

Human-driven spatial and temporal shift in trophodynamics in the Gulf of Maine, USA

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Abstract Utilizing marine protected areas (MPAs) to isolate the ecological effects of human influence can help us understand our effect on systems and foster ecosystem-based approaches to management. Specifically, examining invertebrate prey community dynamics inside and outside an MPA may provide a measure of how altering human influence (i.e., certain fishing pressures) affects ecosystem interactions. We measured trophic interactions inside and outside a deep-water temperate MPA over 2 years. Predation rates on tethered, preferred groundfish prey (crabs) were initially identical inside and outside the MPA, but decreased outside the MPA after the commercial groundfish fishing season commenced. Predation trials using a ubiquitous prey species (brittle stars) and a less preferred prey species (urchins) served as controls, showing no MPA effect. Our experiments quantify differential predatory activity resulting from differences in human activity driven by an MPA, demonstrating important effects of fishing and regulations on the strength of trophic interactions.

Introduction

Fishing, even at levels considered sustainable, can affect the structure and function of marine ecosystems (Pauly et al. 1998; Jackson et al. 2001). Biodiversity and species abundance can be altered, either directly (e.g., removal resulting from fishing effort) or indirectly (e.g., through changes in food web linkages). Some systems have even collapsed under intense fishing pressure, which can be further exacerbated when coupled with unfavorable ocean conditions (Steneck and Carlton 2002). Although managers and scientists can mitigate human impacts on ocean ecosystems, our knowledge of how exactly systems are affected by fishing is still fairly rudimentary. In order to better grasp this, and to provide for ecological buffers, conserve biodiversity and protect or help rebuild fisheries to robust population levels, policy makers are implementing various ecosystem-based approaches to management. Along with a handful of other management techniques, marine protected areas (MPAs), including marine reserves, are emerging as important conservation tools that can help enhance the regional abundances of overfished species (Sobel and Dahlgren 2004; Tognelli et al. 2009; Selig and Bruno 2010).

Many studies indicate that the establishment of MPAs can influence local ecosystems as a whole by restructuring benthic communities, boosting populations of large predators, and returning system dynamics to at least a perceived natural state (Babcock et al. 1999; Lester et al. 2009). This is achieved primarily by removing or dampening identified human activities that can adversely affect ecosystem dynamics, such as fishing. Understanding these changes in human activity will shed light on how nutrients and energy move through a system and influence overall productivity and provide a greater understanding of the

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direct and indirect effects of MPAs on local food webs. This will improve our ability to predict the broad-scale effects of fishing and stock rebuilding programs (Gerber et al. 2003; Micheli et al. 2004).

The establishment of an MPA and subsequent increases in large, predatory species may cause a suite of indirect effects that, through top-down processes, may alter the abundance and production of lower trophic level species not directly affected by the fishery closure (Estes et al. 1978; Walters et al. 1997; Sala et al. 1998; Babcock et al. 1999). For example, an increase in the abundance of large predators through MPA protection may decrease the abundances of benthic prey, which in turn, can increase or decrease populations of other trophically linked invertebrates and plants (Edgar and Barrett 1999; McClanahan and Mangi 2000). Furthermore, variation in the composition and abundance of basal prey species (e.g., benthic invertebrates) is likely in turn to cause changes in fish production through bottom-up processes, primarily the provision of food (Holbrook and Schmitt 1986). Benthic invertebrates may therefore be useful to detect the effects of MPAs on targeted fish populations because the invertebrates: (1) are often important prey for fish, (2) are more tractable due to lower mobility, (3) have shorter population recovery times from impacts due to shorter generation times and faster population growth, and (4) can illustrate the relative strength of functional processes through the selection of prey from different trophic guilds. Thus, shifts in community structure caused by fishing may be rapidly assessed through measuring responses of invertebrate prey species where fished predators are protected by MPAs.

If the goals of an MPA are to provide spatial refuge for commercially valuable fish species and help rebuild fish populations, then trophic interactions may be expected to change between areas where fishing is allowed (e.g., outside the MPA) and not allowed (e.g., inside the MPA). In order to better understand the effect of human fishing activity on lower trophic levels, we studied the effects of a fishery closure on the mortality rate of three species of benthic prey that characterize different trophic roles in the Western Gulf of Maine (Fig. 1). By comparing rates of predation over 2 years inside versus outside the MPA, and by executing our studies at various times of the year when fishing pressures change, we were able to test the effect of fishing activity in this deep-water temperate system. Because the MPA bisects both open and closed fishing grounds, we could conduct paired comparisons holding physical and environmental variables constant between sites. In addition, we supplemented this study by examining potential predator diet through stomach sampling. We predicted that the difference in human activity within versus outside the MPA (which varies throughout the year)

should translate into a measureable difference in predation rates on experimentally supplied prey.

Materials and methods

Study sites: the Western Gulf of Maine closure area

Populations of commercially valuable groundfish have declined more than 50% since the 1950s, due to overfishing the Gulf of Maine (Fogarty and Murawski 1998; Murray et al. 1999; National Oceanic and Atmospheric Administration 1999; Steneck and Carlton 2002; Safina et al. 2005). Due to rapid decline associated with human harvest, groundfish stocks have been deemed extensively overfished, and several large MPAs, in conjunction with other regulatory measures, have been established to aid in their recovery (New England Fishery Management Council 2006).

One of the largest MPAs in the United States is the 3,500 km² Western Gulf of Maine Closure Area (WGoMCA; large rectangle, Fig. 1). This area was established in 1997 to reduce groundfish mortality from fishing and to promote ecosystem recovery to support juvenile and adult groundfish (e.g., cod, *Gadus morhua* Linnaeus; haddock, *Melanogrammus aeglefinus* Linnaeus; Pollock, *Polachius virens* Linnaeus; flatfish spp.). The WGoMCA incorporates much of Jeffreys Ledge, a shallow bank that has historically supported large aggregations of groundfish (Collette and Klein-MacPhee 2002). Preliminary studies indicate that cod in the Western Gulf of Maine have smaller ranges than previously suspected (Howell et al. 2008), thus suggesting the closure may be of sufficient size to protect them. Other studies detect a strong recovery of epifaunal benthic species in sandy and gravel environments, which are common on the Ledge (Grizzle et al. 2009) and can help fuel groundfish recovery. The WGoMCA prohibits commercial vessels from gill-netting and bottom trawling within its boundaries; however, recreational (line) fishing, commercial lobster trapping, and mid-water forage fish trawling are still permitted. In addition, bottom trawling is rarely exercised on top of the ledge both inside and outside the reserve as the cobble and boulder-strewn bottom are not conducive to dragging a net.

To make ecological comparisons between the MPA and a contiguous area outside, we utilized a 386-km² rectangular study domain whose midline straddled the MPA boundary (small rectangle in Fig. 1). To minimize edge effects potentially associated with the MPA boundary, 1 km on either side of the boundary was not used. Our study area was situated on top of Jeffreys Ledge, a 53-km long shallow, rocky glacial deposit found both inside and outside the MPA occupying ~80% of our study domain.

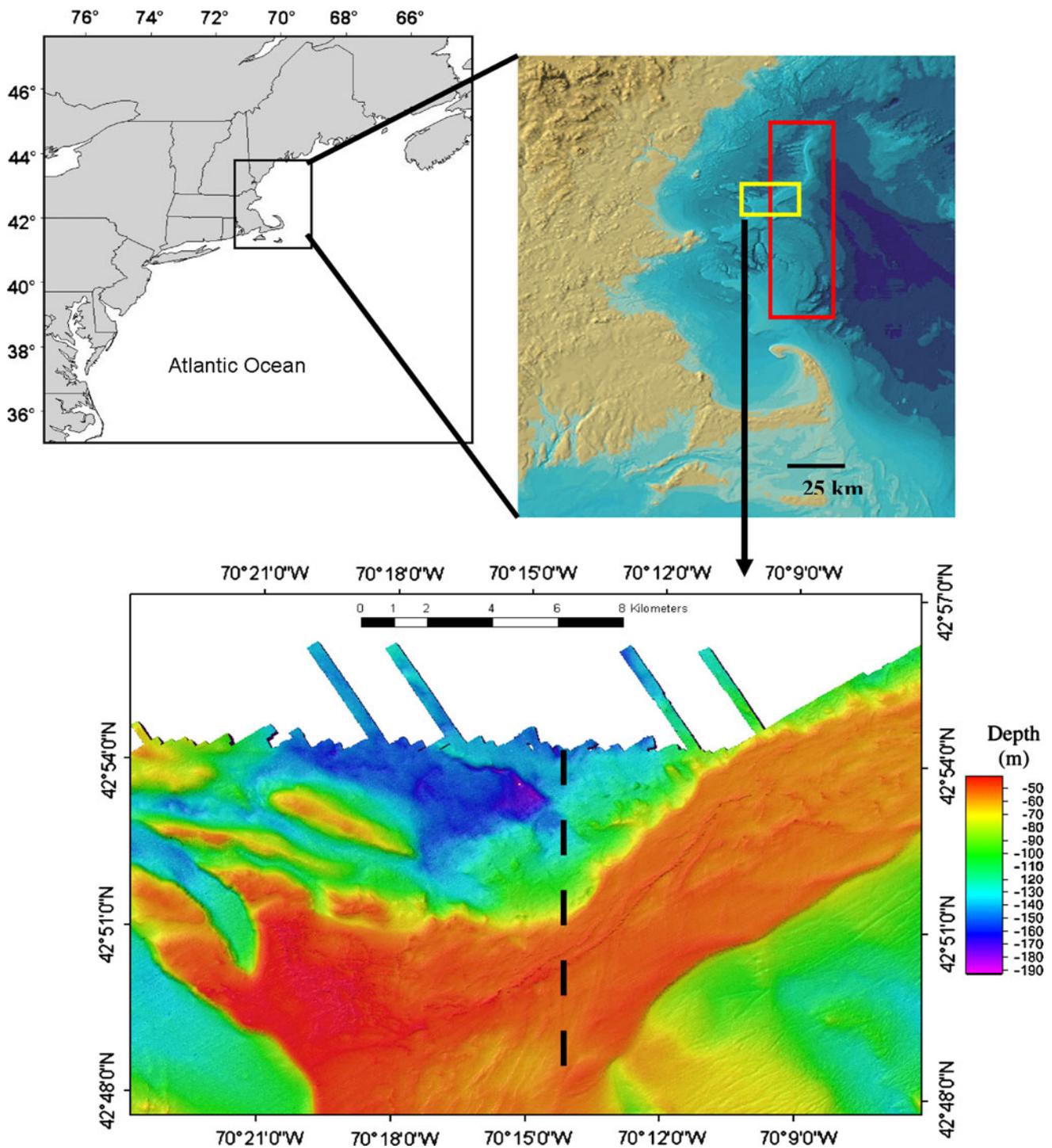


Fig. 1 Map of study area in the Western Gulf of Maine. In the panel on the upper right, the *large rectangle* (3,584 sq km) is the Western Gulf of Maine Closure Area. All experiments were conducted within the *small rectangle* (384 sq km) that straddles the MPA. Jeffreys Ledge is the shallow bank running NE to SW and is a prominent feature throughout the *small rectangle* and the northern portion of the MPA. *Bottom panel* is a high-resolution map generated using

multibeam sonar illustrating the various depths (m) within the *small rectangular* study area on top of Jeffreys Ledge (courtesy of MA Malik 2005). The outline of this map is the exact dimensions of the study area, and the *dashed vertical black line* bisecting the map denotes the western boundary of the Western Gulf of Maine Closure Area. Sites were chosen randomly inside and outside the protected area on any given day

Confining our study to the top of Jeffreys Ledge standardized for depth (50–70 m) and habitat, as the ledge is composed largely of cobble substrate (with occasional boulders). Bottom topography (Malik 2005) and substrate composition were well mapped in this area (McCarthy et al. 1979) enabling us to accurately standardize placements of paired experiments inside and outside the MPA. This study area was used in 2003 and 2004 to examine temporal consistency in measured responses. All trial locations were randomly selected within our study area.

Quantifying trophic interactions

To assess and compare differential predation rates based on location (i.e., inside or outside the MPA) and time of year, we used a tethering protocol with three common groundfish prey: Jonah crabs (*Cancer borealis* Say), the daisy brittle star (*Ophiopholis aculeate* Linnaeus) and the green urchin (*Strongylocentrotus droebachiensis* Muller). The logistics of collecting and maintaining brittle stars in the laboratory proved difficult, thus this species was used less frequently in experiments than crabs and urchins. These prey items were chosen based on the following: (1) their representation of different trophic roles in benthic marine ecosystems, (2) their likely presence within our study site, and (3) evidence of their importance as prey items in groundfish as known through the literature (Collette and Klein-MacPhee 2002) and as verified with our own surveys of prey items in groundfish stomachs (see later).

Tethering trials began in late spring (June 2003 and May 2004) and continued through September of each year. Commercial bottom fishing is off limits in all areas (both inside and outside the MPA) from April 1st–July 1st each year due to the cod's spawning event nearshore (New England Fishery Management Council 1998). Thus, we began deploying tethering trials at least a month before the commencement of fishing outside the MPA to examine predation responses with a BACI (Before-After-Control-Impact) design.

To minimize variability due to size-dependent predation, individuals of each prey species were selected from a small, limited size range (crabs: 45–60-mm carapace width; urchins: 30–45-mm test diameter; brittle stars: 10–15-mm test diameter). Prey was weighed and then attached to 20-cm monofilament tethers (40-lb. test strength for crabs and 15-lb. for urchins and brittle stars). Monofilament line test strengths were chosen to preclude escapement and thus ensure missing prey had been taken by predators. To certify the integrity of tether lines, prey was attached to tethers 24 h before deployment and held in a cold room (10°C) in aerated seawater. Tethers were secured every 5 m along a 75-m polypropylene rope with

the three prey species systematically interspersed, and thus five individuals of each species on each rope line. Previous studies in this area have successfully used similar tethering techniques (Witman and Sebens 1992; Vadas and Steneck 1995).

Three replicate weighted rope lines of tethered prey were deployed on the seafloor simultaneously at a randomly chosen location for each trial both inside and outside the MPA. (A buoy line attached to one of the weights allowed for retrieval of each line at the end of the trial.) At each site, the three lines were spaced approximately 100 m apart, parallel to one another and left at sea for 48 h. Each pair of triplicate deployments constituted one trial, and several trials ($n = 2–8$) were conducted each month.

During retrieval, we enumerated missing and present prey animals on the tether lines. On occasion, portions of killed prey were retrieved. Not only did this represent definitive predation, but often we could deduce the type of predator responsible for predation. On approximately 10 occasions, we retrieved tethered urchins with a large seastar wrapped around the test.

For each species, predation rates were calculated by combining loss rates on the three tether lines at each location for each trial. All trials were categorized according to whether they were executed pre- or post-fishing season commencement. Data were compared between inside and outside the MPA using ANOVA, with protection status (inside and outside the MPA), year (2003 and 2004), and fishing season (pre and post) nested within year treated as fixed factors. For brittle stars, because of insufficient replicates to test the full model, a separate factorial ANOVA was conducted for each year to examine the effect of fishing season and protection status on mortality. Because July 2003 data were obtained very soon after the commencement of commercial fishing season (within 5 days) and thus before substantial reduction in groundfish stock could accrue, these data were treated as pre-fishing season for 2003 analyses. Data were Anscombe square root transformed to compare proportional mortality.

Predator diet

The identity of the most likely predators in the tethering trials was confirmed with gut content analysis of predatory fishes caught periodically by trawl and hook and line throughout each summer within our study area. Predatory fish species were killed, and their gut contents were removed and placed on ice. Gut contents were examined under dissecting microscopes in the laboratory. Stomach items were identified and enumerated, though digestion sometimes precluded identification. Although literature searches identified prominent prey species utilized by predatory groundfish, the collection of these data allowed

us to quantify prey selection patterns by specific fish species in the immediate experimental area.

Results

Effects of fishing on predation/mortality rates of prey

Predation rates on tethered invertebrate prey varied by month, location, and prey species identity. There was a significant, lowered rate of predation on crabs outside the MPA, but only after fishing season had commenced (MPA × season [year]: Table 1a; Fig. 2). This pattern of lower crab mortality outside the reserve during fishing season was consistent in both years.

Urchins exhibited no difference in predation inside compared to outside the MPA regardless of the status of the fishing season outside (Table 1b; Fig. 3). Patterns in 2003 and 2004 were not different. Our analysis included urchins that were killed by seastars, which accounted for approximately 40% of urchin mortality, although it made no statistical difference if these seastar-killed urchins were excluded from analyses. Seastar predation was readily identified by loss of spines and Aristotle’s lantern or in 10 cases (as mentioned earlier), upon retrieval, a seastar was still wrapped around and consuming the urchin.

Brittle star predation also showed no definitive trends inside or outside the MPA, regardless of fishing season, in either 2003 (MPA: $F_{1,6} = 0.09, P = 0.77$; season: $F_{1,6} = 0.0002, P = 0.99$; MPA × season: $F_{1,6} = 0.042, P = 0.84$; Fig. 4, Panel A) or 2004 (MPA: $F_{1,11} = 0.45,$

Table 1 Results of ANOVA on predation rates of tethered invertebrate prey: (a) crabs (*Cancer borealis*) and (b) the green urchin (*Strongylocentrotus droebachiensis*)

| Source | Df | MS | F | P |
|-------------------|----|-----------|-----------|-------|
| (a) | | | | |
| MPA | 1 | 0.13 | 7.19 | 0.010 |
| Season [year] | 2 | 0.0068 | 0.38 | 0.69 |
| Year | 1 | 0.023 | 1.28 | 0.26 |
| MPA*year | 1 | 0.0015 | 0.086 | 0.77 |
| MPA*season [year] | 2 | 0.069 | 3.85 | 0.029 |
| Error | 42 | 0.018 | | |
| (b) | | | | |
| MPA | 1 | <0.000001 | <0.000001 | >0.99 |
| Season [year] | 2 | 0.00093 | 0.058 | 0.94 |
| Year | 1 | 0.010 | 0.64 | 0.43 |
| MPA*year | 1 | 0.0077 | 0.49 | 0.49 |
| MPA*season [year] | 2 | 0.0065 | 0.41 | 0.67 |
| Error | 42 | 0.016 | | |

Factors include MPA (inside vs. outside), year (2003 and 2004), and fishing season (pre and post) nested within year

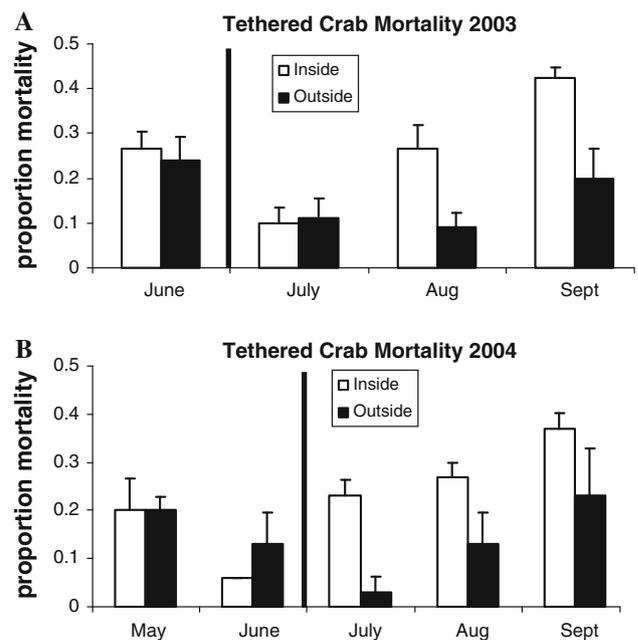


Fig. 2 Tethered crab mortality based on month and location (inside vs. outside the MPA). Panel A presents 2003 data; Panel B is 2004. Error bars denote + 1 SE. In Figs. 2–4, the vertical black line between June and July in both years denotes the commencement of commercial fishing season (fishing is prohibited outside the MPA for 3 months prior to July 1st). Our July sampling in 2003 began only 3 days after commercial fishing began. The minimal difference between crab mortality inside and outside the MPA at this time suggests that increases in crab mortality inside the MPA are lagged behind the commencement of commercial fishing. July samples in 2004 began more than 2 weeks after commercial fishing season began

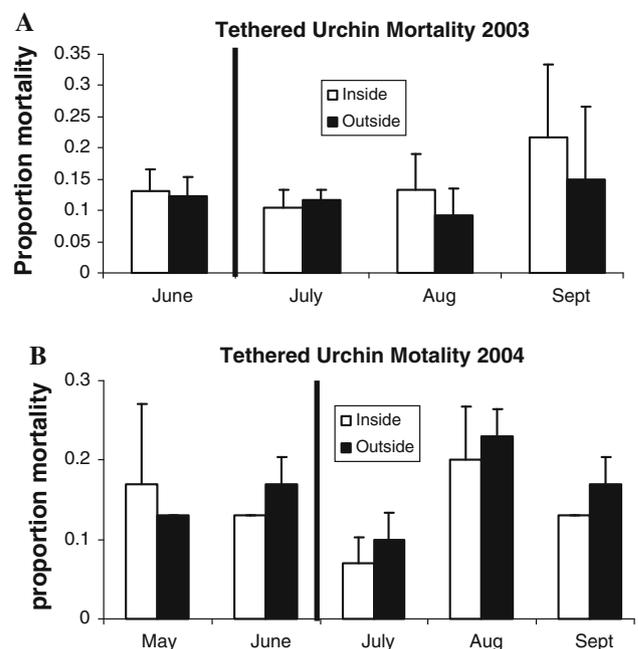


Fig. 3 Tethered urchin mortality based on month and location (inside versus outside MPA). Panel A presents 2003 data; Panel B is 2004. Error bars denote + 1 SE

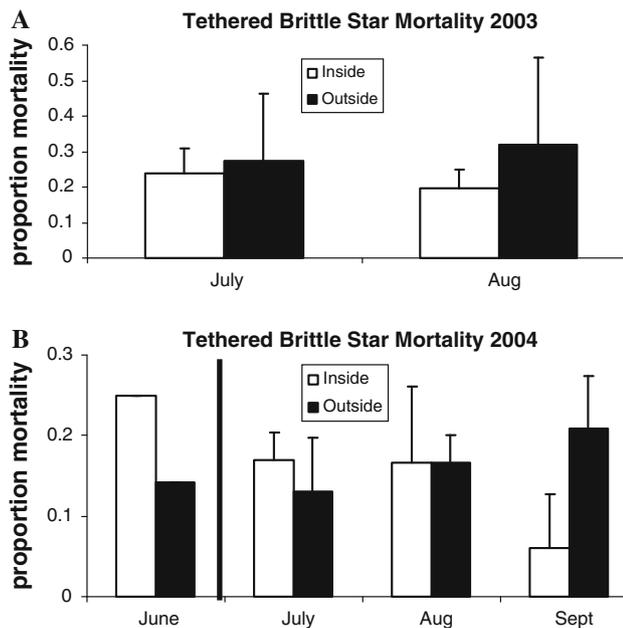


Fig. 4 Tethered brittle star mortality based on month and location (inside versus outside MPA). *Panel A* presents 2003 data; *Panel B* is 2004. Error bars denote + 1 SE

$P = 0.52$; season: $F_{1, 11} = 0.81$, $P = 0.39$; MPA x season: $F_{1, 11} = 1.93$, $P = 0.19$; Fig. 4, Panel B).

Predator diet

Via benthic trawl and hook and line, we caught 47 cod, 23 haddock, 8 Pollock, and 58 dogfish immediately adjacent to the MPA to be examined for their diets. We found in gut content sampling that cod, haddock, and Pollock in our study area readily consumed fish, such as herring, but to varying degrees (Table 2). Additionally, benthic invertebrates comprised a large portion of their diets, especially for cod and haddock. These invertebrates included polychaetes, crabs, shrimp, and brittle stars in cod; bivalves, brittle stars, and amphipods in haddock. Pollock overwhelmingly relied on fish as prey; however, we found shrimp and even sea cucumbers in their stomachs. Every stomach was empty in each of the dogfish sampled; therefore, we could not index

dogfish diet. We also sampled the guts of several other fish species, like wolfish (*Anarhichas lupus* Linnaeus) and monkfish (*Lophius americanus* Valenciennes); however, the number of fish sampled was too low (e.g., <5 each) to confidently infer dietary patterns.

Discussion

Similar initial predation rates on our experimental crabs, followed by differentially lower predation rates outside the MPA after the commencement of the commercial groundfishing season strongly implicates fishing as the mechanism driving the observed differences. This pattern was consistent in both experimental years, suggesting that the MPA is protecting the target fish during the fishing season and in the process, conserving stronger top-down control on the invertebrate community (Babcock et al. 1999). In contrast, outside the MPA, the removal or emigration of predators decreases the relative interaction strength between fish predators and certain prey.

Interestingly, in 2003, our July predation trials were conducted within 5 days of the initiation of groundfishing season, and predation rates on crabs inside and outside the MPA during these trials were highly similar. In 2004, our July sampling began 15 days after the fishery opened, and the differential predation rate was strong. Together these data suggest that there is a slight time lag after the onset of commercial fishing in the reduction in predators that manifests itself in crab predation rates.

Why no effect on urchins or brittle stars?

Although the pattern of lower predation outside the MPA is apparent with crabs, we detected no significant pattern with urchins and brittle stars. Admittedly, replication in our brittle stars was low, but there is still a strong plausible biological explanation for the lack of pattern. Specifically, brittle stars are abundant on Jeffreys Ledge (Meyer, personal observation); thus, the inclusion of brittle stars on our tether lines may have simply added to an already abundant prey source.

Table 2 The percentage of stomachs in which each prey occurred found in the guts of the three regionally important and historically abundant predatory fish species examined in this study

| Species | <i>n</i> | Brittle stars | Crabs | Urchins | Fish | Clams | Nematodes | Amphipods | Shrimp | Cucumbers | Snails | Unidentified |
|---------|----------|----------------------|--------------|----------------|------|-------|-----------|-----------|--------|-----------|--------|--------------|
| Cod | 47 | 17 | 23 | 6 | 60 | 11 | 64 | 9 | 21 | 4 | 9 | 43 |
| Haddock | 23 | 70 | 4 | 17 | 20 | 74 | 13 | 56 | 4 | 0 | 13 | 87 |
| Pollock | 8 | 0 | 0 | 0 | 60 | 0 | 1 | 0 | 38 | 13 | 0 | 63 |

The category “unidentified” indicates remains that were too digested to identify. The natural occurrence in fish diets of the three prey taxa used in our tethering experiments are highlighted in bold

Also, consumption of crabs requires a relatively large predator that can eat larger prey. Cod and wolfish are likely the heaviest consumers of adult crabs because they attain larger sizes than most groundfish and have the capacity to easily ingest crabs whole (Wahle and Steneck 1992, Meyer, personal observation). In contrast, urchins and brittle stars are commonly eaten by small or non-targeted predator species unaffected by fishing regulations, and this could explain their similar predation rates inside and outside the fishery MPA. For example, ~40% of the urchin predation we documented on our tether lines was attributed to seastars (e.g., *Asterias* and *Crassoster*). Likewise, we examined several cunner (*Tautogolabrus adspersus* Walbaum) stomachs and found numerous brittle stars, which were one of the only consistently identifiable contents. Haddock are the groundfish species that most often consumes urchins and especially brittle stars (Table 2). Based on historical literature (McCarthy et al. 1979; Collette and Klein-MacPhee 2002), these fish were not common even inside the MPA. Thus, unlike crabs, observed predation rates on brittle stars and urchins were likely affected by lower trophic level, non-target predators (e.g., cunner, seastars) that were unaffected by MPA status or fishing season.

Significance and conclusions

Ours is one of very few studies that examine predation rates inside and outside MPAs through a controlled, replicated BACI design. Thus, we have eliminated many of the confounding variables that influence the interpretation of many studies that try to draw conclusions about trophodynamics from purely observational data. Thus, our study isolates more soundly than most the influence of MPAs on trophic interactions.

As managers and scientists develop the underpinnings of ecosystem-based approaches to managing human influence on marine systems, it is critical to understand as best we can how fishing—i.e., the removal of high trophic level predators—can affect ecosystem dynamics. Examining invertebrate benthic communities within and outside a deep-water MPA can shed light on how top-level predators can influence the flow of energy in a system. The significantly higher rate of predation on crabs within the MPA after the onset of commercial fishing season was consistent over two consecutive years. These findings highlight that predator–prey interactions can vary as a function of protective status and emphasize the effect large fish predators have on the benthic community assemblage of invertebrates in this MPA. Quantification of such trophic interactions is a substantial, tangible step toward predicting the long-term impact of fishing of predatory groundfish populations and responses of their invertebrate prey.

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