Abstract—The recovery of benthic communities inside the western Gulf of Maine fishing closure area was evaluated by comparing invertebrate assemblages at sites inside and outside of the closure four to six years after the closure was established. The major restriction imposed by the closure was a year-round prohibition of bottom gillnets and otter trawls. A total of 163 seafloor sites (~half inside and half outside the closure) within a 515-km^2 study area were sampled with some combination of Shipek grab, Wildco box corer, or underwater video. Bottom types ranged from mud (silt and clay) to boulders, and the effects of the closure on univariate measures (total density, biomass, taxonomic richness) of benthos varied widely among sediment types. For sites with predominantly mud sediments, there were mixed effects on inside and outside infauna and no effect on epifauna. For sites with mainly sand sediments, there were higher density, biomass, and taxonomic richness for infauna inside the closure, but no significant effects on epifauna. For sites dominated by gravel (which included boulders in some areas), there were no effects on infauna but strong effects on epifaunal density and taxonomic richness. For fishing gear, the data indicated that infauna recovered in sand from the impacts of otter trawls operated inside the closure but that they did not recover in mud, and that epifauna recovered on gravel bottoms from the impact of gillnets used inside the closure. The magnitudes of impact and recovery, however, cannot be inferred directly from our data because of a confounding factor of different fishing intensities outside the closure for a direct comparison of preclosure and postclosure data. The overall negative impact of trawls is likely underestimated by our data, whereas the negative impact of gillnets is likely overestimated.

Effects of a large fishing closure on benthic communities in the western Gulf of Maine: recovery from the effects of gillnets and otter trawls

Raymond E. Grizzle (contact author)[1]

Larry G. Ward[2]

Larry A. Mayer[3]

Mashkoor A. Malik[3]

Andrew B. Cooper[4]

Holly A. Abeels[5]

Jennifer K. Greene[6]

Melissa A. Brodeur[7]

Andrew A. Rosenberg[8]

Email address for contact author: ray.grizzle@unh.edu

[1] Department of Biological Sciences
and Jackson Estuarine Laboratory
University of New Hampshire
Durham, New Hampshire 03824

[2] Department of Earth Sciences
Center for Coastal and Ocean Mapping
and Jackson Estuarine Laboratory
University of New Hampshire
Durham, New Hampshire 03824

[3] Center for Coastal and Ocean Mapping
University of New Hampshire
Durham, New Hampshire 03824

[4] Resource and Environmental Management
Simon Fraser University
Vancouver, British Columbia V6B 5K3

[5] Coastal Watershed Institute
Florida Gulf Coast University
Fort Myers, Florida 33965

[6] The Nature Conservancy
Eastern Resource Office
11 Avenue De Lafayette, 5th Floor
Boston, Massachusetts 02111

[7] Consortium for Ocean Leadership
1201 New York Avenue, NW, Suites 400–420
Washington, D.C. 20005

[8] Department of Natural Resources and
Ocean Process Analysis Laboratory
University of New Hampshire
Durham, New Hampshire 03824

The Western Gulf of Maine (WGOM) closure area was implemented by the National Marine Fisheries Service on 1 May 1998 as part of an overall effort to rebuild overfished New England groundfish stocks such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), other gadids, and flatfish. The WGOM closure is one of the largest year-round closures in the United States, designed to protect habitat and help in the recovery of overfished species. The major restriction imposed by the closure was year-round prohibition of commercial fishing gear that is capable of capturing groundfish, principally otter trawls and gillnets. A variety of other fishing gears (e.g., lobster pots, recreational hook-and-line gear), however, have been deployed in the area since its establishment. The WGOM closed area fits the definition of a marine protected area (MPA) because it provides some level of protection of habitat and resources (NRC, 2002). In many areas, MPAs have been useful management tools but the causal mechanisms for their effectiveness in protecting habitat and meeting other management objectives differ widely, largely because MPAs vary widely in design and other characteristics (Fogarty and Murawski, 2005; Shipley, 2004). Hence, there is a need to assess individual MPAs in the context of environmental and other characteristics, as well as in regard to the particular combination of restrictions placed on each area. For assessing the data presented here, the closure was considered as an area that was potentially recovering from the impacts of gillnets and otter trawls.

There have been no published studies on the effects of the WGOM closure on seafloor habitats, and none designed specifically to address the effects of the closure on groundfish

stocks. Recent analyses of commercial trawl data (Murawski et al., 2004, 2005) have shown no appreciable effect of the closure on stock rebuilding in the region, although there has been substantial recovery of some groundfish stocks since the closure was implemented. From studies of MPAs in other areas, for example, New England (e.g., Collie et al., 2005), it seems reasonable to expect that a closure of the magnitude of the WGOM area would have a measurable effect on habitat recovery and fish stock rebounds. Its role in these respects, however, remains to be demonstrated.

In this article, we present data from grab and box core samples of sediments and infauna, underwater video surveys of benthic fauna, and general seafloor conditions four to six years after the closure of WGOM, all of which indicate that the closure has resulted in substantial recovery of some bottom habitat types. We offer hypothetical causes for the recovery in the context of gear removal, and we discuss the implications for ecosystem-level management of the closure.

Materials and methods

Study area

The study was restricted to a 515-km^2 area that comprised a section of the central western WGOM closed area and a section outside the closed area (Fig. 1). The overall closure area, which covers much of Jeffreys Ledge, is about 30 km wide (east–west) and 110 km long (north–south) and is located off the southern Maine, New Hampshire, and northern Massachusetts coasts. The location of the study area was chosen mainly because it has similar environmental characteristics both inside the closure and outside the closure.

A 5-m pixel resolution bathymetric map covering about 85% of the area and produced from multibeam sonar data collected between December 2002 and January 2003 (Malik and Mayer, 2007) was used as a general base map for the present study. It functioned as a guide for the final selection of sampling-site locations and for the interpretation of data related to potential gear impacts on bottom habitats.

An important feature of the study area for our research was the level of fishing activity, historically as well as after implementation of the closure. Data on date, location, and gear type (acquired by the National Marine Fisheries Service from federally permitted commercial fishing vessels) were acquired and plotted. For map production, the raw data (which were submit-
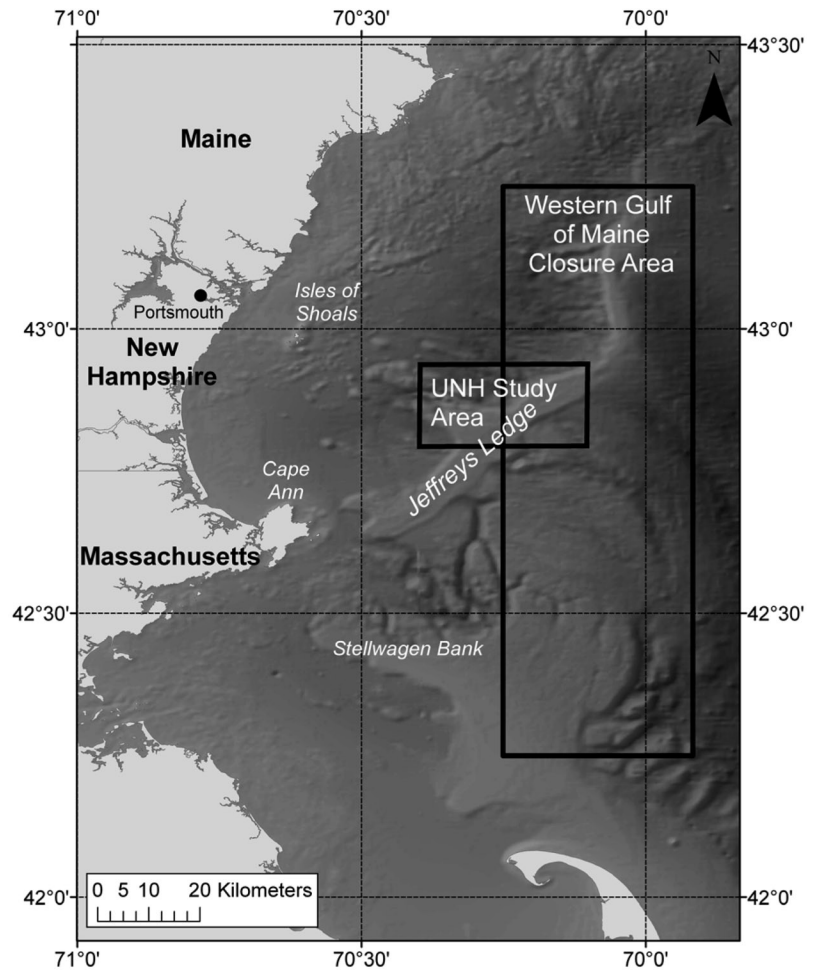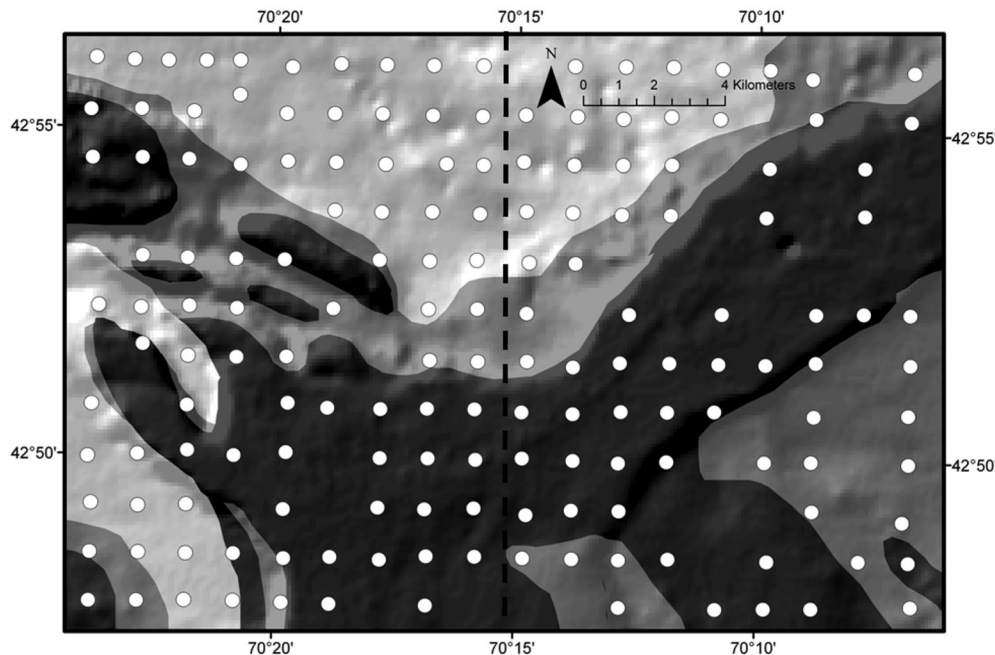

Figure 1

Location of the 515 km^2 University of New Hampshire study area (UNH Study Area) in relation to the western Gulf of Maine closure area. The map has a resolution of 90-m to one pixel and indicates bathymetric contours with light gray (shallow water) and dark gray (deep water).

ted at 1-min intervals of longitude and latitude) were plotted. All locations with fewer than five trip records were deleted from our analysis to eliminate potentially spurious data arising from reporting mistakes or for other reasons. Vessel trip report data from 4.5-yr preclosure (1994–98) and postclosure (1998–2002) were obtained for all reported gear types. Bottom gillnets and otter trawls were represented in >95% of the data records, and therefore other gear types were not analyzed.

Study design

The study was a control-impact assessment (Osenberg et al., 1994) for which there was systematic sampling of the seafloor at approximately equal numbers of sites distributed inside and outside the closed area (Fig. 2). Sampling sites were located on a grid with sampling points at approximately 1.3-km intervals (0.75 min of

Figure 2

Locations of 163 seafloor sampling sites (white circles) within the 515 km^2 University of New Hampshire study area that were sampled by some combination of Shipek grab, Wildco box corer, and towed video camera. Distribution of three major bottom sediment types: light gray=mud; medium gray=sand; dark gray=gravel (which includes all hard bottom types ranging from gravel to boulders).Vertical dashed line is the western boundary of the WGOM closure.

latitude and 1 min of longitude), yielding a total of 216 target sampling sites (not all were sampled). A combination of techniques was used at each site, including grab and box samples for infauna and sediments, and towed video for epifauna and general seafloor conditions, as described below.

Field and laboratory methods

All seafloor sampling occurred from June 2002 through September 2005. However, most sampling occurred during 2002 (~65% of the grab and box core sampling) and 2004 (~90% of the video sampling, and ~30% of the grab and box core sampling). Hence, 90–95% of all seafloor sampling occurred during 2002 and 2004, and there was no temporal bias in sampling inside compared to outside of the closure. In other words, approximately equal numbers of sites inside and outside of the closure were sampled during each year of the study. All sampling gear was deployed from chartered commercial fishing vessels.

Bottom sediments were sampled with either a Shipek grab (Wildlife Supply Co., Buffalo, NY) with a design sampling area of 0.04 m^2, or a Wildco box corer (Wildlife Supply Co.) with a design sampling area of 0.0625 m^2. The depth of sediment penetration was measured to the nearest 0.5 cm for each sample, and a subsample of sediment was taken for grain size and organic content

analyses. Grab samples were rejected if they did not penetrate at least 2 cm into the sediment, and box core samples with less than 5 cm penetration were rejected. The contents of the box corer were subsampled with a 10.4-cm inside diameter (0.0085 m^2 surface area) acrylic core tube. The entire grab contents and box core subsamples were washed through a 0.5-mm mesh sieve, fixed in 3% unbuffered formalin, and preserved in 70% isopropanol. In the laboratory, all invertebrates were removed under 3× magnification, sorted by major taxa, identified to family level in most cases, counted, and weighed (wet weight of preserved specimens).

Bottom sediments were analyzed for grain-size composition (texture) by using standard sieve and pipette analytical techniques (Folk, 1980). Organic content was determined by loss-on-ignition (% LOI) after 4 hours at 450°C (Byers et al., 1978).

Epifaunal assemblages were determined from bottom videographs taken with a custom-made camera system composed of a video camera mounted on a frame with synchronized strobe lights and an integrated positioning system. At each station the camera was suspended near the bottom (within 50 cm) and 6 to 10 minutes of downward looking video footage was recorded along a drift transect at least 50 m long. For quantitative analyses, the videotape from each transect was subsampled to isolate still images of sufficient quality to characterize seafloor features so that a series of nonoverlapping

images (n=13 to 94 per transect) along the length of each transect was produced. Each still image was analyzed for bottom characteristics (predominant sediment type), visible burrow characteristics (size, density), and epifauna (taxa, density). A trio of laser beams fixed at known distances apart allowed the total area of each image to be determined.

Data analysis

The major focus of this study was to determine the effects of the WGOM closure by comparing samples taken inside the closure with samples taken outside the closure. Thus, potential confounding factors (e.g., sediment type, water depth, and sediment organic content) that might have affected comparisons between samples taken inside the closure with those taken outside (hereafter referred to as "in vs. out" comparisons) were assessed. Also, for the infauna analyses, data from the two sampling devices (grab and box corer) were analyzed separately to avoid complications with different sample sizes and selectivity of the gear.

Infauna (sampled by grab and box corer)

For both sampling devices, the role of sediment grain size (mud, sand, or gravel), water depth, sediment organic content (% LOI), and relative penetration of the sampling device were assessed, along with the factor of primary interest: whether the sample was taken from inside or outside the closure. Separate analyses were performed to examine each of the three dependent univariate infauna community variables: 1) density, 2) biomass, and 3) taxonomic richness.

All analyses were performed by using generalized linear models (GLM; McCullagh and Nelder, 1989) in S-PLUS 7.0 (Insightful Corporation, Seattle, WA). For normally distributed data or data that could be transformed to approximate normality, significance for main effects and interactions were examined by using a combination of forward and backward model selection based on the C_p statistic and sequential F-tests in an analysis of deviance with alpha levels of 0.05 and 0.10, respectively. For non-normally distributed data, significance for main effects and interactions were examined by using sequential chi-square tests in an analysis of deviance with alpha levels of 0.05 and 0.10, respectively. For each model, the inclusion of either Gaussian or exponential spatial correlation was examined with the extended generalized linear modeling capabilities in the S-PLUS correlated data library.

Epifauna (documented along video transects)

A generalized linear mixed-effects (GLME) model with Poisson error and log link was used to analyze the video count data of epifauna taxa and density (Breslow and Clayton, 1993). The mixed-effects portion of the model was necessary to account for multiple images within each transect and the images that may have been cor-
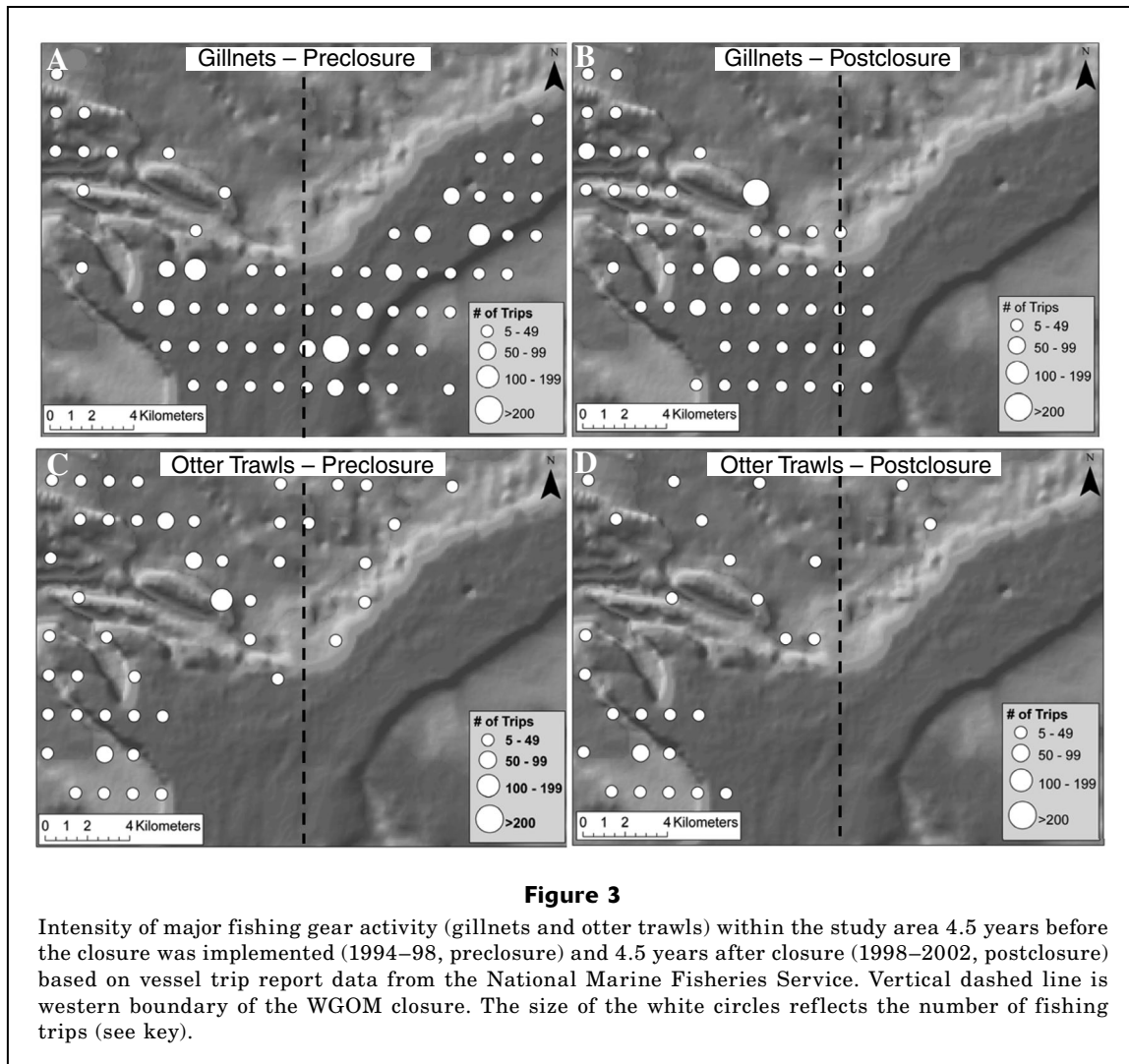
related. The use of GLME allowed individual transects to differ from one another for reasons unaccounted for by the data and directly accounted for the repeated-measures nature of the data. S-PLUS 7.0 and the GLME extension from the S+ Correlated Data library (vers. 1.0, release 1) were used for all analyses. The significance of each fixed-effect, both main effects and interactions, was tested in an ANOVA framework by using marginal F-tests (Pinheiro and Bates, 2000) based on the (restricted) penalized quasi-likelihood with an alpha-level of 0.05 for main effects and 0.10 for interaction effects (Sokal and Rohlf, 1981). In addition to the main effect of inside or outside of the closure, water depth and sediment type were assessed as potential confounding factors. Offsets were included in each model to account for the fact that the total surface area observed varied from image to image because of the variations in the height of the camera. Separate analyses were performed on the two dependent variables: total density and taxonomic richness.

Results

Preclosure and postclosure plots of the report data from fishing vessel trips showed several relevant patterns (Fig. 3). First, both preclosure and postclosure trip data verified the general expected pattern that trawls are mainly used on soft sediments in deeper water (greater than 60 m), and gillnets are used mainly on rocky bottoms in shallower areas (less than 60 m). These patterns indicate that a major effect of the closure was the removal of trawl impacts from the deeper, mainly finer sediments, and the removal of gillnet impacts from rocky areas along the top and southeast flank of Jeffreys Ledge.

The report data indicated that total gillnet fishing intensity in the overall 515-km^2 study area was similar before closure (2056 trips) and after closure (1812 trips); however, gillnet intensity nearly doubled in the area outside of the closure after closure (761 trips before closure compared to 1494 trips after closure). This pattern indicates that any data interpreted as showing recovery of benthic communities in rocky areas where gillnets were the major gear type needs to be tempered because of increased postclosure gillnet fishing intensity in the "control" area outside the closure.

In contrast, trawling intensity in the overall 515-km^2 study area decreased from 1103 trips before closure to 581 after closure (Fig. 3). There was a 39% decrease for trawl intensity outside the closure, from 894 trips before closure to 544 trips after closure. Moreover, the only portion of the study area inside the closure that was likely strongly affected by trawls before the closure was the deeper area north of Jeffreys Ledge. This information indicates that any data interpreted as showing recovery of benthic communities in soft sediment areas needs to be tempered because of the decreased trawling intensity after closure in the control area outside the closure.
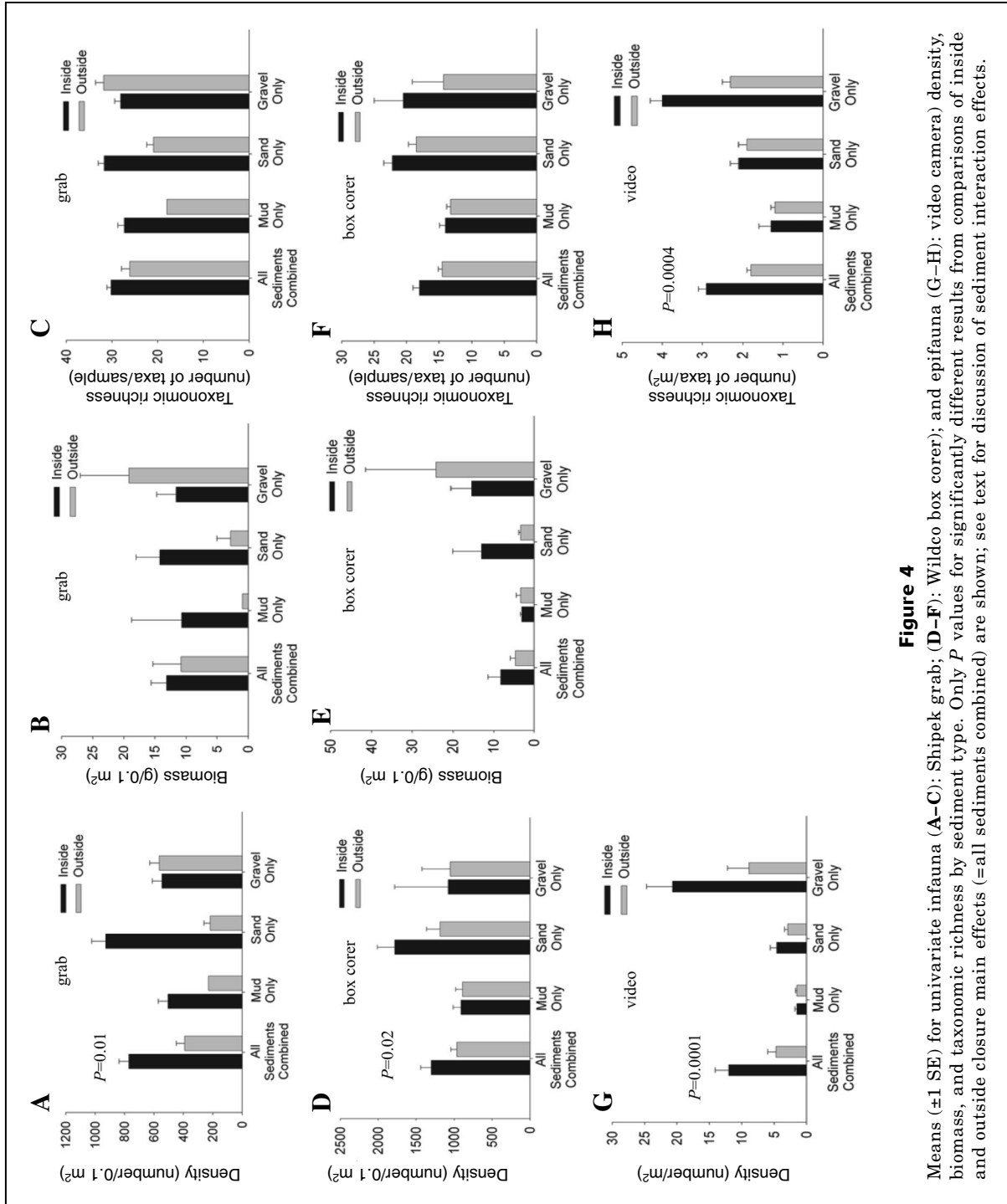
Figure 3

Intensity of major fishing gear activity (gillnets and otter trawls) within the study area 4.5 years before the closure was implemented (1994–98, preclosure) and 4.5 years after closure (1998–2002, postclosure) based on vessel trip report data from the National Marine Fisheries Service. Vertical dashed line is western boundary of the WGOM closure. The size of the white circles reflects the number of fishing trips (see key).

A total of 163 sites in the 515-km² study area were sampled with some combination of grab, box corer, and videotape recording (Fig. 2). Bottom types ranged from organic-rich muds in deeper water (greater than 100 m) to hard bottom (gravel and boulders) in water less than 80 m deep. Hard bottom areas typically were composed mainly of gravel and in many cases sufficient amounts of sand to allow grab samples to be successfully obtained for infauna analysis. Some hard bottom sites also had boulders present, as determined from the video imagery, and these sites were classified as gravel (Fig. 2). No plants were collected in the grab and core samples or observed in the video imagery. Infauna dominated the soft sediments in deeper waters (and were mainly sampled by box corer and video recorder), and epifauna dominated the shallower hard bottom areas (mainly sampled by grab and video recorder).

There were strong differences across the three sediment types for both infauna and epifauna. For the infauna, there were three significant sediment interaction effects for density, biomass, and taxonomic richness from grab data; all three measures were substantially higher in sand sediments inside the closure than outside the closure (Fig. 4). For the epifauna, there were significant sediment interactions for density and taxonomic richness; both variables were substantially greater only in gravel sediments inside the closure. Although the interaction effects clouded interpretation of the main effects (i.e., all sediments combined), there was consistency in that all measures were higher inside the closure compared to outside the closure. There were two significant main effects (Fig. 4, A–F): higher densities of infauna from grab ($P=0.01$) and box corer ($P=0.02$) data inside compared to outside the closure. There were two significant main effects comparisons for epifauna (Fig. 4, G–H): total community density ($P=0.0001$) and taxonomic richness ($P=0.0004$), which were both higher inside.

Overall, these data indicate the following trends by sediment type. For mud, there were no consistent trends

Figure 4

Means (±1 SE) for univariate infauna (**A–C**): Shipek grab; (**D–F**): Wildco box corer); and epifauna (**G–H**): video camera) density, biomass, and taxonomic richness by sediment type. Only P values for significantly different results from comparisons of inside and outside closure main effects (=all sediments combined) are shown; see text for discussion of sediment interaction effects.

for significant in vs. out differences for infauna or epifauna. For sand, there were strong and consistently greater density, biomass, and taxonomic richness for infauna inside the closure, but no in vs. out differences for epifauna. For gravel, there were no in vs. out differences for infauna, but greater density and taxonomic richness for epifauna inside the closure. In the context of fishing gear use, these data indicate recovery inside

the closure from the negative impacts of otter trawls on infauna in sand, but not mud, and recovery inside the closure from the impacts of gillnets on epifauna on gravel bottoms. The magnitude of recovery, however, cannot be directly inferred from these data because of the confounding factor of different fishing intensities when the preclosure and postclosure data were compared (Fig. 3). The overall negative impact of trawls

(on sand sediments) was likely underestimated by our data, and the negative impact of gillnets (on gravel) was likely over estimated.

Discussion

In control-impact studies like this one, spatial effects cannot typically unambiguously be distinguished from temporal effects of the activity of interest, because no data are available from before the activity was started (Osenberg et al., 1994). Hence, such studies (in contrast to the more rigorous before-after, control-impact [BACI] designs) must be assessed with respect to how factors that may have changed over time in relation to the control and impact areas might have contributed to any observed differences. Thus, it is possible that there were differences in the benthic communities before the WGOM closure was implemented that could have affected our interpretation of the data. Although this possibility cannot be unequivocally discarded, several lines of evidence indicate it is reasonable to assume similar conditions in both areas before the closure. First, the overall study area was chosen so that the control sites with continued fishing outside the closure were in close proximity to the treatment sites inside the closure where fishing impacts were removed; this proximity of the two areas minimized potential confounding differences related to distance. Second, the range of habitat types and relative coverage area by each type were similar inside and outside the closure. Finally, we know of no other events since establishment of the closure—other than fishing gear restrictions and subsequent intensity patterns—that may have differentially affected the study areas inside and those outside the closure. Therefore, although we feel it is reasonable to interpret the differences inside and outside the closure in our data mainly to be the result of the removal of gillnets and otter trawls from the closed area, details on the spatial distribution patterns for each type of gear use must be considered in order to fully assess these impacts.

The obvious intent behind the WGOM closure was to eliminate negative impacts from both gear types inside the closure. Implementation of the closure, however, also caused a shift in fishing intensity, particularly for gillnets. Although this shift did not affect the overall conclusion of significant impacts for both gear types and subsequent recovery inside the WGOM closure, it does indicate that the relative levels of impact of the two gear types may have been exaggerated by our data: the impacts of gillnets may have been over-estimated because of the substantially increased postclosure fishing intensity outside, and the trawl impacts may have been under-estimated. Displacement of fishing effort and intensity may be the general trend for fishing closures, and there is no straightforward way to estimate the magnitude of this effect (Ward, 2004; Fogarty and Murawski, 2005).

The major conservation concerns regarding the use of gillnets have been bycatch and entanglement of non-

target species (He, 2006). Our data, however, strongly indicate that gillnets have been responsible for substantial reductions in epifauna on Jeffreys Ledge. Although Malik and Mayer (2007) reported seafloor marks on top of the ledge which may be evidence of the use of other bottom fishing gear in this area, available fishing activity data on preclosure and postclosure gear use in the study area indicate that gillnets are the major gear used on rocky bottoms in the area. Therefore, the substantial and significant differences between epifauna densities and taxonomic richness inside (compared to outside) the closure would indicate that macrofaunal communities on hard bottoms were damaged by gillnets and are recovering from these effects.

Our data from soft-sediment areas where otter trawls were the dominant gear type reflect the general trends observed in other studies (see reviews by Dorsey and Pederson, 1998; Watling and Norse, 1998; Johnson, 2002; and Kaiser et al., 2006): decreased density, biomass, and taxonomic richness in benthic communities. To our knowledge, only one previous study of bottom habitats inside the WGOM closure has been completed, an M.S thesis by Knight (2005). This research focused on areas north of our study area that were mainly affected by trawls, and it also had a similar study design of inside vs. outside a closure. The sampling occurred from 2002 through 2004, covering nearly the same time interval as our project, but also included areas in the easternmost portion of the WGOM closure that were not incorporated into the closure area until 1999 (two years after the initial closure area was implemented). These differences aside, Knight (2005) reported findings similar to ours: much higher abundances for some infaunal and epifaunal taxa inside the closure compared to outside. Knight (2005) also noted that a shift in taxonomic composition of infauna (e.g., increases in sabellid polychaetes inside the closure) and epifauna towards taxa less tolerant of physical disturbances had occurred at sites inside the closure.

As already noted, our data indicate substantial recovery but cannot be used to accurately infer the magnitude of recovery because of concurrent and confounding changes in fishing intensity during the study period. Additionally, our understanding of the recovery process for seafloor habitats disturbed by fishing gears is in the early stages—in large measure because of the number of factors involved (e.g., gear type, frequency and intensity of gear disturbances, and seafloor sediment type). Recent meta-analyses of gear effects have revealed widely variable recovery times, and no consistent trends for many combinations of gear and bottom types (Collie et al., 2000; Kaiser et al., 2006). In two recent studies on nearby Georges Bank in the Gulf of Maine few measurable effects of two large fishing closures were found for epifauna and infauna. Link et al. (2005) reported no significant differences in a variety of measures of benthic communities from video recordings and grab samples when comparing sites fished mainly by scallop dredges outside the closed areas with those inside the closures 4.5 years after closure. They attributed their

findings to the naturally dynamic nature of the seafloor that is frequently affected by storms and strong tidal currents (also see Auster and Langton, 1999; DeAlteris et al., 1999; Henry et al., 2006). Stokesbury and Harris (2006) reported similar findings for a video study of epifauna in the same general study areas. In contrast, Collie et al. (2005) showed substantial recovery of benthic epifauna (megafauna) on gravel bottoms inside one of the closed areas on Georges Bank, but differences did not occur until 2.5 years after closure, and increases in biomass and abundance of some taxa were still occurring after five years. They suggested that recovery times for faunal communities on gravel bottoms in their study area were on the order of ten years. In sum, these data further indicate that long-term studies will be needed to fully assess the effects of the WGOM closure on the recovery process for benthic communities on hard bottoms.

A similar conclusion can be drawn for recovery of benthic communities on muddy bottoms inside the closure: the recovery process is still ongoing. Previous studies that indicate otherwise, however, need to be considered. For example, two studies in the western Gulf of Maine indicated rapid recovery of mud bottom communities. Sparks-McConkey and Watling (2001) reported recovery to ambient levels for the infauna on muddy bottoms within 3.5 months after experimental trawling disturbance. Simpson and Watling (2006) also found only short-term (less than three months) effects on mud-bottom infaunal communities regularly fished by shrimp trawls with rock hopper gear compared to an adjacent unfished area. In both studies, the dominant taxa were small, nearsurface-dwelling species (mostly polychaetes) with high reproductive rates and thus potentially able to recover quickly from disturbance. It should also be noted that both these studies involved much smaller spatial scales (two study areas, each <40 km^2) than that of our study (515 km^2) such that immigration over smaller distances may have resulted in faster recovery rates. In contrast to these findings of minimal effects and fast recovery, some studies have shown substantial effects of otter trawls on mud-bottom communities and long recovery times, and the differences can in part be explained by differences in dominant taxa. If mud bottom communities include long-lived species, many of which are also structure-forming, then trawls (and other mobile gear) can have substantial adverse effects, as was found in the meta-analysis of Collie et al. (2000). Jennings et al. (2001) and Queirós et al. (2006) found significant decreases in infaunal biomass and production on muddy bottoms related to trawling intensity, as well as differential responses in relation to size spectra of the dominant taxa. Hixon and Tissot (2007) documented 600% higher densities of epibenthic invertebrates (and 23% more fish) based on video transects in untrawled (compared to trawled) mud bottom areas. Long-lived, slow-growing sea pens (*Stylatula* spp.) dominated the invertebrate communities in untrawled areas, but were rare in trawled areas. Tillin et al. (2006) reported similar sea-basin scale patterns in benthic communities in the North Sea in relation to fishing intensity; large, suspension-feeding epibenthic taxa dominated in lightly trawled areas, whereas mobile taxa and infaunal and scavenging species were dominant in areas that were more heavily trawled. Therefore, the level of effect and recovery times for benthic communities on mud bottoms affected by bottom trawls can be expected to vary widely, dependent in part on characteristics of the dominant species, and areas dominated by large or structure-forming taxa can be the most negatively affected. Further studies will be required to characterize the process over the long term, and such research should include more rigorous assessment of variations in fishing intensity than was possible in our study (Hiddink et al., 2006).

A final topic here concerns possible indirect effects on benthic communities caused by removal of fishing pressure on species that consume benthic invertebrates (Pinnegar et al., 2000). Unfortunately, little information is available on how fish populations have responded to the WGOM closure. However, available data indicate little or no increase in populations of fish such as gadids, skates, and flatfish that prey on benthic invertebrates (Murawski et al., 2004, 2005). However, recent experimental tethering studies showed greater predation rates on adult crabs (*Cancer* spp.) in rocky areas inside the closure (Meyer, 2005). Meyer also found very slow colonization rates on experimental habitat plots inside and outside of the closure, and no significant effects of predator exclusion cages on these rates. In sum, these data suggest that any indirect effects caused by differential predation rates inside compared to outside of the closure would have been weak. Meyer's (2005) colonization experiments (which were conducted over 4- to 12-month periods) also indicate that any recovery rates occurring inside the closure would be relatively slow.

The WGOM closure area is achieving a very important management goal: protection and enhancement of seafloor habitats. How are these changes related to ongoing recoveries of some fish populations and what are the management implications?

Closed area management measures are expected to have two separate effects on productivity and sustainability of fisheries (Stefansson and Rosenberg, 2005). First, if the closure is properly designed, it may reduce fishing mortality rates on some stocks by shifting limited effort away from areas where catchability is high to areas where it is lower. Effort control is essential to ensure that effort increases don't compensate for reduced catchability. Reduced fishing mortality rates on overfished stocks should increase productivity through higher stock and recruitment levels.

Secondly, closed areas that protect habitat may increase productivity of stocks by increasing growth, reproduction, and survival rates. This effect of closed areas is much harder to quantify or demonstrate with respect to recovery of the fish stocks. But, one important aspect of inferred habitat quality is the abundance of food resources for fishes, including both infauna and epifauna.

The management implications from this study are also two-fold. The observed differences in infauna and epifauna indicate that the closed area has been an effective measure for protecting habitat and potentially aiding stock recovery, although the latter has yet to be quantified. This conclusion is important regionally because closed area effects on reducing fishing mortality in New England have been generally accepted, but habitat protection benefits are still controversial.

A second important implication from this study is in the design of closed areas. The results presented here indicate that the particular bottom types that benefit most from protection depend on the type and intensity of fishing gear use before the closure is established. For example, the rocky bottoms in our study area were heavily fished with gillnets before the closure was implemented, and they showed the most recovery for epifauna, but little difference for infauna. As management of closed areas is modified in the future, these results will help clarify design criteria and refine the design of closures. Coupled with the improved ability to accurately monitor the position of vessels during fishing operations, these data may enable managers to more finely tailor spatial characteristics of closed areas thereby improving the effectiveness of management measures while potentially reducing the restrictions on fishing operations.

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