to avoid overfilling the dredge bag with gravel and losing the sample. Once the gravel sample was brought on board, all living animals were removed and preserved in a buffered solution of formalin in seawater. The gravel was shoveled into 9-liter (L) metal pails to measure the sediment volume and discarded overboard. One 9-L subsample was sieved on a 5-mm screen to check for any animals that were missed in the initial sorting. On average, about one tenth of the total sample was sieved.

Photo transects were made at the same locations as the dredge samples and at additional locations at each site The primary tool was a grab sampler equipped with video and still cameras (SEABOSS; Valentine et al., 2000; Blackwood and Parolski, 2001). This sampler drifted with the tidal current over the sea bottom at a height of ~1 m for a duration of 15-20 min. Photo transects were also made with a remotely operated vehicle (1996, 1997, 1999) and a submersible (1998). With each type of sampler, still photographs were taken with a downward looking 35-mm camera at 30-60 s intervals, depending on drift speed over the bottom. Paired lasers were used to define a linear scale in each photo.

In the laboratory, the dredge samples were sorted to species and counted. The aggregate mass of each species was measured to 1 mg after blotting excess moisture on paper towels. The 9-L sieved subsamples from each dredge tow were sorted and enumerated separately. These subsample analyses were extrapolated by the total sediment volume of the dredge tow to account for any animals missed during the initial sorting. Each final sample was standardized by the total volume of sediment collected, such that the resultant data had units of numbers/L and g/L. The combined species list was searched for taxa that could not be reliably sampled or identified. These included colonial taxa that could not be counted (presence/absence only), macrofaunal species (mainly amphipods and small polychaetes) that were too small to be retained consistently on a 5-mm sieve, and animals that could only be identified to a higher taxonomic level because of missing body parts. This filter resulted in a list of 124 selected species out of 319 taxa.

For each sample, we calculated a number of aggregate ecological indices including numerical abundance, biomass, and number of species (S). Shannon-Wiener species diversity (H') was calculated with base 2 logarithms. Pielou's evenness was calculated as $J' = H'/\log S$ (Krebs 1989). To determine the appropriate transformation for each variable, we calculated the within-replicate mean and variance at each site and year combination. The transformation was selected that made within-replicate variance independent of the mean. Biomass and abundance were log transformed; no transformation was necessary for number of species. Species diversity and evenness were exponentiated, as these indices were calculated from base 2 logarithms. The diversity index $2^{H'}$ is the expected number of species (Krebs 1989). After appropriate transformation, analysis of variance was used to test for differences among sites, cruises, and before/after the area closure at the shallow sites.

Multivariate analyses were conducted with the PRIMER software package (Clarke and Warwick 1994). Bray-Curtis similarity matrices were calculated on square-root transformed species abundance data. Ordination was performed with non-metric multidimensional scaling (MDS). The ANOSIM (Analysis of Similarities) routine was used to test for significant differences in species composition among sites and years. The SIMPER (Similarity Percentages) routine was used to determine which species accounted for most of the similarity and dissimilarity among sites. The sites were also compared with *k*-dominance curves and Abundance-Biomass Curves.

Results

Consistent differences in the benthic megafaunal communities were found on two cruises in 1994. Numerical abundance and biomass were significantly higher at the deep sites and also significantly higher at undisturbed sites compared with disturbed sites at each depth (Collie et al. 1997). There were however, significant interaction effects, such that the disturbance effect on abundance was greater at the deeper sites. Though the differences between sites are quite clear-cut, they depend on the interpretation of the disturbance level at each site. High-resolution data on fishing patterns are a necessary element of gear-impact research. We therefore determined the fishing history at each sampling site and followed the community structure over time. Because of depth×disturbance interactions in the 1994 samples, different fishing patterns, and sampling schedules, we analyzed data from the deep and shallow sites separately.

<u>Deep sites (80–84 meters)</u>

Since 1992, there has been scallop dredging at Site 13 but not at Site 20 (Fig. 2). There has been some bottom trawling at Site 20, but always less than at Site 13 except in 1999 and 2001. These effort data are consistent with our interpretation of the side-scan sonar data in 1994, except that Site 20 has been lightly trawled, especially since 1998. Though the fishing locations are reported to the nearest minute, high intensities are evident at regular intervals, suggesting that some fishermen round to the nearest 10 min (Fig. 2C). Therefore the precision of these location data is somewhat less than 1 min and they can only be used to approximate bottom fishing intensity at our sampling sites.

The biomass and abundance of benthic megafauna has remained significantly higher at Site 20 than at Site 13 (Table 2); in fact the differences between Sites 13 and 20 appear to have increased since 1994 (Figs. 3A,B). Shannon-Wiener species diversity was significantly higher at Site 13 (Table 2, Fig. 3C). The reason for lower diversity at Site 20 is not that there are fewer species; there were significantly more species (*S*) at Site 20 (Table 2, Fig. 3D). The difference between the two sites is due to the distribution of numbers of individuals among species. Evenness was significantly higher at Site 13 ($p<0.001$), which causes species diversity to be higher there. There were also significant site×cruise interactions for diversity and evenness; these indices were significantly different between sites in 1997, 1998, and 1999 but not in 1994. At Site 20 the lower species diversity in 1997-1999 matches the high numbers during those years and is due to higher dominance in the community composition, with single species (the polychaete, *Thelepus cincinnatus*) accounting for up to 50% of the individuals sampled. In contrast, at Site 13 single species accounted for at most 15% of the individuals. It is this high numerical dominance at Site 20 that accounts for the lower species diversity, despite a greater number of species.

Multivariate analysis of the community composition data from Sites 13 and 20 included 102 species. The complete species list is not included here but can be requested from the first author. The 50 most abundant megafaunal species were listed by Collie et al. (1997). Multidimensional scaling of the similarity matrix shows clear separation of the community composition of the two sites, as well as changes with time (Fig. 4). According to the two-way crossed ANOSIM, the between-site differences were highly significant (R=0.995, p=0.001) as were differences among years (R=0.825, p=0.001). A SIMPER contrast of Sites 13 and 20 indicated an average dissimilarity of 75%. The top ten species accounting for this dissimilarity were fragile taxa such as the polychaetes *Thelepus cincinnatus* and *Potamilla neglecta*, the brittle star *Ophiopholis aculeata*, the toad crab, *Hyas coarctatus*, and six shrimp species (Table 3). The among-year differences at Site 20 were due to higher abundances of some species in 1997, 1998, and 1999, especially, *T. cincinnatus* and *P. neglecta*, and *Spirontocaris spinus*. The benthic community at Site 13 was dominated by echinoderms (*Asterias vulgaris*, *Strongylocentrotus droebachiensis*) and bivalves (*Astarte* spp. and *Cyclocardia borealis*). The bivalves in particular have heavy shells that apparently can resist encounters with bottom fishing gear.

Shallow sites (45-49 meters)

Prior to the area closure in January 1995, Site 17 (47 m) had high levels of scallop fishing effort (Collie et al. 1997); since the closure there has been no bottom fishing in this area except for very limited experimental fishing in 1998 (Table 4, Fig. 5). Site 18 was lightly fished before the closure but has had more fishing effort directed at it since then. Site 17W is a heavily fished site just outside Closed Area II, adjacent to Site 17. The distribution of scallop fishing, and of the scallops, matches the gravel habitat, as shown in Fig. 1. The effort data confirm our designation of Sites 17W and 18 as fished control sites for the recovering Site 17. Both sites have been fished with otter trawls and scallop dredges during the period our samples were collected. Fishing intensity has been greater at Site 17W than at Site 18 (Table 4).

Two-way ANOVA was used to test the univariate indices from the shallow sites, with site and closure (before-after) as fixed effects. The first set of ANOVAs omitted the data from Site 17W, which was not sampled before the closure. The site×closure interaction term tests for the effect of the closure of Site 17 relative to Site 18. Prior to the closure, biomass was significantly lower at Site 17 than 18 (Collie et al. 1997). After 1995, this pattern was reversed, with a significant site×closure interaction (Table 5). On average, biomass increased by a factor of two per year (Fig. 6A). By 2000, average biomass was 18 times higher inside than outside the closed area. Likewise, abundance increased significantly at Site 17 following the closure (site×closure interaction, Table 5). On average, abundance increased by a factor of 1.5 per year inside the closed area (Fig. 6B). In 1999, mean abundance was four times higher inside than outside; in 2000 this difference was reduced to a factor of two. The indices at Site 17W can only be compared with Sites 17 and 18 for the years 1997 through 1999 (Fig. 6). According to Sidak's multiple comparison test, biomass was significantly higher at Site 17 than both Sites 17W and 18, except in 1999 when Site 17 and 17W were not significantly different (Fig. 6A). Likewise abundance was higher at Site 17 than at both 17W and 18, except in 1997 when Sites 17 and 18 were not significantly different (Fig. 6B).

Species diversity increased at both Sites 17 and 18, but the increase was significantly greater at Site 17 (Table 5, Fig. 6C). The increase in species diversity reflects the increase in number of species per sample (Table 5, Fig. 6D). The number of species also increased at Site 18, but the increase was greater at Site 17, as indicated by the significant site×cruise interaction term (Table 5). Evenness at Sites 17 and 18 was not significantly different and the closure effect was insignificant. In 1999, Site 17W had significantly higher abundance than Site 18 (Fig. 6B) and lower species diversity (Fig. 6D).

Multivariate analysis of the community composition data from the shallow sites included 100 species. Multidimensional scaling of the similarity matrix separated the samples by sites on the vertical axis (Fig. 7); temporal shifts in species composition are also apparent along the horizontal axis of the MDS plot. Species composition changed more at Site 17 inside the closed area than at the two sites (17W and 18) outside the closed area. Species composition at Sites 17 and 18 was most similar in 1996 when total abundance and biomass at these sites was also similar (Fig. 6A,B); since 1996, species composition at these sites has diverged.

The Similarity Percentages (SIMPER) routine in PRIMER was used to identify the species that contributed most to the similarity and dissimilarity of species composition in samples collected at the shallow sites. Averaged across years, Site 17 had greater abundance of the brittle star, *Ophiopholis aculeata*, the polychaete, *Nereis zonata*, the sea star, *Asterias vulgaris*, and the sea urchin, *Strongylocentrotus droebachiensis* than either of the open sites 17W and 18. Site 17W was distinguished by having greater abundance of the sand shrimp, *Crangon septemspinosa*, than either sites 17 and 18. Site 18 differed by having more *Cancer irroratus* crabs than the other two sites.

Changes in epifaunal cover are apparent in the bottom photographs from Site 17, within the closed area (Fig. 8). In 1994, prior to the closure, the gravel was barren with very little epifauna. In 1996, the gravel was covered with a biogenic layer, which was being grazed by the nudibranch *Coryphella*. By 1997 we saw colonization of the gravel by sponges and hydrozoans, and increased abundance of crabs and small scallops. The 1999 photo shows an increase in sponge cover, in particular, colonies of *Polymastia* and *Isodictya*. Though uncommon, we also observed small colonies of *Filograna implexa*, a colonial polychaete with fragile calcareous tubes that characterized the deep, undisturbed Site 20 (Collie et al. 2000a).

Many megafaunal species increased in abundance at Site 17 following the closure in January 1995, with the differences becoming most apparent in 1997 (Figs. 6, 7). Twelve species accounted for most of the dissimilarity in species composition at Site 17 and hence the increase in biomass and abundance following the closure (Fig. 9). This species group includes three crabs (*Cancer irroratus*, *Hyas coarctatus* and *Pagurus acadianus*), three echinoderms (*Ophiopholis aculeata*, *Strongylocentrotus droebachiensis*, and *Asterias vulgaris*), three bivalves (*Crenella glandula*, *Astarte borealis*, and *Placopecten magellanicus*), one gastropod (*Buccinum undatum*), one shrimp (*Dichelopandalus leptocerus*), and one polychaete (*Nereis zonata*). Three of the 12 species—*O. aculeata*, *H. coarctatus*, and *D. leptocerus*—were among those that distinguished the deep undisturbed Site 20 from disturbed Site 13. Hence the presence/absence of these three fragile species can be considered indicators of disturbance and recovery. Conversely, the abundance of the crab, *Cancer irroratus* and the sand shrimp, *Crangon septemspinosa* (not shown in Fig. 9) remained relatively constant at Site 17 following the closure; these two scavenging species appear less sensitive to bottom fishing disturbance and potentially benefit from the increased feeding opportunities associated with disturbance.

Marked shifts in species dominance occurred over time at Site 17 (Fig. 10). In 1994, prior to the closure, the abundance dominance curve lay above the biomass curve, because there were few large animals at this site. Following the closure, the biomass dominance curve was shifted upwards, reaching its highest level in 2000. Starting in 1996, the biomass came to be dominated by the sea scallop, *Placopecten magellanicus*, the sea urchin, *Strongylocentrotus droebachiensis*, the sea star, *Asterias vulgaris*, and the gastropod, *Buccinum undatum*. Shifts in the abundance dominance curve mirror the changes in species diversity and evenness (Fig. 6C), with high dominance corresponding with low evenness. The abundance dominance curve generally shifted down with time, except in 1999, when the brittle star, *Ophiopholis aculeata* was numerically dominant. The number of species found in the samples at Site 17 increased from 24 in 1994 to 54 in 2000 (Fig. 10).

Discussion

Univariate indices

We have demonstrated significant differences between sites in the abundance and biomass of benthic megafauna sampled from gravel habitats on Georges Bank. Moreover, we measured significant increases in abundance and biomass at Site 17, following its closure to bottom fishing. The most likely explanation of the differences is bottom fishing intensity. However, our study is subject to the same caveats inherent in most spatial comparisons of fishing effects in benthic communities (Hall 1999), namely that fishing effort is not experimentally controlled, and that the sites may differ in characteristics other than fishing intensity. This study was limited to a small number of sites sampled systematically over time. Despite sampling constraints, the multi-year nature of the study has allowed us to document trends of change over time in the composition of benthic communities on gravel habitats.

At the deep sites (80-84 m), fishing effort was greater at Site 13 than at Site 20. Some bottom-trawling effort was recorded at Site 20, so it can be classified as lightly trawled, especially after 1998. In bottom photographs we have observed trawl cables snagged on boulders. The effort data are consistent with our personal observations of increased trawling intensity at Site 20. It is possible that, with improved navigation, fishermen are identifying trawl corridors in what was previously considered untrawlable bottom. Given the light trawling that occurred at Site 20, it appears that scallop dredging is responsible primarily for the difference in megafauna between Sites 13 and 20. This conclusion is consistent with other studies, which found that, on a per-tow basis, scallop dredges cause more disturbance than otter trawls (Collie et al. 2000b).

Why are there fewer scallops, and hence no scallop dredging at Site 20, compared with Site 13? These two sites are adjacent and located at virtually the same depth. Therefore they share similar bottom currents and most likely a similar supply of larval scallops. Both sites have gravel substrates, though Site 20 has slightly more cobbles and less small pebbles (Collie et al 2000a). Site 20 is characterized by a high percent cover of hydroids and bryozoa (on which post-larval scallops are known to attach; Thouzeau et al.

1991; Stokesbury and Himmelman 1995) and of colonies of colonial polychaete tubeworms (*Filograna implexa)*. Predation rates on recently settled scallops may be greater at Site 20 due to the higher densities of invertebrate predators associated with attached epifauna (see below). As in our study, Thouzeau et al. (1991) found higher scallop densities on gravel substrates but not at sites with a high cover of *Filograna implexa.*

At the shallow sites (45-49 m), interpretation of the effort data is more clear-cut, thanks to the area closure. Since the closure, Site 17W and 18 have been subject to both scallop dredging and bottom trawling, with effort levels somewhat lower at Site 18 than 17W. Site 17W was thus a good choice of fished control for Site 17. Site 18 remains an important control because it was sampled prior to the closure and therefore enables BACI comparisons with Site 17. These shallow sites are at similar depths and thus subject to similar current regimes. Again there are subtle differences in the gravel substrate (Collie et al. 2000a) that could contribute to the differences in community composition.

The patterns in species diversity were inconsistent between the deep and shallow sites. At the deep sites the difference was due primarily to greater evenness at the disturbed Site 13. The increase in diversity observed at the shallow sites was due primarily to an increase in the number of species per sample. Interestingly, the number of species per sample at Site 17 increased to about 40 following the closure, which is about the same S as the undisturbed Site 20. It is well recognized that S depends on sample size (Krebs 1989), but we presented these results to aid in interpreting the patterns in species diversity. Species diversity is known to be an insensitive indicator of disturbance (Clark and Warwick 1994) and we therefore rely more heavily on the multivariate analyses.

<u>Multivariate indices</u>

Significant differences in species composition were found among sites, which can be attributed to differences in bottom fishing intensity. We also observed shifts in species composition, particularly at the deep sites (compare 1994 samples with other years at Sites 13 and 20, Fig. 4) that appear unrelated to fishing intensity. These shifts could be explained by natural variability in the megafaunal populations. We did not sample at the same time each year, and though the dominant megafaunal species live longer than one year (Hermsen et al. 2003), they do have seasonal recruitment and mortality patterns. Seasonality could explain the lower biomass and abundance at Site 20 in November 1994 (Fig. 3A,B) and the decline in abundance at Site 17 in November 2000 (Fig. 6B).

Though we used the same sampling methodology over time, different groups of people picked the samples from each cruise, possibly introducing sampling variability. Likewise, we have taken pains to standardize the taxonomic lists from one cruise to the next. However as our taxonomic skill increased with time, it is possible that we identified more species in recent cruises. We are confident that sampling and identification biases are small, considering that over 40,000 individual specimens weighing 242 kg were included in this analysis. If there were a bias in species identification it would not affect comparisons made among sites on the same cruise.

From the differences in species composition we can identify sensitive taxa and species that can be considered as indicator species. At the deep sites, the polychaete, *Thelepus cincinnatus* accounted for the greatest dissimilarity (15%). This species builds its tubes around cobbles; physical disturbance of the cobbles will abrade and crush the tubes. One of the most apparent visual differences among the sites is that the gravel particles at Site 20 are encased and bound together by worm tubes, whereas the gravel particles at disturbed sites have a polished look. Another major visual difference is that Site 20 has a high percent cover of hydroids, bryozoans and calcareous worm tubes. This matrix of emergent epifauna shelters fragile animals, including pandalid shrimps, the brittle star, *Ophiopholis aculeata*, and the toad crab, *Hyas coarctatus*. The horse mussel, *Modiolus modiolus*, is also known to be an indicator of fishing disturbance (Hall 1999; Bradshaw et al. 2002). Its large, yet relatively thin valves are vulnerable to physical damage and its slow growth rate requires a long recovery time. Though not abundant at our sites, the mussels *M. modiolus* and *Musculus discors* were found at Site 20 and not Site 13.

Some of the same indicator species increased in abundance at Site 17 following the area closure, namely *Ophiopholis aculeata*, *Hyas coarctatus*, and the shrimp, *Dichelopandalus leptocerus*. Increases in these species coincided with increased epifaunal coverage (Fig. 8), as expected from prior studies. Among the other species that increased at Site 17, some are fragile, such as the errant polychaete, *Nereis zonata*, and the northern red sea anenome, *Urticina felina*. Other shelled animals also increased, including the sea urchin, *Strongylocentrotus droebachiensis*, the rock crab, *Cancer irroratus*, and the sea scallop, *Placopecten magellanicus*. Scavengers, such as the sea star, *Asterias*, do not suffer a high mortality from trawling (Ramsay et al. 2000) but may have benefited from increased feeding opportunities following the area closure. The hermit crab, *Pagurus acadianus*, increased in parallel with the gastropod, *Buccinum undatum*, one of its principal sources of housing (Fig. 9). *P. acadianus* was also more abundant at undisturbed Site 20 than at disturbed Site 13.

Among the taxa more resistant to bottom fishing disturbance are small, hard-shelled bivalves such as *Astarte* spp. and *Cyclocardia borealis*. Similar observations have been made in other studies, and it has been suggested that the pressure wave in front of the bottom fishing gear blows these small mollusks out of the way (Gilkinson et al. 1998). Of the six *Astarte* species found in our samples, *A. borealis* appears most sensitive to bottom fishing and *A. elliptica* the least sensitive. In the closed area (Site 17), *A. borealis* increased in abundance while *A. elliptica* fluctuated without trend. Some crustaceans (e.g. *Cancer irroratus* and *Crangon septemspinosa*), though not particularly robust, do not appear as sensitive to bottom fishing, perhaps because of a high rate of population increase coupled with their scavenging lifestyle.

The dynamics of the sea scallop, *Placopecten magellanicus*, are particularly important because it is the target of the dredge fishing that disturbed the bottom. In addition to the fishing mortality, there is substantial mortality to scallops that are crushed by the gear but not retained (Myers et al. 2000). Scallops feed on suspended matter from the water column but require a stable substrate for settlement (Stokesbury and Himmelman 1995). The chief predators of scallops are sea stars, crabs, and lobsters. Sea scallops are a dominant component of the benthic megafauna in the closed area. However they are not solely responsible for the recovery patterns observed at Site 17. We observed numerical responses in numerous species (Fig. 9) and other molluscs and echinoderms contribute to the increased biomass.

Recovery, succession, and dominance

We observed significant increases in abundance and biomass at Site 17 in 1997, 2½ years after the area closure. The recovery time of gravel habitats is clearly longer than for soft-sediment communities (Collie et al. 2000a). In 2000, five years after the closure, we were still seeing increases in biomass and in the abundances of certain taxa. Our results so far, suggest that the recovery time of the gravel habitats is on the order of 10 years, but continued sampling is required to validate this prediction. Similar recovery rates were observed during 10 years of sampling a gravelly habitat off the Isle of Man following closure to scallop dredging (Bradshaw et al. 2000).

The pattern of succession at Site 17 can be interpreted with respect to the lifespan of the different species, as listed in Hermsen et al. (2003). We expect short-lived species to recover more quickly but to exhibit more variability in abundance ("r-selected" species). In contrast, longer-lived species should exhibit slower and steadier recovery patterns ("K-selected" species). Many species were absent or rare at Site 17 prior to the closure. Some species increased rapidly after the closure, then declined. For example, the nudibranch, *Coryphella*, was abundant at Site 17 in 1996 only. Several short-lived (on the order of up to 5 years) species first became abundant in 1997 and then their numbers leveled off (e.g. *Hyas coarctatus*, *Astarte borealis*, and the mussel, *Crenella glandula*). Other longer-lived species (10-20 years) continued to increase throughout the time series (e.g. *Placopecten magellanicus*, *Buccinum undatum*, and *Asterias vulgaris*). With higher numerical densities, species abundance will be increasingly affected by competitive and predator-prey interactions.

The successional end point of the benthic megafaunal community at Site 17 is still unclear. There does not appear to be a linear succession of the community composition at Site 17 toward that at Site 20. Instead the successional pattern seems more like the indeterminate pattern suggested by Auster and Langton (1999, Fig 5B). Site 20 is almost twice as deep as Site 17 and therefore has weaker bottom currents (Butman 1987); stronger bottom currents at Site 17 may reduce settlement rates of some taxa. It remains unclear to what extent the sea bottom at Site 17 will become covered with colonial epifauna. Analysis of recent bottom photos at Site 17 is not yet complete and will be the subject of future analyses.

Dominance curves from Site 17 are consistent with shifts in benthic community structure that have been observed along pollution gradients. At unpolluted sites, the biomass curve lies above the abundance curve, but with increasing pollution the position of the curves is reversed (Clarke and Warwick 1994). Abundance-biomass (AB) curves and the difference between them (the *W* statistic) can therefore be used as indicators of pollution. Prior to the closure at Site 17, the abundance curve was above the biomass curve, on both cruises in 1994. Following the closure in 1995, the biomass curve shifted above the abundance curve, and the separation between the two curves has increased since then, as reflected in the *W* statistic (Fig. 10). Thus the AB curves gave the earliest indicator of recovery at Site 17 following the closure. This initial response was due to an increased biomass of echinoderms (*Asterias vulgaris* and *Strongylocetrotus droebachiensis*); scallop biomass did not increase until 1996.

Links to fish production

The main results of this study show that there is a higher abundance and biomass of benthic megafauna at undisturbed gravel habitat sites and that the community composition is significantly different from that of disturbed sites. What are the implications of our results for the production of demersal fish? One prediction is that emergent epifauna provides juvenile fish with shelter from predators (Lindholm et al. 2001) but our study did not address this hypothesis. A second prediction is that bottom fishing reduces the abundance of prey species that are important in the diets of demersal fish. In a related analysis, Hermsen et al (2003) estimated production from the size-frequency distributions of benthic megafauna from the same samples. They found significantly lower production of benthic megafauna at Site 13 than at Site 20. Likewise, there was an increase in production at Site 17 following the closure, to levels comparable with Site 20. The differences in production between disturbed and undisturbed sites are substantial when viewed in the context of the Georges Bank food web. Our results echo those of Jennings et al. (2001), who found reduced macrofaunal production with increasing trawling intensity in the North Sea. Taken together, these new results indicate that bottom fishing alters the flow of energy through continental shelf ecosystems.

Many of the species that were more abundant at the undisturbed sites are also important in the diets of demersal fish species. Not all benthic invertebrates in fish stomachs can be identified to species level, yet some important prey species stand out. Numerous demersal fish species, including flatfish and skates (Bowman et al. 2000), specialize on eating shrimp (*Dichelopandalus leptocerus*, *Pandalus montagui*, *Crangon septemspinosa*, and other pandalids) and crabs (*Hyas coarctatus*, *Cancer irroratus*, *Pagurus* spp.). Haddock eats the brittle star, *Ophiopholis aculeata*, and American plaice also specializes on eating ophiuroids (Bowman et al. 2000). To the extent that these prey species are reduced in abundance, demersal fish must spend more time foraging, and the juveniles will be exposed to increased predation risk (Walters and Juanes 1993).

What actions should be taken to mitigate the effects of bottom fishing disturbance? The National Research Council (NRC) committee that studied the effects of trawling and dredging on seabed habitats recommended that a combination of effort reduction, gear modifications, and area closures be tailored to fit specific combinations of fisheries and habitats (NRC 2002). Effort reduction—the cornerstone of fisheries management—should result in commensurate decreases in bottom fishing disturbance (Hall 1999). Sensitive habitats with long recovery times require the additional protection of area closures. There are some incentives and opportunities for "reduced-impact" fishing gears to operate within closed areas. However, bottom contact is required to catch species such as flatfish and scallops, and for these fisheries there is limited scope to reduce bottom impacts with gear modifications.

Rotational harvest strategies may increase the yield-per-recruit of scallops by reducing the mortality of small scallops (Myers et al. 2000). However, the rotation times of that are being considered (3-5 years) are shorter than the recovery times of gravel habitats (~10 years). The result of a rotational harvest strategy on gravel habitats could be to maintain all the areas in a chronically disturbed state. During a temporary trawl closure in the North Sea, fishing effort was displaced outside a closed area, but then returned when the area was re-opened (Rijnsdorp et al. 2001). The net result was a more homogeneous distribution of fishing effort and increased effort in areas that formerly were less impacted by bottom gear. From a habitat perspective, it is preferable to keep fishing effort patchy (Duplisea et al. 2002) because repeated tows of the same area cause a diminishing mortality of benthic species and large areas remain unfished. Thus, permanently closed areas of gravel habitat are preferred over temporary or rotating closures to mitigate the effects of fishing on benthic communities. However, rotating closures of other kinds of habitats (e.g. those sand and mud habitats that recover more rapidly than gravel) might be an appropriate management strategy.

These management issues are especially topical on Georges Bank, as the New England Fisheries Management Council considers different closed area options as amendments to the groundfish and scallop fishery management plans (NEFMC 2003). The existing areas closed to mobile bottom fishing gear have been successful in reducing fishing mortality and have protected benthic habitat (Murawski et al. 2000). In fine-tuning the existing closed areas, the primary considerations are 1) to reduce fishing mortality on overfished stocks while allowing harvest of abundant stocks; (2) to protect vulnerable habitats; and (3) to create informative spatial comparisons that will allow the benefits and costs of the closed areas to be measured and evaluated.

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Table 1. Cruise dates, water depths, and numbers of dredge samples collected at sampling sites on northern Georges Bank. See Fig. 1 for the locations of these sites.

	Sampling Site				
	13	20	17	17W	18
Depth (meters)	80	84	47	49	45
Disturbance level	disturbed	undisturbed	Recovering[a]	disturbed	disturbed
Sampling Dates					
1994 April 10-13	7	-	5	-	3
1994 Nov. 12-16	8	6	3	-	6
1995 July 30	-	-	3	-	3
1996 May 25-27	-	-	6	-	3
1997 July 18-22	3	3	6	3	3
1998 June 15-22	3	1	3	3	3
1999 June 19-23	3	3	4	4	3
2000 Nov. 5	-	-	3	-	2

a. Site 17 was closed to mobile bottom fishing in January 1995.

Table 2. Analysis of variance of univariate indices at the deep Sites 13 (80 m) and 20 (84 m). See Figure 3 for graphical plots of these indices. The ANOVA table is calculated from Type-III Sums of Squares. H' is Shannon-Wiener diversity. In comparing Sites 13 and 20, the *F* statistic and the Probability in the Site column show that Sites 13 and 20 are significantly different, with Site 20 having higher biomass, abundance, and number of species and Site 13 having higher species diversity. The data are from four cruises in the years 1994, and 1997 through 1999.

Source of variation	Site	Cruise	Site×Cruise	Residual
Degrees of freedom	1	3	3	20
Response variable		Log (Biomass)		
Mean square	9.226	0.309	0.480	0.274
F statistic	33.647	1.218	1.750	
Probability	<0.001	0.362	0.189	
Response variable		Log (Abundance)		
Mean square	38.321	0.422	0.510	0.198
F statistic	195.974	2.130	2.577	
Probability	<0.001	0.128	0.083	
Response variable		Species Diversity ($2^{H'}$)		
Mean square	340.782	9.308	54.784	10.317
F statistic	33.031	0.902	5.310	
Probability	<0.001	0.457	0.007	
Response variable		Number of species (*S*)		
Mean square	588.000	106.784	122.080	38.450
F statistic	15.293	2.777	3.175	
Probability	<0.001	0.68	0.047	

Table 3. Percent dissimilarity between the megafaunal communities at Sites 13 and 20. Dissimilarity was calculated with the SIMPER routine in PRIMER, based on square-root transformed data. Average dissimilarity of the entire communities (102 species) was 75%. The 10 species contributing most to the dissimilarity are listed. Mean abundance is standardized per liter of gravel.

	Mean abundance		Dissimilarity		Percent	
Species	Site 13	Site 20	Mean	Mean/ StDev.	Contri- bution	Cumu- lative
Thelepus cincinnatus polychaete	0.09	22.47	11.48	1.84	15.24	15.24
Ophiopholis aculeata brittle star	0.04	3.23	4.91	3.45	6.52	21.75
Hyas coarctatus toad crab	0.13	2.78	4.18	2.23	5.55	27.30
Dichelopandalus leptocerus shrimp	0.09	1.63	3.01	1.93	3.99	31.30
Potamilla neglecta polychaete	0.02	2.32	2.94	1.03	3.90	35.20
Lebbeus groenlandicus shrimp	0.00	0.77	2.54	1.90	3.37	38.57
Pandalus montagui shrimp	0.00	0.72	2.34	1.58	3.10	41.68
Eualus pusiolus shrimp	0.03	0.68	2.04	1.70	2.71	44.38
Crangon septemspinosa shrimp	0.01	0.71	1.88	0.92	2.49	46.88
Spirontocaris spinus shrimp	0.01	1.00	1.84	0.76	2.44	49.31

Table 4. Relative fishing intensity at the shallow sites (45-49 m). Days absent from port were extracted from vessel trip reports, calculated from the date and time the vessel left and returned to port. The entire trip is assigned by the fisherman to a single location, and the data have been summed by 10 minute squares (David Stevenson, NMFS, Gloucester, MA, pers. comm.). We then selected the 10-min square that contained each of our sampling sites. The scallop fishing hours come from the satellite vessel monitoring system (Rago and McSherry 2001). We summed scallop fishing hours within 2 nautical miles of our sampling sites.

Sampling Site	17	17W	18
Days absent from port 1995-2000			
Bottom trawl	0	1770	463
Scallop dredge	0	1373	544
Scallop fishing hours within 2 nautical miles of sites			
1998	0	2244	1267
1999	0	234	11
2000	0	756	7

Table 5. Analysis of Variance of univariate indices at the shallow Sites 17 (47 m) and 18 45 m). See Figure 6 for graphical plots of these indices. The ANOVA table is calculated from Type-III Sums of Squares. H' is Shannon-Wiener diversity. Of primary interest are the *F* statistics and corresponding Probabilities in the Site×Closure interaction column. Comparing the differences in biomass, abundance, species diversity, and number of species between Site 17 and Site 18, highly significant changes occurred following the closure at Site 17. The data are from eight cruises from 1994 through 2000.

Source of variation	Site	Closure	Site×Closure	Residual
Degrees of freedom	1	1	1	58
Response variable		Log (Biomass)		
Mean square	0.949	20.895	16.268	0.800
F statistic	1.879	26.130	20.344	
Probability	0.280	<0.001	<0.001	
Response variable		Log (Abundance)		
Mean square	0.0405	24.902	6.917	0.347
F statistic	0.117	71.832	19.955	
Probability	0.734	<0.001	<0.001	
Response variable		Species Diversity ($2^{H'}$)		
Mean square	0.916	477.689	58.713	12.839
F statistic	0.071	37.206	4.573	
Probability	0.790	<0.001	0.037	
Response variable		Number of species (*S*)		
Mean square	53.365	3274.569	146.487	33.511
F statistic	1.592	97.715	4.371	
Probability	0.212	<0.001	0.041	

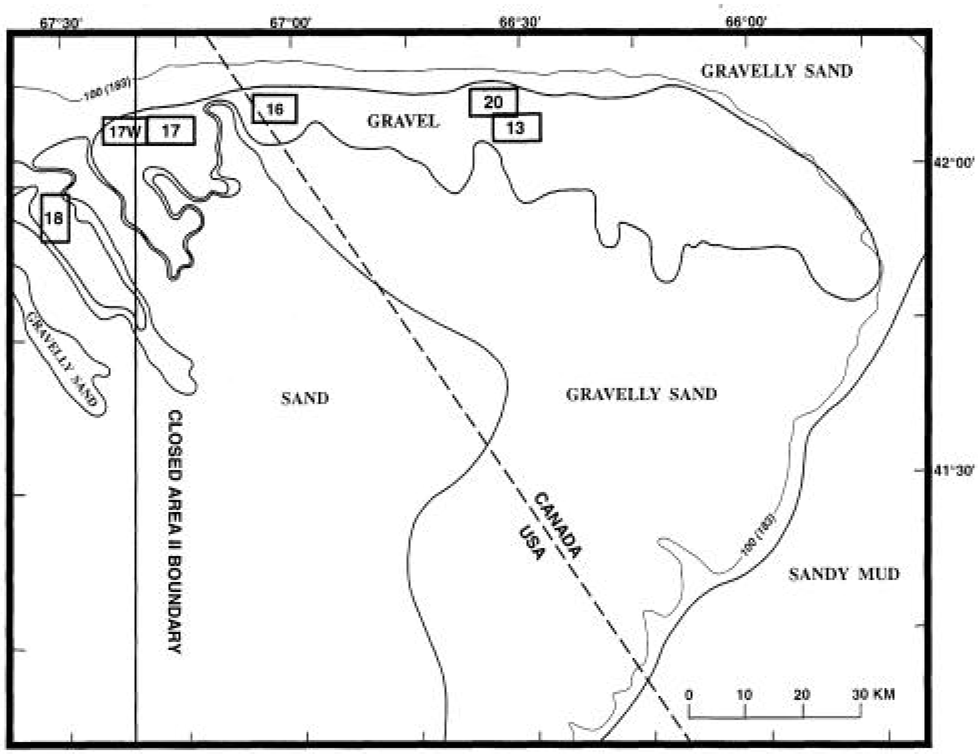

Fig.1. Location of sampling sites on northern Georges Bank. The numbered rectangles are sites on the gravel habitat that were surveyed with side-scan sonar in 1994 by the U.S. Geological Survey.

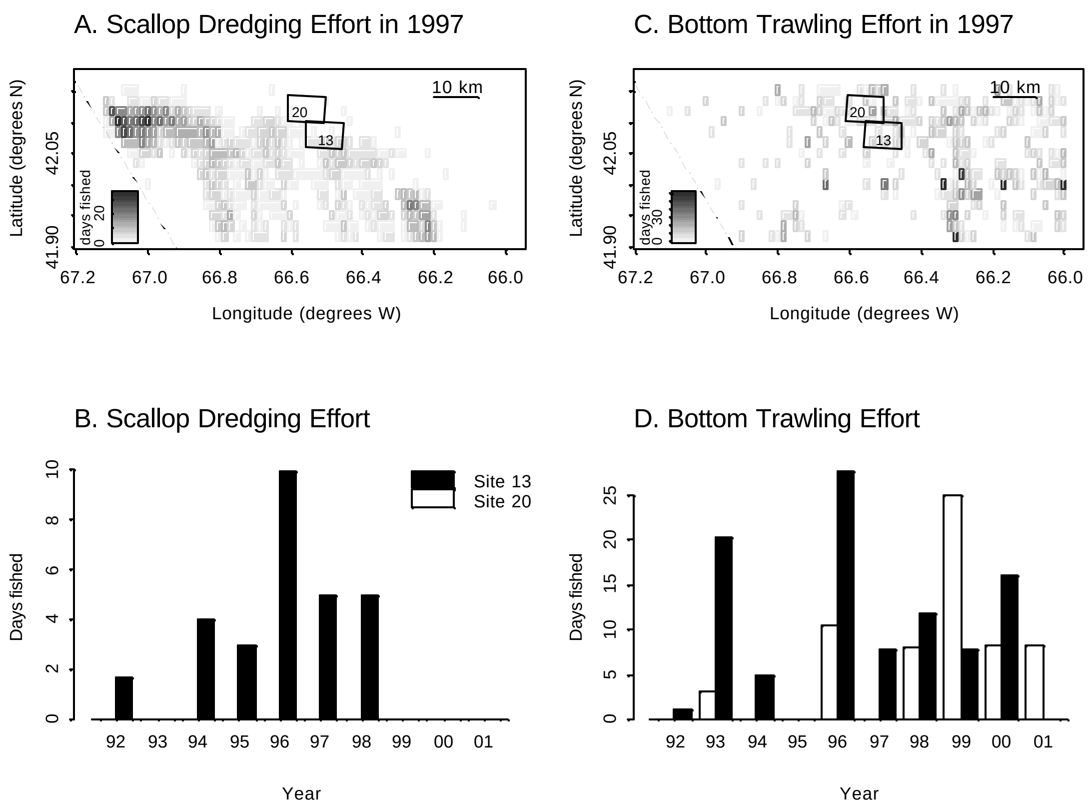

Fig. 2. Spatial distribution of bottom fishing on northeastern Georges Bank. Fishing locations were reported to the nearest minute of latitude and longitude. A. Distribution of scallop dredging effort in 1997. The diagonal line is the Hague Line and the rectangles are quadrants that have been surveyed with side-scan sonar. The numbered sites show the locations where dredge samples were taken. B. Scallop dredging effort in the 1-min. quadrants corresponding to dredge Sites 13 and 20. C. Distribution of bottom trawling effort in 1997. The high-density quadrants suggest that some locations have been rounded to the nearest 10 min. D. Bottom trawling effort in the quadrants corresponding to dredge Sites 13 and 20. These location data were extracted from the Zonal Interchange Format database by Jerry Black, Canada Department of Fisheries and Oceans, Dartmouth, Nova Scotia.

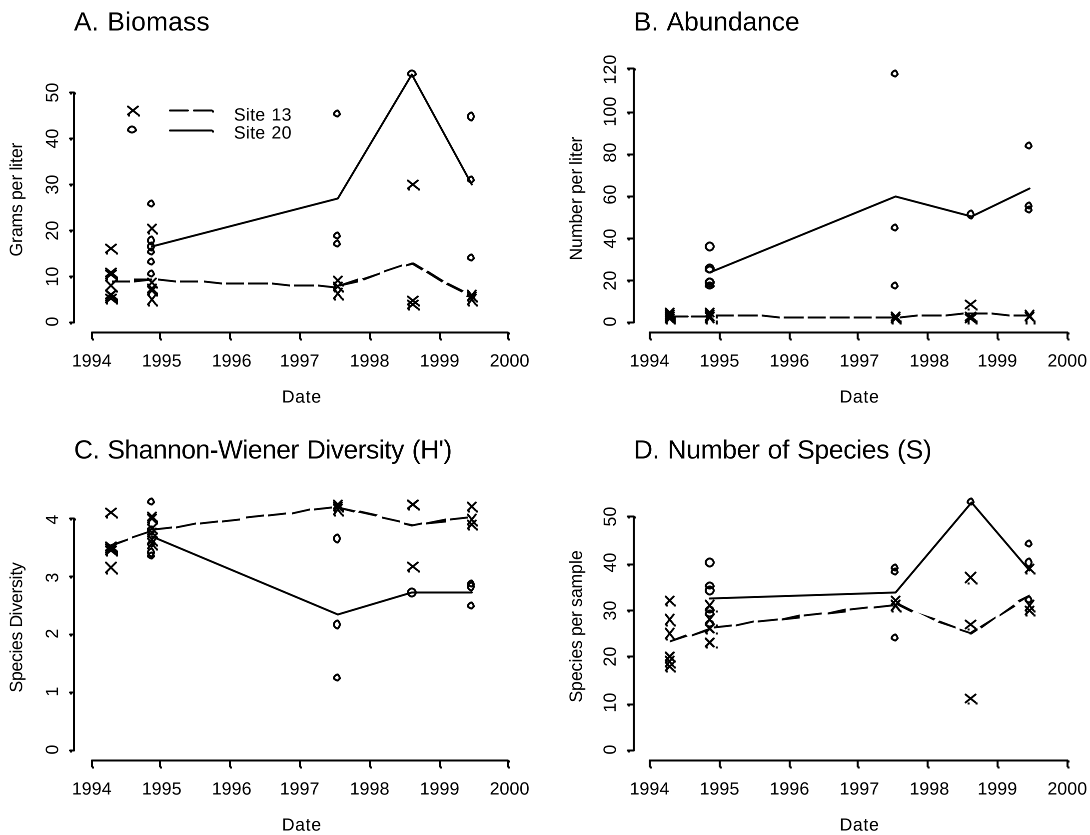

Fig. 3. Univariate ecological indices at the deep sites. Each symbol represents one dredge sample and the lines connect the means from each sampling cruise.

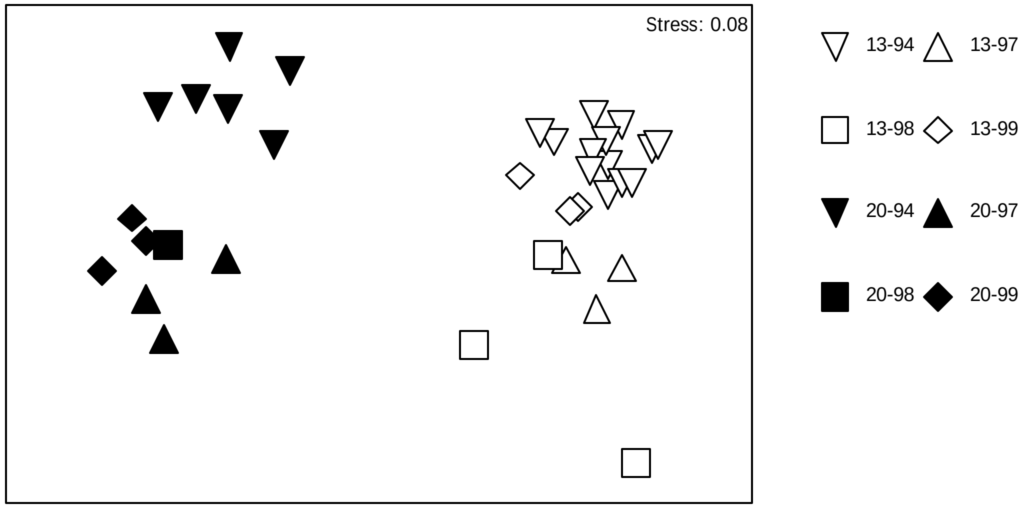

Fig. 4. Non-metric multidimensional scaling of megafaunal communities at Sites 13 and 20. Each symbol represents one dredge sample. This ordination is based on the Bray-Curtis similarity matrix of square-root transformed data on the abundance of 102 species.

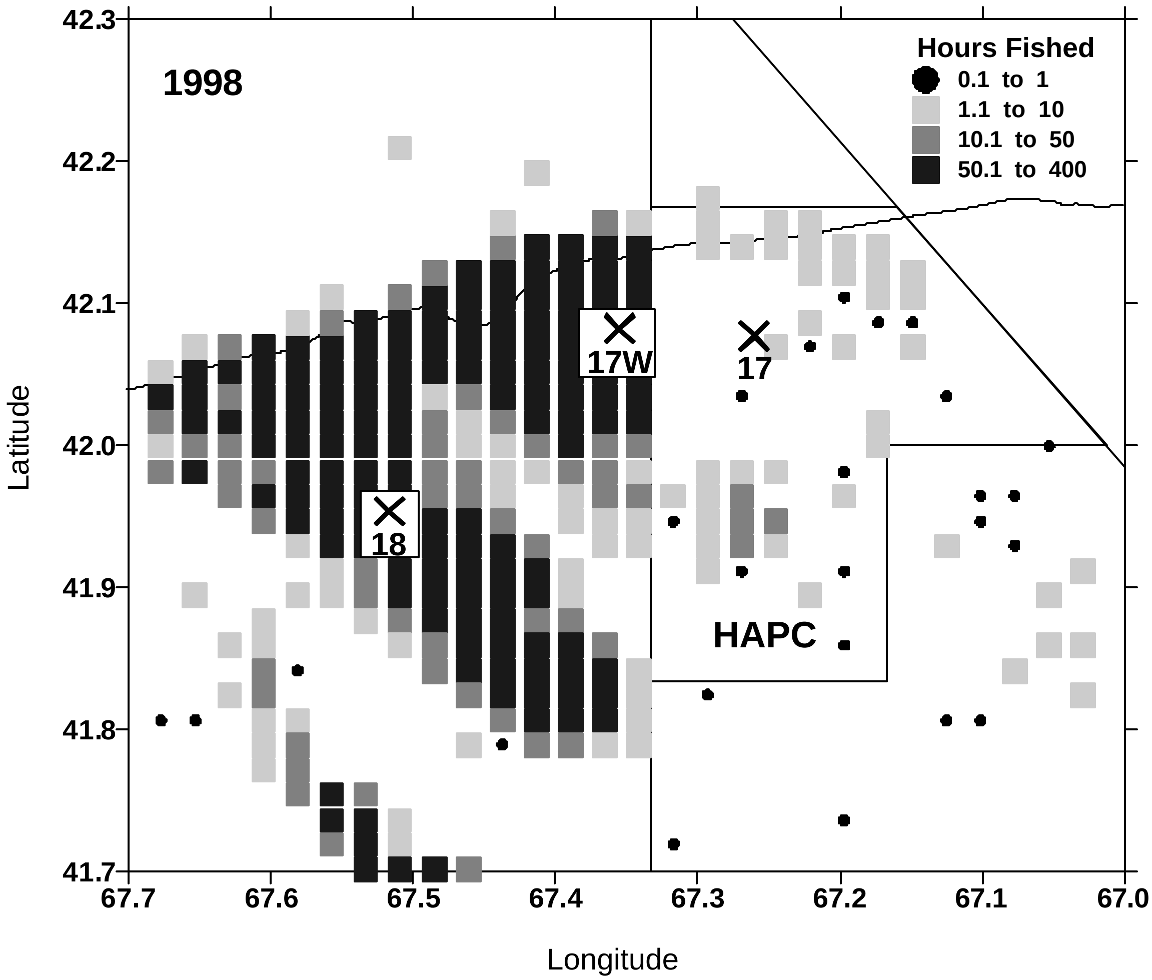

Fig. 5. Spatial distribution of scallop fishing in 1998. Location data were obtained from the satellite vessel monitoring program. Total fishing time in each 1 nm^2 cell was calculated by Rago and McSherry (2001) as the sum of vessel hours at speeds less than 5 knots. HAPC is the Habitat Area of Particular Concern established for juvenile cod inside Closed Area II.

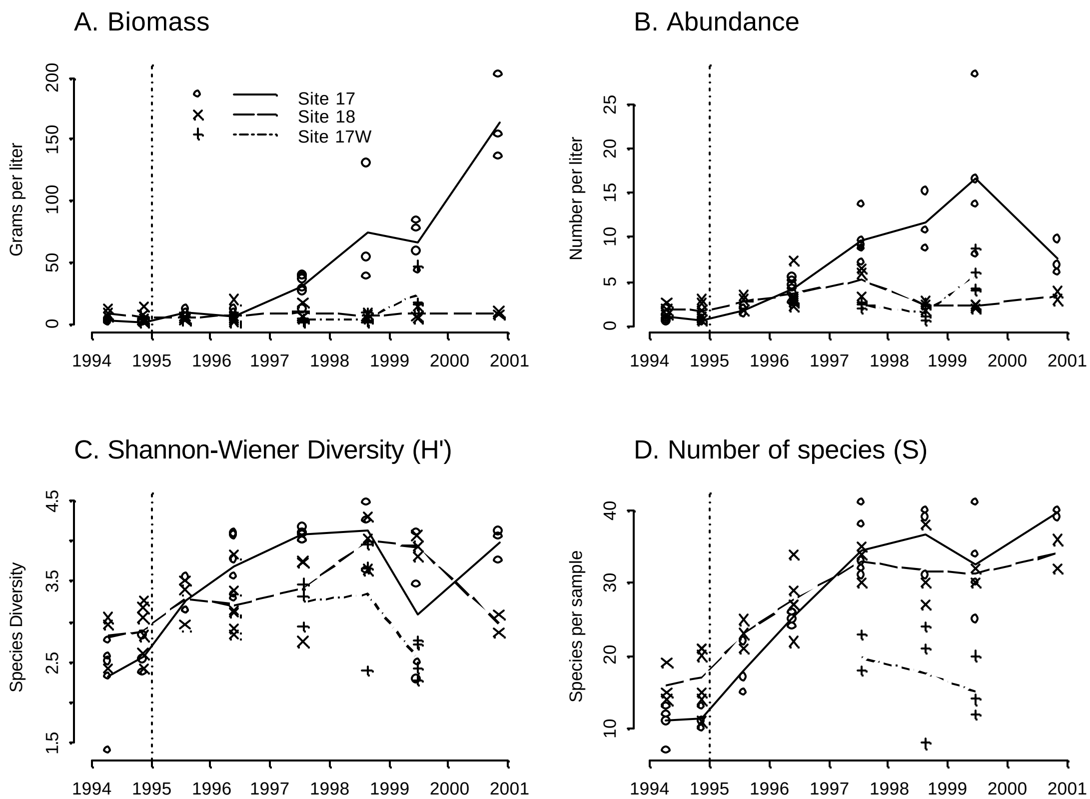

Fig. 6. Univariate ecological indices at the shallow sites. Each symbol represents one dredge sample and the lines connect the means from each sampling cruise. The vertical broken line indicates the date that Site 17 was closed to all bottom fishing. Sites 18 and 17W remained open throughout this period.

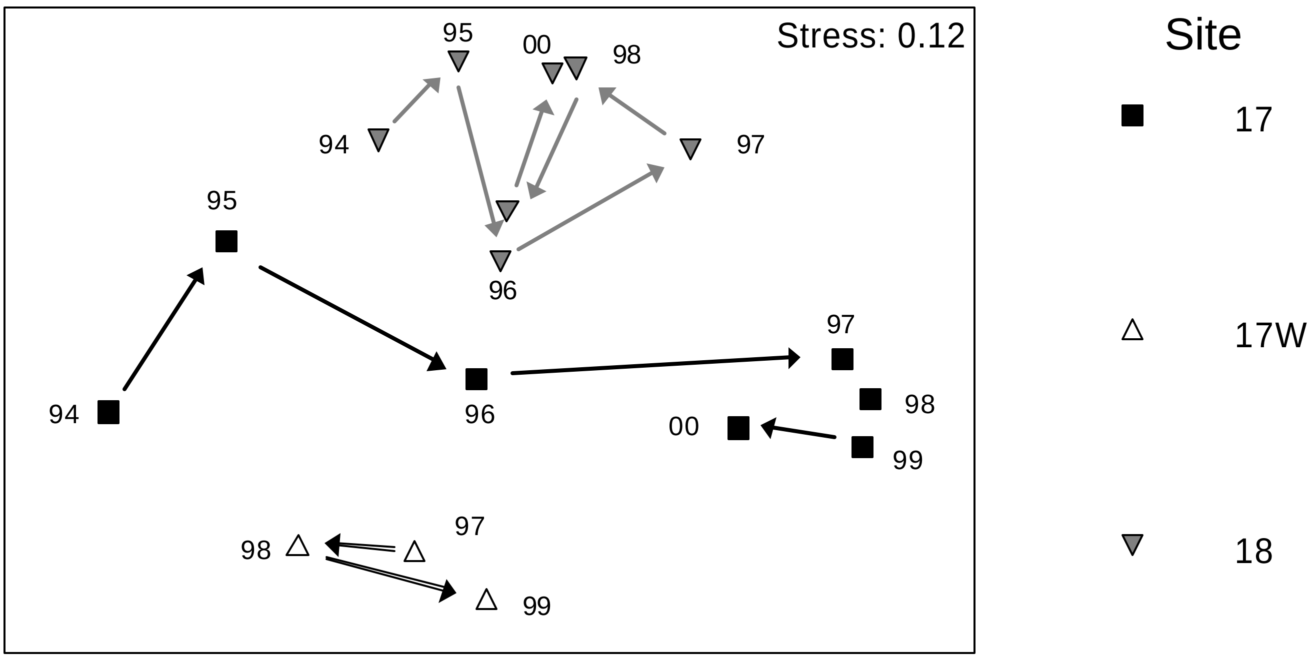

Fig. 7. Non-metric multidimensional scaling of megafaunal communities at Sites 17, 17W, and 18. To simplify the graph, each symbol represents the mean of replicate dredge samples taken at each site and cruise. This ordination is based on the Bray-Curtis similarity matrix of square-root transformed data on the abundance of 100 species.

Fig. 8. Photographs of the sea floor at Site 17. The field of view in each photograph is approximately 76 cm by 51 cm (30 by 20 inches). 1994: prior to the closure only a few burrowing anemones (ba) can be seen. 1996: many burrowing anemones and a hermit crab (hc) can be seen in the top right corner. 1997: Sponges, bryozoans (br), a sea urchin (su) and small scallop (sc), a hermit crab and toad crab (tc) can be seen. 1999: sponges (*Polymastia* and *Isodictya*) and a large scallop are evident. Photographs by Dann Blackwood, USGS.

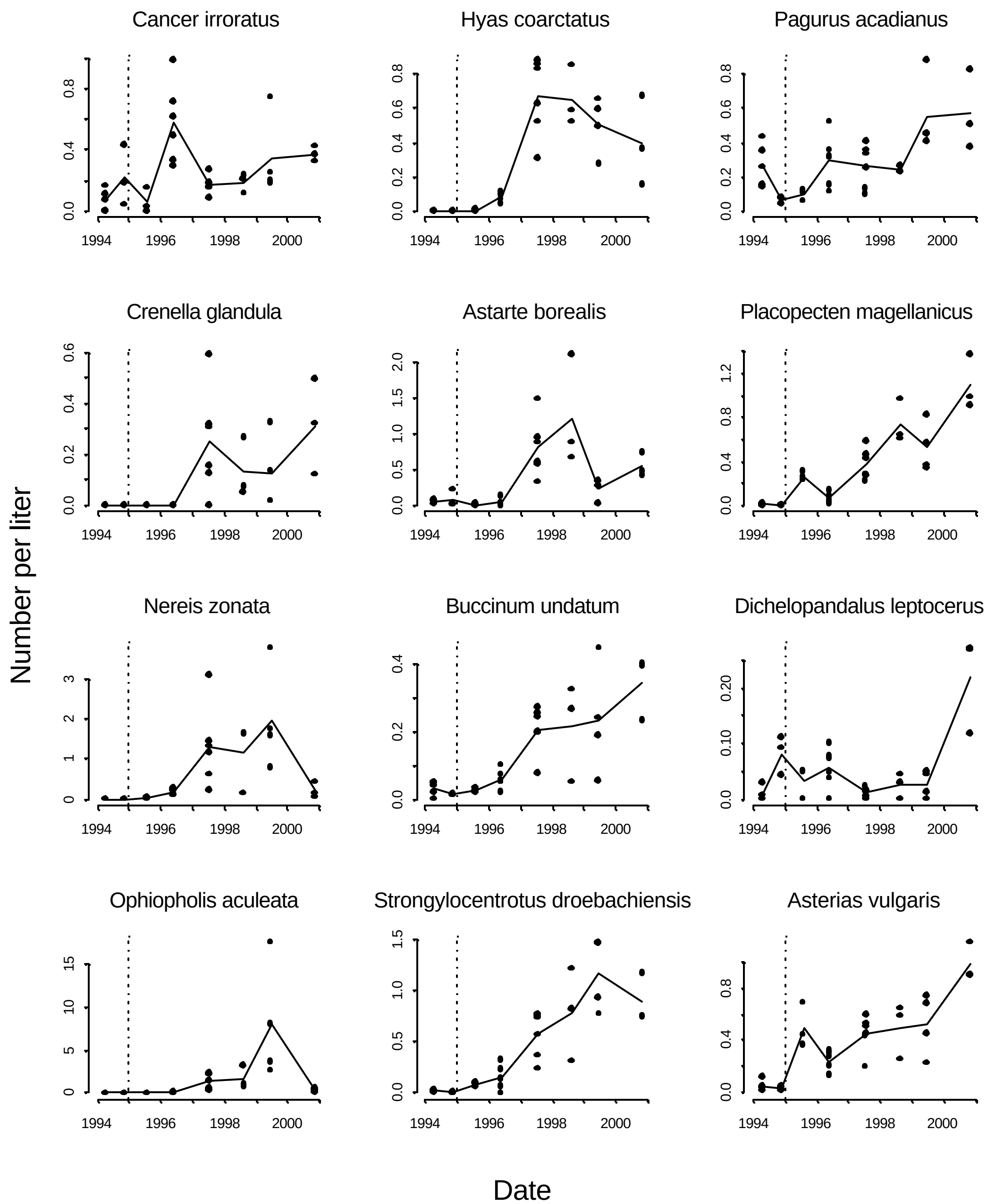

Fig. 9. Abundance of 12 megafaunal species that contributed most to the changes in community composition Site 17. Each point represents one replicate dredge sample; solid lines connect the means at each sampling date. The broken vertical lines indicate the date this site was closed to bottom fishing.

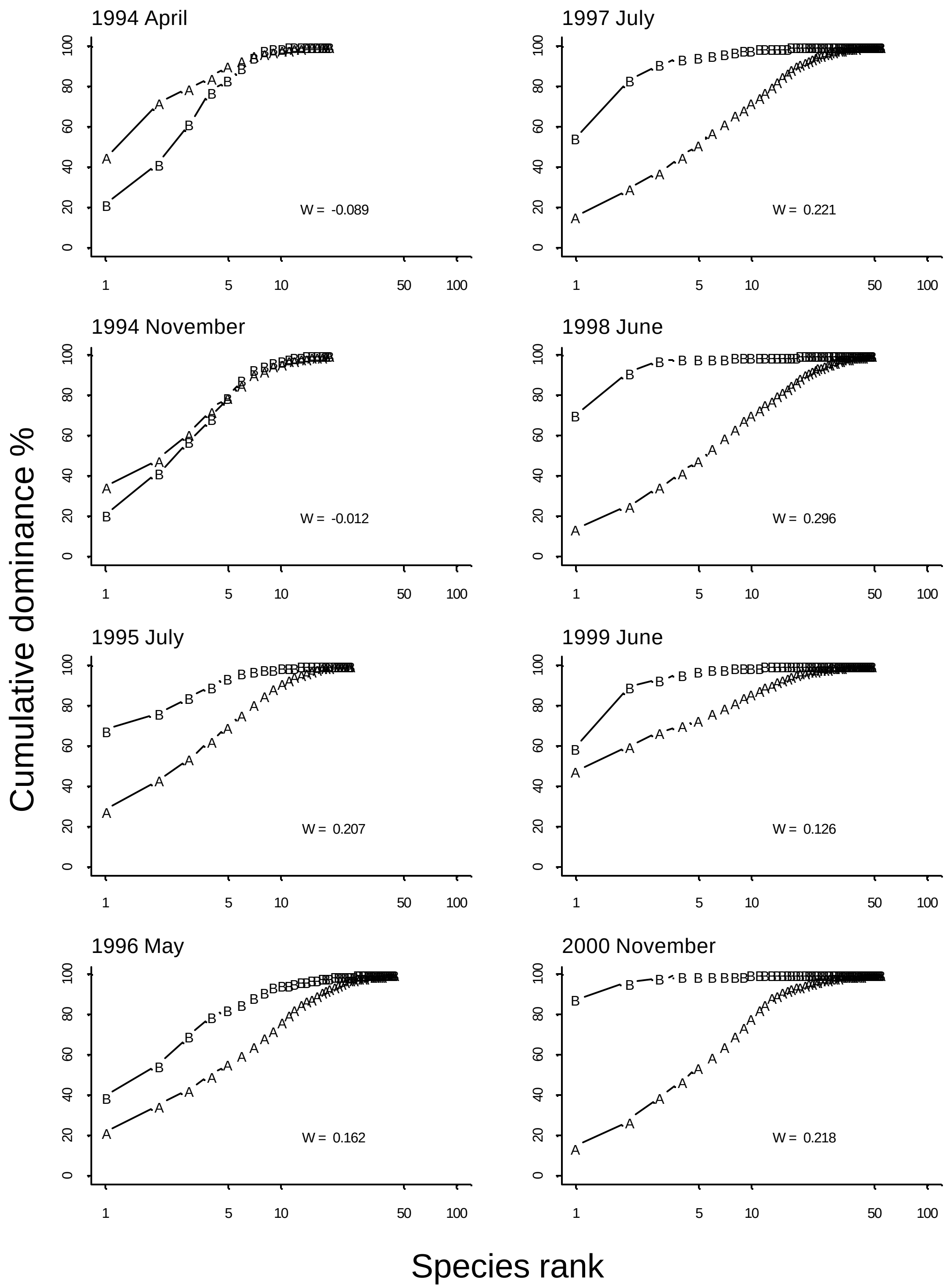

Fig. 10. Cumulative dominance curves calculated from the Abundance (A) and Biomass (B) of benthic megafauna at Site 17. The W statistic sums the differences between the biomass and abundance curves (Clark and Warwick 1994).