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Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure

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Abstract—Trawling and dredging on Georges Bank (northwest Atlantic Ocean) have altered the cover of colonial epifauna, as surveyed through *in situ* photography. A total of 454 photographs were analyzed from areas with gravel substrate between 1994 and 2000 at depths of 40–50 m and 80–90 m. The cover of hydroids, bushy bryozoans, sponges, and tubeworms was generally higher at sites undisturbed by fishing than at sites classified as disturbed. The magnitude and significance of this effect depended on depth and year. Encrusting bryozoans were the only type of colonial epifauna positively affected by bottom fishing. Species richness of noncolonial epifauna declined with increased bottom fishing, but Simpson's index of diversity typically peaked at intermediate levels of habitat disturbance. Species that were more abundant at undisturbed sites possessed characteristics that made them vulnerable to bottom fishing. These characteristics include emergent growth forms, soft body parts, low motility, use of complex microhabitats, long life spans, slow growth, and larval dispersal over short distances. After the prohibition of bottom fishing at one site, both colonial and noncolonial species increased in abundance. Populations of most taxa took two years or more to increase after the fishing closure. This finding indicates that bottom fishing needs to be reduced to infrequent intervals to sustain the benthic species composition of Georges Bank at a high level of biodiversity and abundance.

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Commercial fishing with mobile gear (e.g., otter trawls, beam trawls, scallop dredges) has become such a widespread practice that it is estimated that an area equivalent to approximately 75% of the world's continental shelves is trawled annually (Kaiser et al., 2002). Because bottom fishing can kill and injure benthic invertebrates that are either caught as bycatch or crushed underneath fishing gear, heavily fished areas often exhibit decreased abundance, biomass, and diversity of epifauna (Collie et al., 1997). Trawling and dredging can modify the composition of marine sediments through the dispersal of piles of boulders (Collie et al., 1997; Freese et al., 1999) and the resuspension of fine sediments. The latter process may subsequently release contaminants and excess nutrients, expose anoxic sediment layers, smother filter feeders, and alter biogeochemical fluxes (Kaiser et al., 2002). Bottom fishing also affects benthic community structure by augmenting the abundance of scavengers (Ramsay et al., 1998) and depleting organisms that serve as ecosystem engineers or keystone species (Auster et al., 1996). Similarly, ecosystem function and population dynamics can be indirectly altered because bottom fishing may reduce levels of epifaunal productivity (Hermsen et al., 2003), lower the diversity of prey available to demersal fish (Jiang and Carbines, 2002), and decrease the structural complexity of the benthic environment (Auster et al., 1996).

A meta-analysis of the effects of bottom fishing revealed that less than one-half of the studies addressing this topic examined the long-term recovery of the benthic community (Collie et al., 2000b). In studies where recovery rates were investigated, most tracked recovery for a period of less than two years, which may not be long enough to evaluate the final outcome of ecological succession in disturbed habitat patches. For example, at the completion of a study that involved experimental trawling in a Scottish sea loch, physical signs of trawl damage had disappeared after 18 months, but differences in the benthic community structure at treatment and reference sites persisted (Tuck et al., 1998). Similarly, at the end of a six-month study of the effects of experimental trawling, the polychaete *Terebellides atlantis* and the nemertean *Cerebratulus lacteus* had not yet returned to pretrawling levels of abundance (Sparks-McConkey and Watling, 2001). Knowledge of epifaunal recovery from natural and fishing-induced disturbance is especially lacking on the continental shelf, an area subjected to heavy bottom fishing. Compared to intertidal zones and shallow subtidal areas where benthic responses to natural disturbance have long been studied, relatively little research has been undertaken to track the colonization of sessile epifauna to hard substrata at depths greater than 30 m after natural or anthropogenic disturbances. In the Gulf of Maine, those studies on this subject (Sebens et al., 1988; Witman, 1998) had relatively short durations (less than two years), which may not have

provided adequate time for the completion of ecological succession.

We evaluated fluctuations in the abundance of colonial and noncolonial epifauna in benthic photographs taken between the years 1994 and 2000 in areas of Georges Bank (northwest Atlantic) that have been classified as either disturbed or undisturbed by bottom fishing. Colonial epifauna are ecologically important because many taxa generate three-dimensional microhabitats that augment the structural complexity of the benthic environment. These microhabitats may directly benefit invertebrates and demersal fishes by aggregating food sources and providing refuge from visual predators (Henkel and Pawlik, 2005). Comparisons were made between two depth strata in order to determine how depth may modulate the response of epifauna to bottom-fishing disturbance. Because noncolonial species of megafauna were examined in both photographs and previously analyzed benthic samples collected at the same study sites with a 1-m wide "naturalist" dredge (a dredge design described in Eleftheriou and Holme, 1984), trends in noncolonial epifauna distribution, abundance, and species composition are analyzed to facilitate comparisons between sampling techniques. The effect of bottom fishing on the diversity of noncolonial species is also examined.

One of our study sites was located in an area where bottom fishing has been prohibited since December 1994. Because this site had previously been fished with mobile gear, much of its resident epifauna had been destroyed at the beginning of our study. This situation allowed us to examine patterns of ecological recovery. Our research represents one of the first published studies conducted in this geographic region on the long-term processes (i.e., greater than two years) affecting ecological recovery from disturbance among colonial epifauna on the continental shelf.

Materials and methods

Description of study sites

In December 1994, bottom fishing was prohibited in three large sections of Georges Bank and the southern New England continental shelf to decrease levels of fishing mortality on Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Limanda ferruginea*). Closed (fishing) area II (CA-II), which is the focus of the current research, is located 150 km offshore on the Northeast Peak of Georges Bank (Fig. 1A). The northern section of CA-II where the seafloor is principally covered by gravel substrate was designated as a habitat area of particular concern (HAPC) in 1998. The gravel substrate in this area forms an important habitat for Atlantic sea scallops (*Placopecten magellanicus*), provides a nursery ground for juvenile *G. morhua* and *M. aeglefinus*, and serves as a spawning ground where Atlantic herring (*Clupea harengus*) deposit their demersal eggs (Lough et al., 1989). Sections of the gravel substrate contain dense patches of sponges, hydroids, bushy and encrusting bryozoans, colonial ascidians, and the lacy tubeworm (*Filograna implexa*) (Collie et al., 2000a; Valentine et al., 2007).

During the year before the establishment of CA-II, scientists from the University of Rhode Island (URI) and the United States Geological Survey (USGS) traveled to this area on two occasions to conduct sidescan sonar surveys, collect samples of benthic megafauna, and record the fauna observed on the seafloor along transect lines by means of video and still cameras. Initial assessments of the benthic megafauna and colonial epifauna at these study sites were published in Collie et al. (1997, 2000a). Between 1994 and 2000, the URI and USGS research team returned to Georges Bank on a nearly annual basis to track the recovery of the megafaunal community in CA-II and to evaluate interannual variations in community structure at other sites (Collie et al., 2005).

Because some sites on Georges Bank contain scattered boulders that can damage fishing gear, certain areas are generally avoided by fishermen and can, therefore, be classified as undisturbed by bottom fishing. To identify which regions were disturbed by bottom fishing, a 10-km^2 area at six different sites was surveyed with a 100-Khz high-resolution sidescan sonar in April 1994. Sonograms from these surveys were inspected for trawl and dredge marks. Areas containing such marks were classified as disturbed, and areas with no visible signs of recent trawling or dredging activity were considered undisturbed. Sediment maps were consulted to ensure that only sites dominated by gravel substrate were sampled (Valentine et al., 1993). Disturbed and undisturbed sites were examined at shallow depths (40–50 m) and at deeper depths (80–90 m) in U.S. and Canadian waters (Collie et al., 1997).

The original classification of study sites as disturbed or undisturbed was validated with data on scallop dredging and bottom trawling effort provided by the National Marine Fisheries Service (NMFS) and the Canadian Department of Fisheries and Oceans (DFO) (Table 1). For sites located within the U.S. Economic Exclusive Zone, data from the NMFS satellite vessel monitoring program were used to compute the number of hours that scallop fishing boats spent dredging each square nautical mile of Georges Bank from 1998 through 2000 (Collie et al., 2005). Before 1998, the classification of sites as disturbed or not disturbed on the U.S. portion of Georges Bank was verified with NMFS data on scallop dredging effort which had a 10-minute latitude resolution. At shallow sites, both NMFS data sets consistently confirmed the accuracy of the original disturbance classifications that had been based on sidescan sonar surveys. The disturbance classifications at Canadian sites were authenticated with data from DFO logbook reports from the commercial scallop fishery that had a 1-minute latitude resolution. Because the number of days fished at deep sites varied both inside individual study sites and between years (Collie et al., 2005), we decided that the classifications of sites located at the

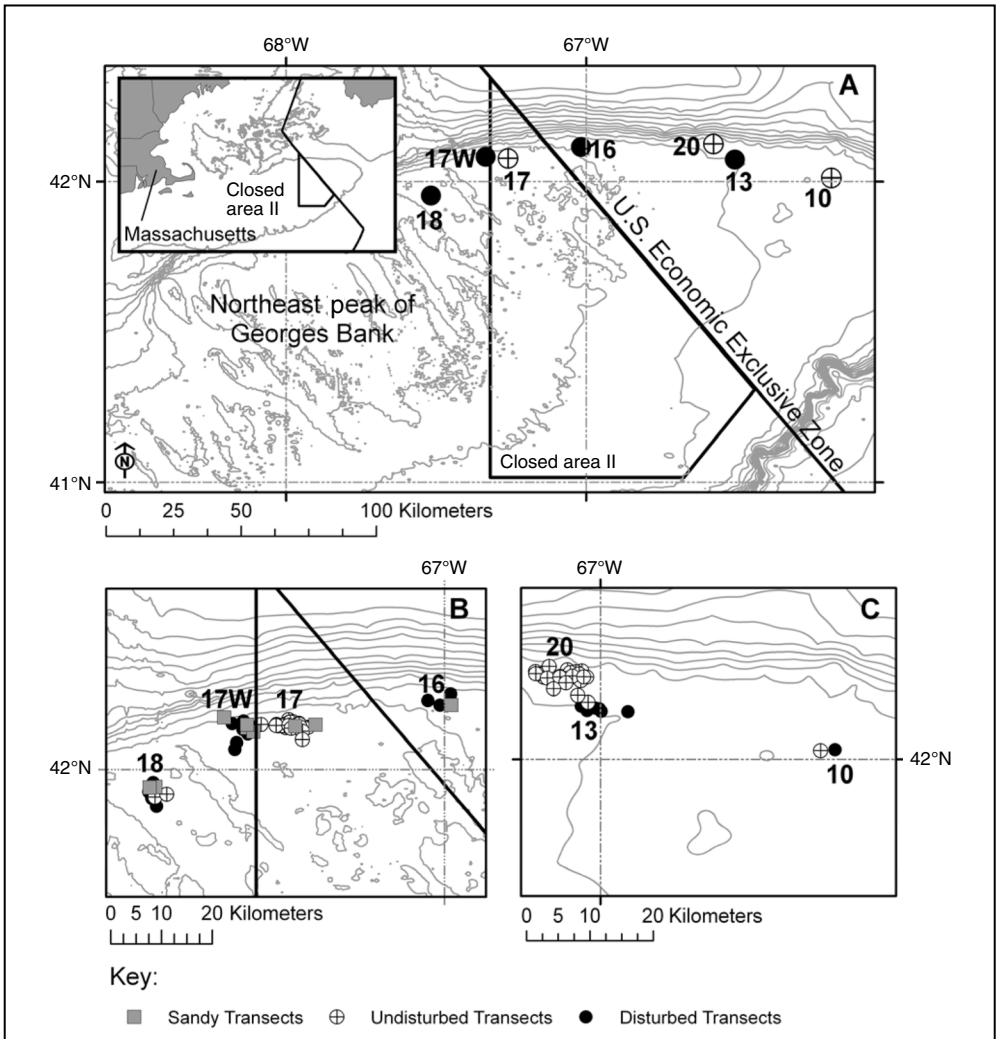

Figure 1

(**A**) Map of the Northeast Peak of Georges Bank displaying closed area II and the study sites surveyed between 1994 and 2000. (**B**) and (**C**) Maps of the starting points of each photographic transect conducted at shallow (B) and deep (C) sites. Transects were classified as sandy if more than 50% of the photographs analyzed contained ≥50% cover of sand. Numbers on each map identify study sites. The classification of disturbance at some sites (i.e., 17 and 18) changed throughout the duration of this study. The lines in the background of each map show the bathymetry of Georges Bank; each line represents a 20-m change in depth.

deeper depth strata should be recategorized. According to our revised classification scheme, any photographed transect at a deep site that was fished with a scallop dredge for one day or less per year was classified as undisturbed.

Based on disturbance classification, sediment composition, and depth, five 5 km × 10 km sites were selected for examination during the first year of this study (Fig. 1). Three of these study sites (i.e., sites 10, 13, and 20) were located in deeper water on the Canadian section of Georges Bank. At the 80–90 m depth stratum, site 20 was classified as undisturbed, site 13 was classified as disturbed for all years except 1998 when it contained two undisturbed transects, and site 10 was sampled only in 1994 when it contained one disturbed and one undisturbed transect (Table 1). On the shallower U.S. portion of the bank, two study sites were originally surveyed, one corresponding to an area with little disturbance from bottom fishing (i.e., site 18) and the other representing a heavily fished zone (i.e., site 17). After the incorporation of site 17 into CA-II, much of the fishing effort formerly concentrated at this site was displaced into areas that were unaffected by the closure, including site 18. Consequently, the initial clas-

Table 1

Classifications of disturbance and mean scallop dredging effort at study sites based on data from the National Marine Fisheries Service (NMFS) and the Canadian Department of Fisheries and Oceans (DFO). Dashes indicate years when no photographic samples were collected. D and U indicate shallow sites that were classified as "disturbed" or "undisturbed," respectively, before the development of the NMFS satellite vessel monitoring program in 1998. Classifications made at shallow sites before 1998 were based on trawl and dredge marks seen in side can sonar images. No photographic data were gathered in 1995. Dredging effort from U.S. and Canadian sites cannot be easily compared because data were reported in different units and the type of fishing gear used by each country may have varied.

Site	Classification of disturbance	1994	1996	1997	1998	1999	2000
Shallow sites: Mean dredging effort in hours fished per year within two miles (3.2 km) of site							
16	Disturbed	—	D	D	—	—	—
17	Disturbed before establishment of a fishery closure (i.e., 1994) and undisturbed afterwards (i.e., 1996–2000)	D	U	U	0	0	0
17W	Disturbed	—	—	D	172.6	58.1	—
18	Undisturbed before establishment of a closed area (i.e., 1994) and disturbed afterwards (i.e., 1996–2000)	U	D	D	97.4	1.0	1.2
Deep sites: Mean dredging effort in days fished per year within a square minute latitude of a transect							
10	Mildly to moderately disturbed	2.5	—	—	—	—	—
13	Disturbed, except for two transects surveyed in 1998	3.5	5.0	4.0	2.0	—	—
20	Undisturbed	0	0.2	0.1	0	0	—

sification of bottom-fishing-induced disturbance at sites 17 and 18 was reversed in 1995. In order to evaluate the effectiveness of the fishery closure, other disturbed sites were sampled surrounding CA-II (i.e., sites 16 and 17W) in later years.

Fieldwork and laboratory procedures

Photographs of the seafloor of northeastern Georges Bank were collected during seven research cruises, which were conducted on a nearly annual basis from November 1994 through November 2000. During all cruises, except for one occurring in July 1995, the SEABed Observation and Sampling System (SEABOSS; Woods Hole Science Center, U.S. Geological Survey, Woods Hole, MA) was deployed to take 35-mm photographs of the seafloor. The SEABOSS consists of a tethered van Veen grab sampler that is equipped with two Hi-8 video cameras, one still camera, accompanying lights, and a pressure-depth sensor (Blackwood and Parolski, 2001). The SEABOSS also contains two parallel lasers placed 20 cm apart, which are used to gauge the size of objects on the seabed. The frame of the SEABOSS instrument was attached to a winch and allowed to drift under the research vessel as it traveled at a speed of 1–2 knots (0.5–1.0 m/s). At each study site surveyed during a research cruise, three transects were generally conducted with the SEABOSS. However, depending on weather conditions, research priorities, and available ship time, anywhere between one and ten transects were filmed. Because of changes in tidal speed, transect length varied between 183 and 4316 m (mean distance of 921 m, standard deviation [SD]=527 m). Along transects, photographs were taken at 30–60 s intervals. In addition to the SEABOSS, during the 1996 and 1999 research cruises, videos and photographs of the seafloor were also taken with a MaxRover MK1 remotely operated vehicle (ROV; Deep Sea Systems International, Inc., Falmouth, MA) provided by the National Undersea Research Center at the University of Connecticut. This ROV system included a set of two 35-mm still cameras and two Hi-8 video cameras. As with the SEABOSS, two parallel lasers placed 20 cm apart were used to estimate the size of objects on the seafloor. During the 30-minute ROV transects (approximately 1000 m in length), photographs of the seabed were snapped at 30-second intervals. Each photograph taken with the SEABOSS covered an area of approximately 0.25–0.27 m^2 of the seafloor, whereas approximately 0.31 m^2 of the sea bottom was examined in each ROV photo.

Because of the impracticality of analyzing the hundreds of photographs taken during each cruise, we randomly selected a subsample of 12–30 photographs per site (average=16) to be examined in detail each year. As a result of the scarcity of quality photos (i.e., not blurry or sandy), a reduced number of photographs were chosen from site 13 in 1996 and site 20 in 1999. A total of 454 benthic photographs from 94 transects surveyed from 1994 and 2000 were analyzed. These photographs covered an area of 120.8 m^2 of the seafloor. Following the method described in Collie et al. (2000a), we over-

laid photographs with a transparency containing a grid, in which each grid cell represented a 5 cm × 5 cm area of the seafloor. From 1996 through 2000, the percent cover of hydroids, bushy and encrusting bryozoans, sponges, and *F. implexa* was recorded in each grid cell. Data were summed across grid cells to calculate the total percent cover of each type of colonial organism per photograph. In 1994, the percent frequency of several types of colonial epifauna was measured, instead of percent cover. Results of the 1994 surveys were presented in Collie et al. (2000a). In addition, noncolonial, megafaunal species were enumerated in each grid cell and identified to the lowest possible taxonomic level. Sediment type and the number of pieces of cultch (i.e., broken bivalve shells) were also recorded during analyses of the photographs. Like colonial epifauna, some fish species use the three-dimensional structure generated by cultch to obtain shelter from predators (Auster et al., 1995).

Because hard bottom (e.g., cobble and gravel) and soft bottom (e.g., sand, silt, and mud) environments support fundamentally different benthic communities, we decided to remove from our data set those transects where sand constituted a large percentage of the substratum. Transects where the majority of photographs contained greater than 50% sand cover were usually clustered around a distinct area or were located at the far edge of our study sites (Fig. 1B). To guarantee that only gravel habitat was examined, 34 photographs from sandy transects were removed from the data set. Once photographs that were sandy, blurry, or overexposed had been selected and removed, 386 photographs remained, covering an area of 100.1 m^2.

Throughout this study, benthic photographs were analyzed by five observers. To evaluate the extent to which between year and within-year fluctuations in epifauna abundance might reflect observer bias, calibration tests were performed during which two observers examined the same photograph(s). *T*-tests, in which photographs analyzed by different observers were treated as matched pairs, were used to determine whether observer bias affected estimates of epifaunal abundance. Results indicated that, with the exception of the coiled worm (*Spirorbis* spp.), patterns of observer bias did not match the direction and magnitude of between-year and within-year variations in epifaunal cover or megafaunal abundance (Asch, 2006). Data on *Spirorbis* spp. are not presented here because of concerns about observer bias.

Statistical analyses

Colonial epifauna A series of two-way analysis of variance (ANOVA) tests were conducted to investigate which taxa of colonial epifauna exhibited significant differences in percent cover between disturbance categories and years. Because large variations in organismal abundance with depth may overshadow subtler fluctuations related to bottom fishing, each depth stratum was considered separately in the ensuing analyses. Response variables included six measures of the cover of colonial epifauna taxa and cultch. A previous examination of spatial patterns indicated that autocorrelation existed between photos from the same transect (Asch, 2006). Therefore, percent cover from photos were averaged across transects, allowing us to use transects as our primary sampling unit when conducting parametric tests. All response variables were arcsine square-root transformed in order to ensure that percent cover data would conform to the normal probability density function. Bottom-fishing disturbance classifications and year were used as factors in the ANOVAs. At shallow sites, the interaction term (*disturbance* × *year*) was used to evaluate whether differences between sites inside and outside of CA-II increased over time because of the continued recovery of organisms in CA-II. Since no data from a deep, disturbed site were collected in 1999, this particular year was removed from the data set when we considered the deeper depth stratum, so that the experimental design would be balanced. Because of the nonorthogonal design of these ANOVAs, type-III sums of squares were used. When interannual differences were indicated to be an important factor affecting a particular type of colonial epifauna, Tukey-Kramer multiple comparisons tests were applied to determine which years differed significantly (S-Plus 6, MathSoft, Inc., Seattle, WA).

Noncolonial organisms Although many noncolonial organisms were identified to the species level, other organisms could only be identified to genus or family because of the limited resolution of photos or the need for microscopic examination of distinguishing features. In cases where some organisms belonging to a particular taxonomic group could be identified to species, but others could not, all members of the taxonomic group in question were lumped together in order to guarantee that classifications were mutually exclusive. Ninety-eight percent of the noncolonial organisms identified in photographs belonged to five extremely abundant taxa: *Spirorbis* spp., the tubeworm *Protula tubularia*, the jingle shells *Anomia* spp., the barnacles *Balanus* spp., and an unidentified species of burrowing anemones (order Ceriantharia). For each depth and disturbance category, the R statistical package (Free Software Foundation, Boston, MA) was used to fit the negative binomial distribution to the data on the abundance of these five species. Next, a *U* test was applied to evaluate the goodness-of-fit of the negative binomial distribution (Krebs, 1999). Because in all cases but one (i.e., *Anomia* spp. at deep, undisturbed sites) the negative binomial distribution provided an adequate fit, we determined that these five highly abundant species have an aggregated spatial distribution, whereby they were absent from many photographs but obtained very high densities in a few areas. For example, *Anomia* spp. and *Balanus* spp. were not identified in two-thirds of the photographs sampled but were occasionally observed at concentrations as high as 1328 per m^2 and 760 per m^2, respectively. Because random sampling of such dense aggregations could result in the detection of artificial

differences among depths, disturbance categories, and years, data on the abundance of these five species are not presented in this manuscript. However, information on trends in the abundance of these five taxa can be referenced in Asch (2006).

All other noncolonial taxa were collectively examined as a multivariate data set. Differences in the species composition of these noncolonial organisms among depth strata, years, bottom-fishing disturbance categories, and sites were explored by constructing nonmetric multidimensional scaling (MDS) plots in PRIMER 6 (Plymouth Marine Lab, Plymouth, UK). MDS plots were constructed with a Bray-Curtis similarity matrix containing information on the mean number of individuals of each taxon per photograph, aggregated across each transect (Clarke and Warwick, 2001). To ensure that patterns in the MDS plot were not dictated solely by trends in the abundance of a few ubiquitous species, data were square-root transformed before this analysis and all other multivariate statistical routines (i.e., analysis of similarity [ANOSIM] and similarity of percentages [SIMPER]). ANOSIM tests were used to evaluate whether differences in noncolonial species composition between disturbance categories and years were statistically significant (Clarke and Warwick, 2001). In cases where significant differences were detected, the SIMPER routine in PRIMER 6 was used to determine the mean percent dissimilarity that each species contributed to differences between disturbance categories (Clarke and Warwick, 2001).

In addition to examining the effect of bottom-fishing-induced disturbance on species composition, its influence on two measures of noncolonial diversity was investigated. Jackknife species richness and Simpson's index of diversity ($1–\lambda'$) were calculated according to the methods described in Krebs (1999). These two diversity indices were selected, because 1) they are either unaffected by differences in sample size (e.g., Simpson's index) or incorporate estimates of the number of rare species that are unlikely to be sampled (e.g., jackknife species richness) (Clarke and Warwick, 2001), and 2) together these indices measure several aspects of biodiversity (e.g., richness, heterogeneity, and evenness). The diversity indices were computed for five levels of disturbance at both shallow and deep sites. Data were binned into five disturbance levels to achieve sufficient sample sizes because the jackknife species richness index requires that the size of samples is large enough to include at least half of the species in an area (Krebs, 1999). Only data from shallow sites collected during years when the NMFS satellite vessel monitoring program was in operation (i.e., 1998–2000) were analyzed. Linear and polynomial regressions were performed to evaluate the relationship between bottom-fishing disturbance and these two measures of noncolonial diversity. The most parsimonious regression model was selected on the basis of the results of the analysis of deviance test included in the R statistical package.

Results

Colonial epifauna

At shallow sites, the cover of five out of six taxa of colonial epifauna differed significantly between undisturbed and disturbed sites located, respectively, inside and outside of CA-II (Fig. 2). Hydroids were the only taxon of colonial epifauna whose percent cover was not significantly affected by disturbance at shallow sites. During most years, structurally complex taxa of colonial epifauna, such as sponges and bushy bryozoans, were more abundant at shallow, undisturbed sites, whereas encrusting taxa, such as encrusting bryozoa, cultch, and *F. implexa*, exhibited a higher percent cover at shallow, disturbed sites (Fig. 2). With the exception of *F. implexa* whose cover at each shallow site remained fairly stable throughout the time series, all other colonial epifauna taxa demonstrated significant between-year variations in abundance at shallow sites. Several of these taxa showed marked changes in abundance beginning in 1997 and 1998, indicating that it took at least two years for these species to respond to the establishment of CA-II or to the increased bottom-fishing effort at sites that remained open to mobile fishing gear. For example, sponges were absent from all photographs taken at the shallow site in CA-II during 1994 and 1996 but were seen in 97% of the photographs taken in this area in 1997 (Figs. 2 and 3A). Similarly, bushy bryozoans experienced a temporary spike in their percent cover at the shallow, undisturbed site in 1997. The cover of encrusting bryozoans was fairly similar at all shallow sites at the initiation of this study, but then began to increase in disturbed areas beginning in 1998. By the year 2000, 62% of the substratum at shallow, disturbed sites was covered by encrusting bryozoa (Fig. 3B). Temporal variations in the abundance of hydroids and cultch are unlikely to reflect changes in bottom-fishing effort because similar between-year changes were seen at all shallow sites regardless of closure status.

The only two taxa that clearly exhibited significant differences between disturbed and undisturbed sites at the deep depth stratum were *F. implexa* and hydroids, both of which consistently had an elevated percent cover in undisturbed areas (Fig. 4). Bushy bryozoans also had a higher cover in 1997 and 1998 in deep areas that experienced little to no bottom fishing. However, this pattern was reversed in 1996 when deep, disturbed sites exhibited slightly greater cover of bushy bryozoans than deep, undisturbed sites. Cultch and encrusting bryozoans at deep sites were frequently more abundant in disturbed areas, but this trend was inconsistent between years, causing ANOVA results to be only marginally significant (i.e., $P=0.08$ and $P=0.07$ for cultch and encrusting bryozoans, respectively). Sponge abundance was depressed at all deep sites from 1996 through 1998, and its mean percent cover never exceeded 0.5% during these years. Temporal variations in colonial epifauna cover appeared to be of lesser importance at deep sites than at shallow sites because encrusting bryozoans were

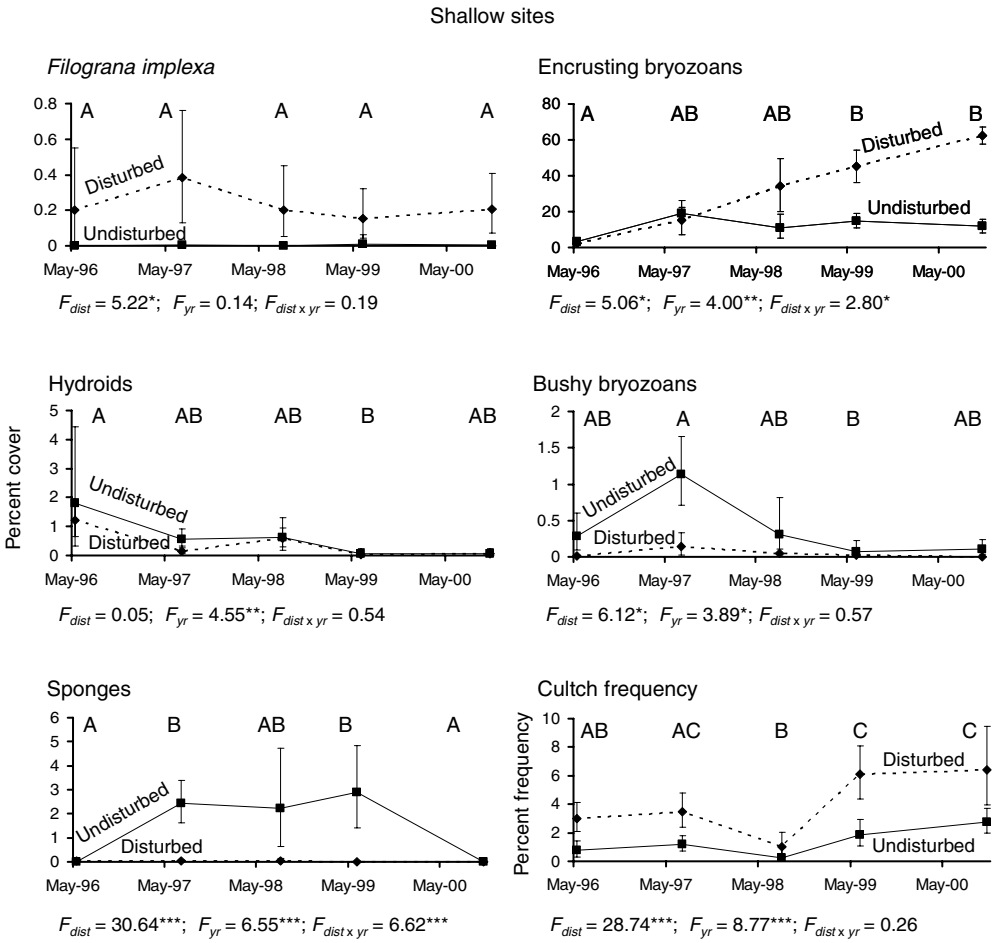

Figure 2

Temporal trends in colonial epifaunal percent cover and cultch percent frequency at shallow sites (40–50 m). Trend lines from sites that were either disturbed or undisturbed by bottom fishing are shown. Shallow undisturbed data came from site 17, whereas shallow disturbed data were derived from sites 16, 17W, and 18. The scale of the *y* axis varies between graphs of different epifaunal taxa. Markers (i.e., black squares and black diamonds) are back-transformed means, and error bars are 95% confidence intervals. Different letters above data points represent annual means that differ significantly from each other in multiple comparison tests. *F* statistics from two-way analyses of variance (ANOVAs) on the effects of disturbance (*dist*), year (*yr*), and disturbance × year (*dist* × *yr*) are shown below each graph (df=1,4,4). Significance levels from ANOVA tests are indicated as follows: **P*<0.05; ***P* <0.01; ****P*<0.001.

the only taxon to have a significant year term in the two-way ANOVAs performed on deep sites (Fig. 4).

The greater between-year variability at shallow sites can be interpreted as a sign of the effectiveness of CA-II. Because there can be subtle, pre-existing differences in habitat quality between areas inside and outside a marine reserve, a conclusive demonstration of reserve effectiveness typically requires that biological distinctions between fished and unfished areas become amplified over time (Murawski et al., 2004). As a result, variables truly affected by the establishment of CA-II should have significant interaction terms in their corresponding two-way ANOVA, as well as exhibit significant differences between disturbance categories and among years. Sponges and encrusting bryozoans were the two colonial epifauna taxa that exhibited significant interaction terms in the ANOVAs performed for shallow sites. No interactions between disturbance and year were detected at the deep sites. This finding reflects the fact that bottom-fishing effort was fairly consistent over time at deep sites (Table 1; Collie et al., 2005), whereas fishing effort at shallow sites showed a more distinct temporal trajectory related to the establishment of CA-II.

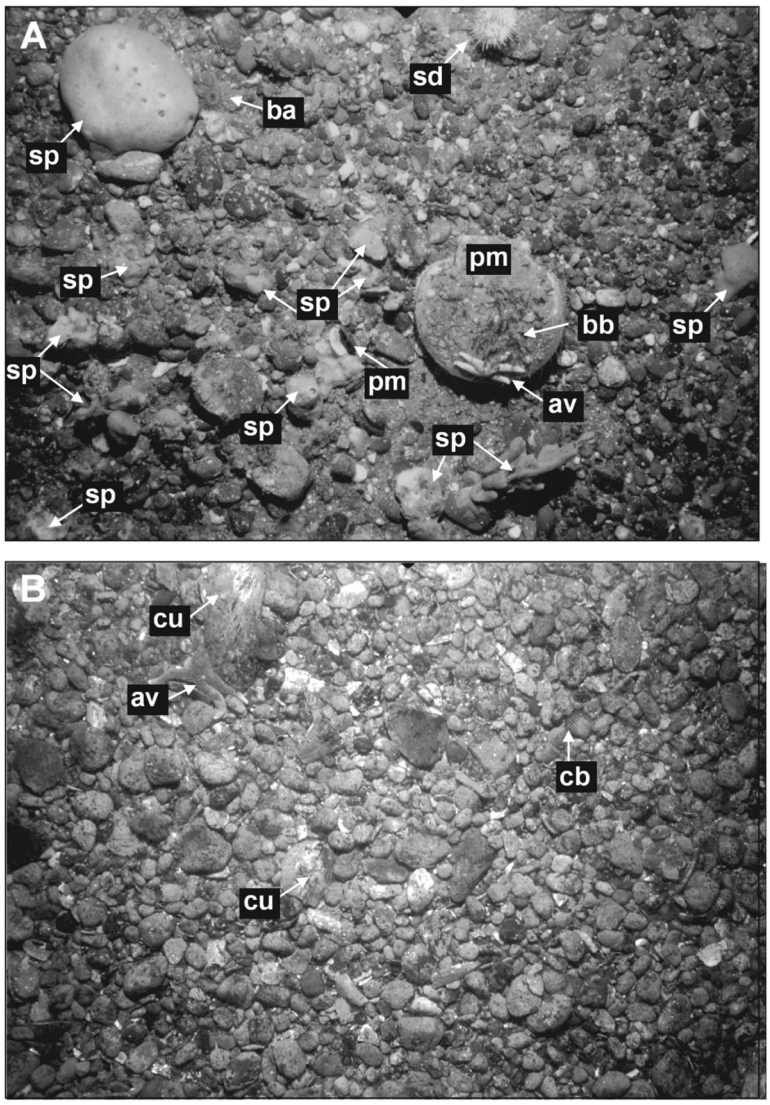

Figure 3

Photographs of the seafloor taken in 1999 at sites 17 (**A**) and 18 (**B**). (A) Sponges (sp) cover 10.4% of the seafloor in this photograph, and bushy bryozoans (bb) cover an additional 2.5%. Species of noncolonial epifauna seen in this photograph include the sea scallop (*Placopecten magellanicus* [pm]), the Northern seastar (*Asterias vulgaris* [av]), the green sea urchin (*Strongylocentrotus droebachiensis* [sd]), and a burrowing anemone (ba). (B) Encrusting bryozoans cover 74.2% of the seafloor in this photo from a shallow, disturbed site. Areas where the gravel substrate is a light grey color contain encrusting bryozoans. Two pieces of cultch (cu) are visible, as well as *A. vulgaris* (av) and a northern cyclocardia (*Cyclocardia borealis* [cb]). Photographs by Dann Blackwood, Woods Hole Science Center, U.S. Geological Survey, Woods Hole, MA.

Noncolonial organisms

In the 454 benthic photographs that were analyzed, a total of 117,315 noncolonial organisms were identified, which included 73 distinct taxa. After removing data on five abundant species with extremely aggregated spatial distributions, we found that this data set contained 1561 individuals. Clear differences between deep and

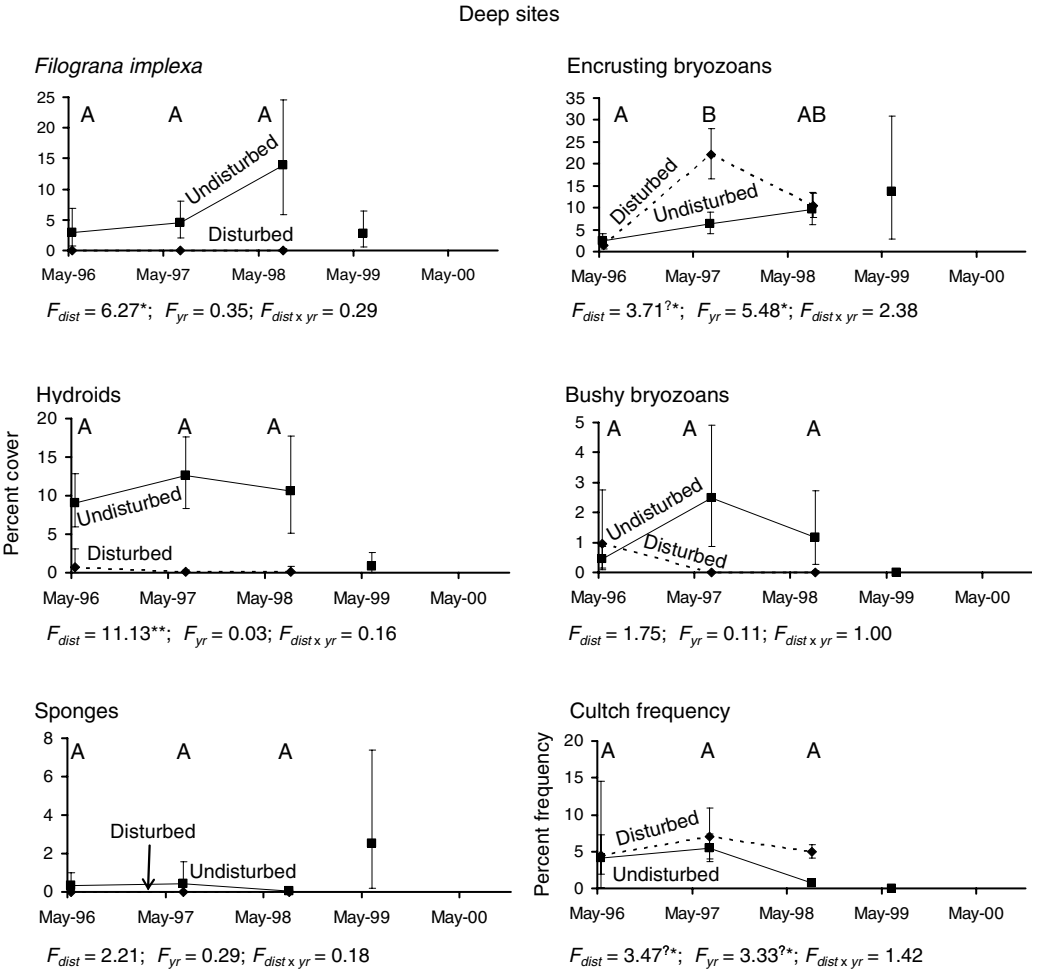

Figure 4

Temporal trends in colonial epifaunal percent cover and cultch percent frequency at deep sites (80–90 m). Trend lines from sites that are either disturbed or undisturbed by bottom fishing are shown. Data representing deep, disturbed sites originated from sites 10 and 13, and data representing deep, undisturbed sites were primarily from site 20, but also included a few unfished transects from sites 10 and 13. The scale of the *y* axis varies between graphs of different epifaunal taxa. Markers (i.e., black squares and black diamonds) are back-transformed means, and error bars are 95% confidence intervals. Different letters above data points represent annual means that differed significantly from each other in multiple comparison tests. *F* statistics from two-way analyses of variance (ANOVAs) on the effects of disturbance (*dist*), year (*yr*), and disturbance × year (*dist* × *r*) are shown below each graph (df=1,2,2). Significance levels from ANOVA tests are indicated as follows: ?* $P<0.10$; *$P<0.05$; **$P<0.01$. There are no lines connecting data from 1998 and 1999 at deep, undisturbed sites because the 1999 data were not included in two-way ANOVAs.

shallow transects in terms of noncolonial megafaunal abundance were apparent when we examined MDS plots (Fig. 5A). Compared to the evident effect of depth on noncolonial species composition, the influence of bottom-fishing disturbance in MDS plots was subtle. Transects recorded at disturbed site 18 could be distinguished from transects at all other shallow sites. Relatively few differences in noncolonial species composition could be seen among sites 16, 17, and 17W (Fig. 5B). At the deep depth stratum, disturbed sites 10 and 13 generally exhibited a community composition that was distinct from undisturbed site 20, as indicated by the positioning of disturbed transects to the left of the MDS plot (Fig. 5C). The two transects from site 13 that were more interspersed among transects from site 20 in the MDS were filmed in the northwestern extent of this study site, which was subjected to less bottom-fishing pressure. The greater dispersion of deep, undisturbed transects across the MDS revealed a wider variation in species composition at site 20 than at other deep sites.

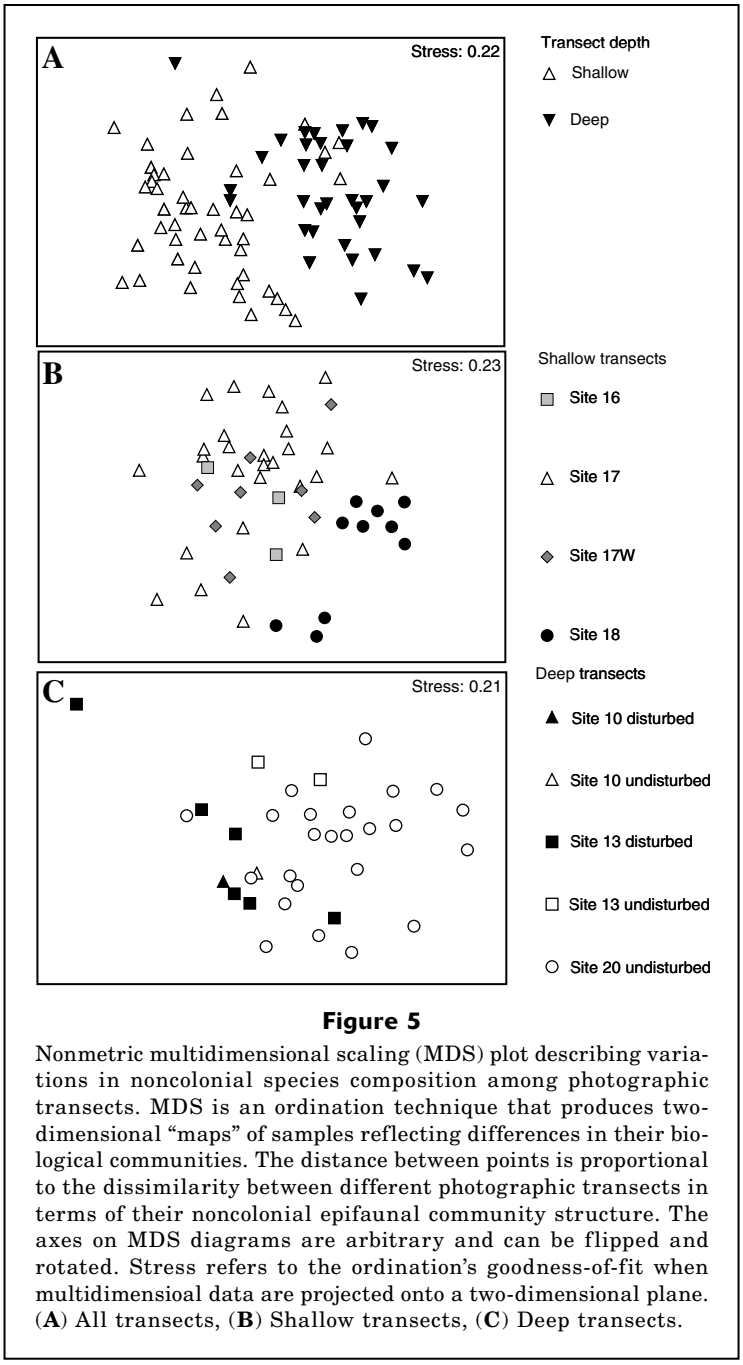

Figure 5

Nonmetric multidimensional scaling (MDS) plot describing variations in noncolonial species composition among photographic transects. MDS is an ordination technique that produces two-dimensional "maps" of samples reflecting differences in their biological communities. The distance between points is proportional to the dissimilarity between different photographic transects in terms of their noncolonial epifaunal community structure. The axes on MDS diagrams are arbitrary and can be flipped and rotated. Stress refers to the ordination's goodness-of-fit when multidimensioal data are projected onto a two-dimensional plane. (**A**) All transects, (**B**) Shallow transects, (**C**) Deep transects.

The majority of noncolonial species were most abundant at undisturbed sites, but hard-shelled mollusks and scavengers tended to dominate in heavily fished areas. Significant variations in community structure were detected at both depths between different disturbance levels and years by means of ANOSIM tests (Tables 2A and 3A). A total of six taxa contributed to 50% of the cumulative dissimilarity between disturbed and undisturbed sites at the shallow depth stratum (Table 2B). Of these six taxa, *P. magellanicus*, the green sea urchin (*Strongylocentrotus droebachiensis*), and the hermit crabs *Pagurus* spp. exhibited higher levels of abundance at shallow sites inside CA-II. Scavenging seastars (*Asterias* spp.) and bivalves (astartes *Astarte* spp. and the northern cyclocardia *Cyclocardia borealis*) were more abundant along shallow, disturbed transects recorded outside the closed area. The elevated numbers of the latter two species at site 18, as well as siphons from an unidentified, infaunal bivalve, explained why transects from site 18 were separated from other shallow sites in the MDS (Fig. 5B). Of the four species that defined 88% of the similarity among undisturbed

Table 2

(**A**) Effects of disturbance from mobile fishing gear and year on the composition of noncolonial organisms at shallow sites. In this two-way crossed analysis of similarity (ANOSIM) test, the sample global R is the test statistic. Data were permuted 9999 times to generate an empirical frequency distribution for global R. Significance levels: *P<0.05; ***P<0.001. (**B**) Similarity of percentages (SIMPER) results identifying species that are characteristic of disturbed and undisturbed sites at the shallow depth stratum. Cumulative percentage refers to the contribution that species make to either the cumulative similarity within each group or the cumulative dissimilarity between two groups. Results are presented in terms of similarity among disturbed transects, similarity among undisturbed transects, and dissimilarity between disturbance groups.

A ANOSIM results

Factor	95th percentile of permuted global R's	Sample global R
Disturbance	0.14	0.20*
Year	0.12	0.30***

B SIMPER results

Similarity among disturbed transects (i.e., outside CA-II)

Scientific name	Mean density per photograph	Cumulative percentage
Pagurus spp.	0.40	27.55
Asterias spp.	0.32	48.41
Placopecten magellanicus	0.59	63.17
Siphons of unidentified bivalves	0.51	74.24
Cyclocardia borealis	0.24	82.70

Similarity amongst undisturbed transects (i.e., inside CA-II)

Scientific name	Mean density per photograph	Cumulative percentage
Placopecten magellanicus	0.72	43.58
Pagurus spp.	0.42	67.24
Strongylocentrotus droebachiensis	0.30	78.10
Asterias spp.	0.27	88.39

Dissimilarity between disturbance groups

Scientific name	Mean density at disturbed sites	Mean density at undisturbed sites	Cumulative percentage
Placopecten magellanicus	0.59	0.72	12.68
Siphons of unidentified bivalves	0.51	0.09	21.74
Pagurus spp.	0.40	0.42	30.46
Asterias spp.	0.32	0.27	39.07
Strongylocentrotus droebachiensis	0.04	0.30	46.32
Astarte spp.	0.47	0.06	52.49

transects inside CA-II (i.e., *P. magellanicus*, *Pagurus* spp., *S. droebachiensis*, and *Asterias* spp., Table 2B), all increased in abundance from 1994 through 2000 (Figs. 3A and 6). Of particular note was the nearly tenfold increase in the mean density of *P. magellanicus* during this time period. At deep sites, seven of the ten taxonomic groups that contributed the most to dissimilarity among disturbance categories were more abundant along undisturbed transects (Table 3B). As was the case at shallow sites, hard-shelled mollusks (*Astarte* spp. and the waved whelk [*Buccinum undatum*]) and scavengers, such as *Pagurus* spp., characterized deep, disturbed sites.

At both depths, species richness of noncolonial epifauna peaked along undisturbed transects (Fig. 7). The negative relationship between species richness and bot-

Table 3

(**A**) Effects of disturbance from mobile fishing gear and year on the composition of noncolonial organisms at deep sites. In this two-way crossed analysis of similarity (ANOSIM) test, the sample global R is the test statistic. Data were permuted 9999 times to generate an empirical frequency distribution for global R. Significance levels: *P<0.05; ***P<0.001. (**B**) Similarity of percentages (SIMPER) results identifying species that are characteristic of disturbed and undisturbed sites at the deep depth stratum. Cumulative percentage refers to the contribution that species make to the cumulative similarity within each group or the cumulative dissimilarity between these groups. Results are presented in terms of similarity among disturbed transects, similarity among undisturbed transects, and dissimilarity between disturbance groups.

A ANOSIM results

Factor	95th percentile of permuted global R's	Sample global R
Disturbance	0.25	0.28*
Year	0.11	0.41***

B SIMPER results

Similarity amongst disturbed transects

Scientific name	Mean density per photograph	Cumulative percentage
Astarte spp.	0.55	21.75
Pagurus spp.	0.55	42.10
Caridea unident.	1.03	59.65
Gastropoda unident. (shelled)	0.48	70.37
Zoantharia unident.	0.23	79.04
Placopecten magellanicus	0.15	86.93

Similarity amongst undisturbed transects

Scientific name	Mean density per photograph	Cumulative percentage
Zoantharia unident.	1.74	35.80
Astarte spp.	0.64	47.03
Pagurus spp.	0.44	55.14
Caridea unident.	3.52	62.44
Modiolus modiolus	0.53	69.59
Gastropoda unident. (shelled)	0.39	76.16
Hyas coarctatus	0.33	81.47

Dissimilarity between disturbance groups

Scientific name	Mean density at disturbed sites	Mean density at undisturbed sites	Cumulative percentage
Zoantharia unident.	0.23	1.74	11.32
Caridea unident.	1.03	3.52	20.25
Astarte spp.	0.55	0.64	26.33
Modiolus modiolus	0	0.53	32.24
Thelepus cincinnatus	1.14	0.25	38.12
Pagurus spp.	0.55	0.44	43.90
Gastropoda unident. (shelled)	0.48	0.39	49.52
Hyas coarctatus	0.05	0.33	53.97
Ophiuroidea unident.	0.05	0.75	58.34
Polychaeta unident. (tubicolous)	0.29	0.33	62.68

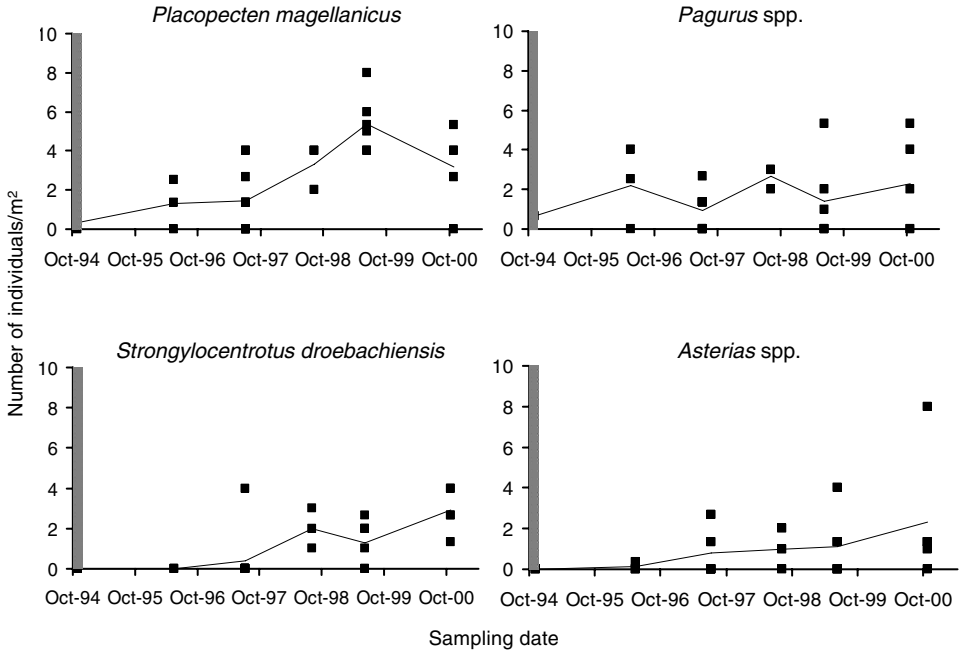

Figure 6

Trends in the abundance of four noncolonial species characteristic of site 17 in closed area II (CA-II). Each black square represents a single photographic transect, and solid lines connect the means from each sampling date. The shaded area indicates the time period before bottom fishing was restricted in CA-II.

tom-fishing effort was statistically significant at shallow sites. Average species richness was greater at deep sites than at shallow sites ($\hat{S}_{deep}$=22 and $\hat{S}_{shallow}$=13), but these two depths did not differ in terms of mean values of Simpson's index of diversity ($1-\lambda'_{deep}$=0.77 and $1-\lambda'_{shallow}$=0.76). The highest values of Simpson's index at shallow sites were recorded in areas with 50–100 hours of scallop dredging per year. At greater levels of bottom-fishing disturbance, a decline in Simpson's index was observed. At deep sites, Simpson's index varied relatively little with disturbance, although its peak value occurred in an area with an intermediate amount of disturbance (i.e., three days of dredging per year). Trends in Simpson's index were not significant when modeled with linear and polynomial regression.

Discussion

Colonial epifauna

Because sessile, colonial organisms cannot avoid the path of mobile fishing gear nor can they quickly immigrate into recently disturbed areas, they may be more adversely affected by bottom fishing than motile species. All six taxa of colonial epifauna examined in this study were affected by bottom fishing, although the magnitude and direction of this effect often depended on depth and varied between years. Because the effect of disturbance on noncolonial species composition was fairly subtle, our study indicates a greater sensitivity of colonial epifauna to disturbance by mobile fishing gear. Similarly, studies conducted in the Gulf of Alaska and Irish Sea show that most motile organisms are less severely affected by chronic and experimental trawling than are anthozoans, sponges, bryozoans, hydroids, tubicolous polychaetes, and barnacles (Freese et al., 1999; Bradshaw et al., 2002). Nevertheless, sessile colonial epifauna exhibit variable morphological forms and possess diverse life history characteristics that can result in different responses to bottom fishing. Colonial organisms whose physical structure can be described as branching, sheet-forming, or mound-forming generally grow slowly but are better competitors for space on the seafloor than encrusting and stoloniferous epifauna (Hughes, 1989). Because of their slow growth patterns, organisms with branching, sheet-forming, and mound-forming structures are typically adapted to stable environments where they are less likely to be detached from their substrate by physical forces associated with natural disturbances. Anthropogenic disturbance causes formerly stable environments to become unstable, thus leaving colonial epifauna with a branching structure maladapted to their new environment.

On Georges Bank, sponges appear to be the colonial epifaunal taxa most negatively affected by bottom fish-

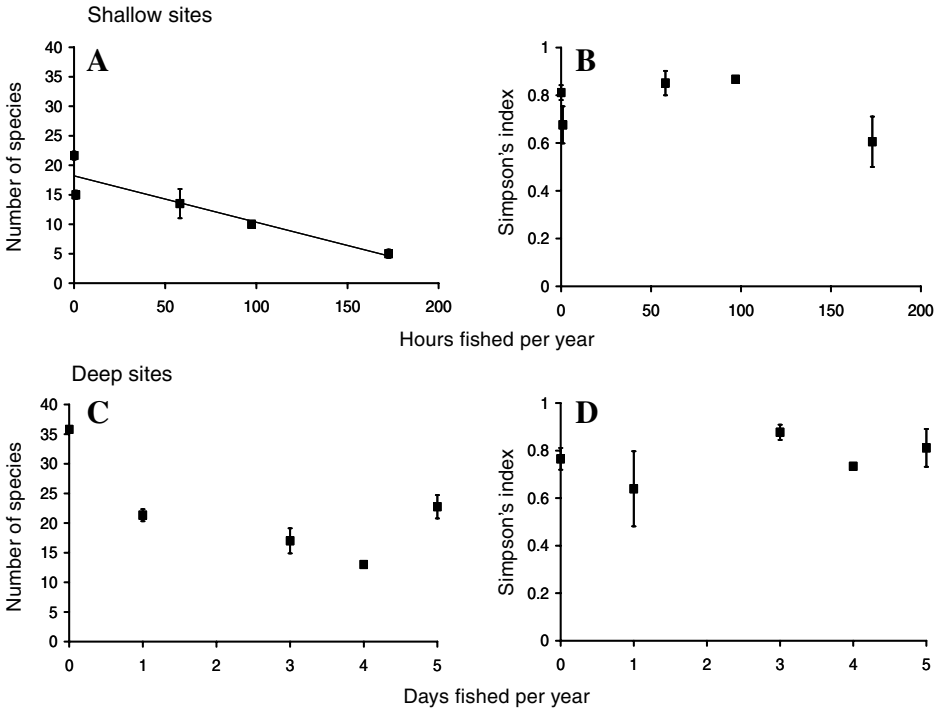

Figure 7

Species richness (number of species) and Simpson's index of diversity ($1-\lambda'$) for noncolonial epifauna at shallow and deep sites. Black squares indicate mean species richness or diversity for a given level of disturbance; standard error bars are shown. Different units of measurement are plotted on the x axis for shallow and deep sites, reflecting the fact that fishing effort was estimated by different methods in U.S. and Canadian waters. Results of linear regression for species richness versus disturbance at shallow sites (**A**): F=17.69; df=1,3; P=0.02. All other linear and polynomial regressions were not significant.

ing at shallow depths. Most sponges at our study sites had branched or mounding-forming structures, which contributed to their sensitivity to mobile fishing gear. Other characteristics that make sponges vulnerable to mobile fishing gear are aperiodic recruitment and a perennial life cycle that allows colonies to persist over several years (Hughes, 1989). In the southern portion of CA-II that is dominated by sandy substrate, sponges are one of the microhabitats whose abundance differs significantly between fished and unfished areas (Lindholm et al., 2004) as was also recorded in our study. Several studies from other regions have documented that sponges are among the most sensitive phyla to bottom fishing (Van Dolah et al., 1987; Freese et al., 1999).

Arborescent epifauna react inconsistently to bottom fishing, reflecting the fact that these organisms possess life history traits that both facilitate and hinder their recovery from physical disturbances. Past research indicates that the effect of bottom fishing on arborescent epifauna varies between regions and species (Auster et al., 1996; Bradshaw et al., 2002). Like sponges, hydroids and bushy bryozoans have an emergent growth form that makes them vulnerable to being knocked over by trawls and dredges. Yet these types of arborescent epifauna do not generally grow as tall as sponges, thus providing them with a degree of resistance to disturbance. When mobile fishing gear do succeed in removing arborescent epifauna from their substrate, recolonization may occur quickly because these organisms are known for rapid growth and typically have short life spans, ranging in length from ten days to one year (Boero, 1983; Hughes, 1989). Other species of hydroids and erect bryozoans are perennial but exhibit seasonal regression. Despite the swift turnover of hydroid and bushy bryozoan colonies, the spatial extent of recovery may be restricted because many species have limited larval dispersal (i.e., <50 m) or tend to settle close to parent colonies (Hughes, 1989; Bradshaw et al., 2002). The dispersal potential of other species, such as hydroids in the family Sertularidae, is even more constrained, because they do not have a pelagic medusa stage (Boero, 1983). Our study indicates that depth may be an additional factor affecting how hydroids react to disturbance caused by bottom fishing, because deeper

sites display a more pronounced, negative response to increased fishing effort. Depth has also been shown to influence the abundance and biomass of other benthic taxa (i.e., amphipods and the brittle star *Ophiura robusta*) in the southern portion of CA-II (Link et al., 2005).

Species in the class Polychaeta play diverse ecological roles (e.g., carnivores, deposit feeders, suspension feeders), use different habitats (e.g., infauna, epifauna), and display different mobility patterns (e.g., errant and tubicolous lifestyles), all of which influences how they respond to bottom fishing. Many polychaetes exhibit a high intrinsic rate of growth allowing them to quickly colonize barren substrate and recover rapidly from disturbances. This high rate of growth explains why the free-living polychaetes in the North Sea remain unaffected by bottom fishing at trawling frequencies as high as six times per year (Jennings et al., 2002). In contrast, tubicolous polychaetes are often heavily affected by bottom fishing because of both their production of calcareous and sediment-encrusted tubes that can be crushed by fishing gear and their need for stable substrate on which to build tubes. This appears to be the case at the deep depth stratum on Georges Bank, where *F. implexa* was less abundant at disturbed sites. Similarly, the inception of bottom fishing was implicated in the declining abundance of four species of tubicolous serpulid polychaetes in the Irish Sea (Bradshaw et al., 2002) and the sabellid polychaete *Myxicola infundibulum* on Fippennies Ledge in the Gulf of Maine (Langton and Robinson, 1990). A few species do prove that there are exceptions to the rule that most tubicolous polychaetes are negatively affected by mobile fishing gear. Such examples include the tubeheads formed by the serpulid polychaete *Pomatoceros* spp. that were not significantly affected by biannual beam trawling in the eastern Irish Sea (Kaiser et al., 1999) and the *Spirorbis* spp. tubes whose abundance was elevated at fished sites on Georges Bank (Collie et al., 2000a; Asch, 2006). The small size of *Spirorbis* spp. tubes makes them extremely difficult to remove from their substrate and may provide this species with a competitive advantage over other species more sensitive to bottom fishing (Collie et al., 2000a). Similarly, the resistance of the *Pomatoceros* spp. to bottom fishing may be related to the fact their tubes are small enough to pass through the 80-mm mesh used by Kaiser et al. (1999) during experimental trawling.

Because of their low, encrusting growth form, encrusting bryozoans have proven to be resistant to physical disturbances from natural sources (Sebens et al., 1988) and appear to be less sensitive to anthropogenic disturbances, as well. The cover of encrusting bryozoans is generally greatest in disturbed areas of Georges Bank. This effect is significant at shallow sites and marginally significant at deep sites. Encrusting bryozoans whose substrate may be overturned by a trawl or dredge are capable of recovering quickly because of their fast growth rates and rapid ability to repair structural damage (Bradshaw et al., 2002). This set of life history characteristics may provide encrusting bryozoans with a competitive advantage in highly disturbed environments.

The abundance of cultch in disturbed areas of northeast Georges Bank can be explained by the fact that most cultch at our study sites consists of *P. magellanicus* shells that were either discarded by scallop fishing crews or killed by mobile fishing gear, but not landed. In areas where cultch accumulation is linked to high levels of predation on bivalves or to current patterns concentrating shell fragments, bottom fishing may have a negative effect on this resource. Such is the case in studies of the effect of mobile fishing gear on patches of cultch on Stellwagen Bank and in a more southern area of Georges Bank (Auster et al., 1996; Lindholm et al., 2004).

Noncolonial organisms

As part of a related research project, naturalist dredge samples of noncolonial megafauna have been collected since 1994 at the same study sites where benthic photographs in the present study were taken (Collie et al., 2005), allowing for comparisons to be made between these two sampling techniques. The results of the current study are similar to those obtained by Collie et al. (2005) in that they both indicated that *P. magellanicus*, *S. droebachiensis*, and *Pagurus* spp. increased in abundance inside CA-II. The increased density of *P. magellanicus* in the closed area is likely related to both direct and indirect effects of bottom fishing. As a commercially targeted species, *P. magellanicus* is removed from areas where scallop dredging occurs. The adverse effect of dredging and otter trawling on sponge cover may also serve to reduce *P. magellanicus* abundance, because some scallop species maintain a mutualistic relationship with sponges that helps them escape predation. In a laboratory experiment where this mutualistic relationship was examined, scallops with sponges encrusted on their shells had to exert 20–30 times less effort to overcome the adherence of the tubefeet of a seastar predator than did scallops whose shells were cleaned of sponges (Bloom, 1975). A third factor influencing the distribution of *P. magellanicus* may be that the seastars (*Asterias* spp.), which are key scallop predators, obtained slightly higher abundance outside the closed area. *Asterias* spp. may be particularly abundant at disturbed sites because members of this genus are also scavengers that have been reported to feed upon organisms damaged by trawls (Ramsay et al., 1998).

The sea urchin *S. droebachiensis* may have also benefited from the elevated cover of colonial epifauna in CA-II because this species is known to eat sponges, hydroids, bryozoans, tunicates, and amphipod and polychaete tube complexes at locations where macroalgae and kelp (the preferred diet of sea urchins) are absent (Briscoe and Sebens, 1988). The elevated number of *S. droebachiensis* in photos taken in CA-II corroborates the findings of Hermsen et al. (2003), who identified

this species as one of the taxa most responsible for increased megafaunal production in CA-II. Along shallow, disturbed transects outside CA-II, bivalves, such as *Astarte* spp. and *C. borealis*, were more abundant. The hard shells of these two species likely confer some resistance to disturbance by bottom fishing. Similarly, the unidentified infaunal bivalve species (most likely the razor clam *Ensis directus*) whose siphons were frequently seen along transects open to fishing may be less vulnerable to this form of disturbance because it resides deep in the substrate below depths affected by otter trawls.

Many of the species most commonly observed at deep, undisturbed sites belong to the classes Anthozoa, Malacostraca, and Ophiuroidea, which are the classes that a meta-analysis has identified as the taxonomic groups most adversely affected by mobile fishing gear (Collie et al., 2000b). At deep sites, we and Collie et al. (2005) found that bottom fishing results in reduced abundance of multiple species of shrimp, brittle stars (e.g., *Ophiopholis aculeata*), tubicolous polychaetes (e.g., *Potamilla neglecta*), and the toad crab *Hyas coarctatus*. Another species that helps define the dissimilarity between disturbed and undisturbed areas at deep sites is the horse mussel *Modiolus modiolus*, which is a long-lived, thin-shelled bivalve that is known to be sensitive to bottom fishing (Bradshaw et al., 2002; Collie et al., 2005). *M. modiolus* may play an important role in the ecology of Georges Bank because anecdotal information from fishermen indicates that the fishes *G. morhua* and *M. aeglefinus* congregate around their beds (Leach, 1998). As was the case at shallow sites, hard-shelled mollusks (i.e., *Astarte* spp. and *B. undatum*) and scavengers, such as *Pagurus* spp., are among the species characteristic of deep, disturbed sites. Both *Pagurus* spp. and *B. undatum* readily consume organisms injured by bottom fishing (Ramsay et al., 1998).

The exact form of the relationship between bottom-fishing disturbance and the diversity of noncolonial species is highly dependent upon the particular diversity index under consideration. At both depth strata, increased bottom fishing results in a concurrent decrease in noncolonial species richness. However, Simpson's index tends to exhibit its highest value at intermediate levels of bottom fishing. This latter pattern is consistent with the intermediate disturbance hypothesis, which proposes that a moderate amount of disturbance can augment diversity by creating more heterogeneous habitats and reducing the likelihood that a single climax species will dominate an area (Connell, 1978). Because bottom fishing is not boosting the absolute number of species present, as indicated by species richness trends, then the high value of Simpson's index at intermediate disturbance levels must be due to a commensurate increase in species evenness resulting from the reduced dominance of a few abundant species. A similar pattern was identified in a study of the effect of scallop dredging on the benthic community of the Irish Sea (Bradshaw et al., 2002).

Recovery period and recovery rates after disturbance

Time periods associated with the recovery of benthic organisms after disturbance caused by bottom fishing are quite variable. Because of adaptations to high levels of natural disturbance, communities living in unconsolidated sand have been predicted to recover from bottom fishing in as little as 100 days (Collie et al., 2000b). However, recovery in structurally complex habitats and among particularly vulnerable species (i.e., species that are long lived, poorly adapted to withstand frequent natural disturbances, or highly susceptible to capture or removal by mobile fishing gear) may require longer time periods. For example, it is estimated to take at least 15 years for several species of sponges off the northwest shelf of Australia to grow to a height of 25 cm (Sainsbury et al., 1997). Similarly, the fig sponge (*Suberites ficus*) became more abundant in areas protected from bottom fishing within a period of 4.5 years (Lindholm et al., 2004). Deep sea corals, such as the samples of *Desmophyllum cristagalli* caught off Western Ireland and calculated to be 4000–5000 years old (Hall-Spencer et al., 2002), are the type of marine fauna requiring the longest recovery time.

Some estimated recovery rates from bottom fishing reported in the scientific literature may be overly optimistic because of biases in the sampling design of many studies. Frequently, these studies involve trawling a small area (<50 m width) located inside a largely undisturbed site. In the ecological literature, small-scale disturbances surrounded by large, unaffected areas are often referred to as type-1 disturbances. Because of the small spatial scale of a type-1 disturbance and the low temporal frequency of such disturbances, recolonization may occur through immigration from adjacent undisturbed areas or vegetative growth (Auster and Langton, 1999; Kaiser et al., 2002). Recovery through localized immigration and vegetative growth requires less time than would be necessary if recovery were to occur through larval settlement and *in situ* reproduction of remaining organisms within the disturbed area. In the case of type-2 disturbances where the ecological community is perturbed across large areas interspersed amongst small unaffected patches, recovery usually proceeds by the slower process of larval settlement, a process where most larvae originate from either distant areas or from the small unaffected patches. This latter scenario more realistically describes the recovery process after disturbance from large-scale bottom-fishing operations on Georges Bank.

Our study is noteworthy because little research has been published on the long-term processes governing recovery from disturbance among colonial epifauna on the continental shelf of the northwest Atlantic. After the establishment of CA-II, several colonial and noncolonial taxa underwent successive increases and declines in abundance at site 17, thus, providing potential evidence of ecological succession. During 1997, bushy bryozoans briefly peaked in abundance at the shallow undisturbed site. Bushy bryozoans were able to react

quickly after establishment of a closed-area because the life span of individual colonies typically does not exceed one year (Hughes, 1989). The subsequent decline in the percent cover of this taxon may be linked to either increased interspecific competition or greater predation pressure at site 17. Organisms with life spans of five years or greater (i.e., sponges, *P. magellanicus*, *Pagurus* spp., *Asterias* spp., and *S. droebachiensis*) either increased throughout the duration of this study at site 17 or maintained a heightened level of abundance for several years before eventually experiencing a decline in numbers. Because differences between areas inside and outside CA-II, in terms of both sponge and bushy bryozoan cover, became apparent in 1997 (as shown by the error bars in Fig. 2), this finding may indicate that there is an approximately two-year lag in the initial response of colonial epifauna residing in gravel habitat to the fishing closure. This lag implies that even infrequent trawling and dredging can lead to prolonged changes in colonial epifauna composition.

Although no other research on Georges Bank has examined long-term patterns of recovery from disturbance among epifauna, our results are similar to those of two studies conducted at Cashes Ledge (located 130 km east of Gloucester, MA) on the colonization of artificial and disturbed natural substrate by colonial organisms over a period of less than two years (Sebens et al., 1988; Witman, 1998). In an area with rocky substrate at 30 m depth, the seafloor was first colonized by erect bryozoans (*Crisia eburnea* and *Idmidronea atlantica*) and the polychaete *Spirorbis* spp., while later colonizers included the ascidians *Aplidium pallidum* and *Ascidia callosa* (Witman, 1998). At the end of the 15-month duration of the Witman study, bryozoans covered approximately 35% of the disturbed patches of the seafloor, whereas no other species had yet colonized more than 6% of this area. It was predicted that it would require seven years or more for this epifaunal community to return to its natural state where sponges, sea anemones, and ascidians were the dominant fauna (Witman, 1998). In a similar study where four depth strata were examined, bushy and encrusting bryozoans were again the first organisms to settle on barren substrate; smaller patches of *F. implexa* and *Spirorbis* spp. were also early colonizers; colonization by *Aplidium* sp. and crustose coralline algae occurred later (Sebens et al., 1988). At the 50-m site on Cashes Ledge, which is the most comparable to our study area in CA-II, *I. atlantica* covered over 50% of the substrate within one year, and the cover of bryozoans approached 100% by the second year. Although bryozoan cover at our study sites never reached the extremely high percentages observed by Sebens et al. (1988), our results mirror theirs and those of Witman (1998) in that bryozoans were the predominant space holder in areas subjected to recent disturbance, and all other species of colonial epifauna never exceeded a mean cover of 5%. The recovery of the benthic community at Cashes Ledge may differ somewhat from Georges Bank, because 1) certain epifaunal species may prefer the rocky substrate at Cashes Ledge over the gravel substrate of Georges Bank (or vice versa); 2) different currents in these areas may affect the settlement rate of invertebrate larvae, and 3) the spatial scale of disturbance at Cashes Ledge (i.e., 25 cm^2) was much smaller than at Georges Bank.

Some evidence indicates that ecological succession is governing the recovery of epifauna in CA-II, but several generations of data on key benthic species would be needed to conclusively rule out other possible mechanisms controlling recovery. There are two models that describe how marine ecosystems may recover from past bottom-fishing disturbance (Auster and Langton, 1999): 1) Ecological succession may occur where the seafloor is colonized by benthic species in a predictable pattern, namely opportunistic species arrive first only to be later out-competed by climax species; 2) The lottery hypothesis, first proposed by Sale (1978), indicates that the benthic community will be dominated by species whose larvae are the first to colonize the seafloor immediately after a disturbance. This scenario implies that recovery will be greatly influenced by unpredictable, stochastic events. Because many species in CA-II have life spans of ten years or more (e.g., the Northern seastar *Asterias vulgaris*, *B. undatum*, *P. magellanicus*, *S. droebachiensis*; Hermsen et al., 2003), it is not yet possible to use time-series data to quantitatively differentiate between these two hypotheses. However, there are indications that recovery from physical disturbances is not characterized by as much stochasticity as implied by the lottery hypothesis. This lack of stochasticity is implied by the fact that bryozoans are early colonizers at both CA-II and Cashes Ledges. Another tenet of the lottery hypothesis is that early colonizers are able to consistently out-compete late colonizers by denying them access to vital habitats (Munday, 2004). This corollary of the lottery hypothesis is not met on Georges Bank, because encrusting bryozoans can be overgrown by the colonial tunicate *Didemnum* sp. and sponges (Valentine et al., 2007).

After examining six years of data collected since the establishment of CA-II, we do not know whether recovery of colonial epifauna is complete at site 17. Although large increases in the cover of colonial epifauna were not seen during 1999 and 2000, the abundance of several noncolonial species continued to grow. This continued growth of noncolonial species could in turn affect colonial epifauna composition as recovering noncolonial organisms may increasingly compete with colonial taxa for resources or prey more heavily on them. The recovery of some colonial species may still be constrained by the fact that their larvae only disperse short distances ($\leq$50 m) from parent colonies (Hughes, 1989). The final species composition of site 17 is likely to differ from that of undisturbed site 20, because the faster current speeds at the shallow site 17 can transport sand across the gravel pavement, inhibiting the growth of arborescent epifauna and *F. implexa*. In fact, the scouring caused by sand transported to site 17 during a winter storm that coincided with our

November 2000 research cruise may be responsible for the low densities of certain species (e.g., sponges) observed during that year. Overall, an extended period of monitoring is needed to determine which epifaunal species will be most abundant in CA-II once recovery is complete.

In conclusion, the cover of hydroids, bushy bryozoans, sponges, and *F. implexa* was generally higher at sites undisturbed by mobile fishing gear, although the magnitude and significance of this effect depended on water depth and differed between years. Among colonial epifauna taxa, only encrusting bryozoa are positively affected by bottom-fishing disturbance. The species of colonial epifauna and noncolonial megafauna that are more abundant at undisturbed sites generally possess characteristics that make them vulnerable to the effects of mobile fishing gear. These characteristics include emergent growth forms, soft body parts, low motility, use of structurally complex microhabitats, long life spans, slow growth, and larval dispersion over short distances. Following the prohibition on bottom fishing in CA-II, both colonial (i.e., sponges and bushy bryozoans) and noncolonial (i.e., *P. magellanicus*, *S. droebachiensis*, *Pagurus* spp., *Asterias* spp.) organisms increased in abundance. Although research investigating the long-term recovery of epifauna from bottom-fishing disturbance is ongoing in the other areas of the Gulf of Maine (e.g., Stellwagen Bank and western Gulf of Maine closed area), this study is one of the first in the region to track the recovery of the colonial epifaunal community from disturbance for a period extending beyond two years. The fact that it took most taxa two years or more to initially respond to the cessation of bottom fishing indicates that even infrequent trawling can alter benthic communities for years to come. When monitoring of CA-II was first initiated, it was predicted that it would take 5–10 years for the megafaunal community to recover (Collie et al., 1997). After six years of studying transects inside CA-II, we conclude that recovery does not yet appear complete and that the higher end of this projection may prove more accurate.

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