The role of closed areas in rebuilding monkfish populations in the Gulf of Maine

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The use of fish closures as a management tool to protect juvenile fish habitat and adult spawning grounds has become increasingly popular, although knowledge of the direct effects of marine closures on juvenile fish populations is limited. Given that monkfish landings account for a considerable percentage of the monetary value derived from the groundfish fishery in new England, investigating the factors that influence monkfish population dynamics will assist managers in sustaining this important natural resource. We conducted bottom-trawl surveys to determine the effects of closure status [inside vs. outside the Western Gulf of Maine Closure Area (WGMCA)] and habitat type (mud bottom in isolation from gravel or cobble bottom vs. mud that is next to these more complex habitats) on the distribution, abundance, and diet composition of monkfish (*Lophius americanus*) in the Gulf of Maine. Surprisingly, the abundance of adult monkfish did not differ in vs. out of the closure, and juvenile monkfish were more abundant outside of the WGMCA, where they also exhibited higher feeding intensity and consumed more prey biomass. Monkfish diet and condition results implied that the boulder and ledge bottom is essential monkfish habitat and that these effects were independent of the WGMCA.

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Introduction

Fisheries managers have responded to the heightened pressures on fish populations globally through a number of proactive and retroactive measures, such as implementing fish quotas, restricting entry to the fishery, and setting up temporal and spatial closures. The 1996 Amendment to the US Magnuson–Stevens Fishery Conservation and Management Act tasked the National Marine Fisheries Service and fishery management councils with the difficult undertaking of identifying and describing essential fish habitat (EFH) for all federally managed species (National Oceanographic and Atmospheric Administration, 1998). EFHs support the production of fish by promoting better growth and survivorship. Therefore, determination of EFH will require information on which habitats are important foraging and refuge grounds and consequently contribute disproportionately to fish production locally and regionally. Protection of fish populations will hinge upon effective determination of EFH (Lindholm *et al.*, 2001). Yet, data on early life-history phases of the vast majority of fish species are severely lacking and consequently hinder this process. Therefore, studies that increase our understanding of fish demographics as a function of habitat will benefit efforts to manage fisheries more effectively.

Fully understanding the habitat requirements of a demersal fish necessitates identifying all the habitats occupied at each life-history stage and the impacts of those habitats on population dynamics (Lindholm *et al.*, 2001). Although adult habitat usage can be inferred from fishery-dependent catch data, modern fishing gear is designed to reduce or eliminate juvenile catches. Consequently, catch data alone provide little insight into juvenile habitat usage. Catch patterns before reductions in trawl mesh size can provide evidence of habitat usage by slightly smaller subadults, but even the smallest meshes previously fished were not effective at catching very young juveniles (especially 0- and 1-year age classes).

Strong linkages between juvenile habitat and groundfish population dynamics have been identified in many regions of the North Atlantic (Keats *et al.*, 1987; Gotceitas and Brown, 1993; Auster *et al.*, 1995; Gregory and Anderson, 1997; Fogarty and Murawski, 1998; Bjornstad *et al.*, 1999; Robichaud and Rose, 2006). In the Gulf of Maine, field surveys of nursery habitats for demersal fish have demonstrated the importance of vegetated habitats in coastal waters (Lazzari *et al.*, 2001). However, few field studies of habitat usage by juvenile groundfish have been conducted farther offshore in the Gulf of Maine, except some recent work on Stellwagen Bank (e.g. Auster *et al.*, 2001; Lindholm and Auster, 2003; Lindholm *et al.*, 2007). Assessment of juvenile fish usage of and population dynamics in nearshore habitats elsewhere in the Gulf of Maine is necessary to determine which bottom types function as juvenile groundfish habitat (i.e. which habitats should be designated as EFH) and contribute disproportionately to the production of adult fish species such as monkfish (*Lophius americanus*) and cod (*Gadus morhua*).

The habitat of fish includes both non-living physical and biological components. For example, a given habitat may be valuable to a fish because it provides physical shelter from predators and

contains food to consume. However, these biotic and abiotic components are not independent because the nature of the physical substratum largely determines which organisms are present. Although habitat is most often recognized on physical criteria, the importance of different habitat types is as much biological as physical (Auster and Langton, 1999).

Most juvenile fish can utilize a variety of habitats. Therefore, simple evidence of abundance patterns (where fish are and how many are present) may not indicate the true ecological value of each habitat. Juvenile fish utilize critical habitat as foraging grounds and to avoid predators. Coupling an understanding of these processes with abundance patterns will enhance our understanding of which habitats are critical to fish population dynamics. This information in turn can provide fisheries managers with the data needed to more clearly identify and define EFH for groundfish species in the Gulf of Maine.

Monkfish have been fished heavily over the past two decades and have exhibited signs of overfishing. For example, the size of monkfish caught in the Northeast Fisheries Science Center's trawl survey has declined over the past 40 years, during which monkfish landings increased from almost nothing to a peak of nearly 30 000 t in 1997 (Richards *et al.*, 2007). It is unclear which types of habitat limit juvenile and adult monkfish abundance. Furthermore, it is unknown whether closures such as the Western Gulf of Maine Closure Area (WGMCA) will effectively benefit the species. The WGMCA, which encompasses a large section of the western section of the Gulf of Maine, including Jeffreys Ledge, was initially designed in 1998 to reduce fishing mortality of key groundfish species such as cod. It also has been recognized as nursery and spawning habitat for certain commercially important fish species because it contains cobble, gravel, and rock-ledge bottom. We conducted a bottom-trawl survey to determine how closure status and habitat-setting influence the ecology of juvenile stages of important groundfish species, including monkfish, in the Gulf of Maine. We hypothesized that juvenile monkfish abundance, growth, condition factor, and survivorship would be greatest along the edges of structured habitat. We also predicted that sites within the WGMCA would contain elevated abundance of monkfish with high condition and greater gut fullness if the WGMCA was achieving its intended goal of rebuilding groundfish stocks by providing EFH.

Methods
Sampling design
We examined the effects of closures and habitat on the ecology of monkfish using an otter trawl survey. Specifically, bottom-trawl sampling was carried out at four pairs of sites both inside and just outside the northern portions of the WGMCA in autumn 2004 and spring 2005 (Figure 1). The northern section of the WGMCA was selected as the focus of this study because of the lack of ongoing groundfish research relative to the central and southern portions of the WGMCA. Bottom depth ranged from 30.2 to 47.8 m over the 16 sites. Each site pair included one site that was next to rock-ledge and boulder fields ("edge landscape") and one that was isolated by >2 km ("mud landscape") from rock bottom (i.e. two seasons × two closure statuses × two habitats × four replicates = 32 total tow samples). This landscape-scale approach permitted us to identify how these suites of habitats influence the ecology of juvenile groundfish more broadly within marine ecosystems than just focusing on a particular
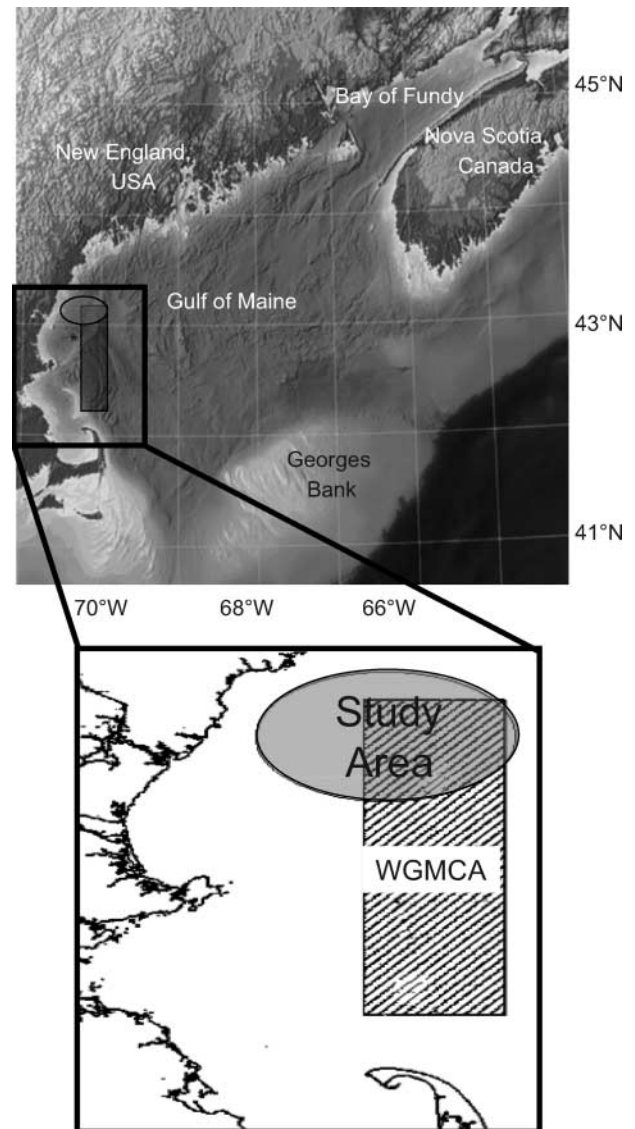

Figure 1. Map of study location in the Gulf of Maine. Bottom-trawl sampling for monkfish was conducted in autumn 2004 and spring 2005.

habitat type. Ecologists elsewhere have demonstrated that mud bottom next to more complex seagrass beds can influence the value of these habitats as foraging grounds for predators and prey that reside within them (Summerson and Peterson, 1984).

Before initiating bottom-trawl sampling efforts, we verified that the "edge" habitats were in fact next to rock ledge and cobble bottom, using a drop camera system. Specifically, we deployed a drop camera along a transect that was perpendicular to the hard bottom and surveyed from within the rock-ledge and boulder habitats to the mud habitat directly next to this hard bottom. This factorial design permitted examination of the effects and interactions of season, closure status, and landscape.

All sampling was conducted aboard the FV "De Dee Mae II". This vessel is a Down East 16.5-m stern trawler of 2.7 m draft with a 6.7-m beam. Monkfish were sampled with a 20-m otter trawlnet with a 50-mm codend fitted with a liner of 25 mm mesh to retain juveniles as well as adults (see Sherman *et al.*, 2005, for net specifications). Trawl tows were fixed at 15 min at

a towing speed of 2.3–2.5 knots. Tow time began when the winch brake was tightened, signifying that the net was on the seabed. The tow ended when the brake was loosened and cable hauling commenced.

Data

All monkfish captured in each tow were enumerated, measured, and weighed. Abundance was quantified as the total number of monkfish per tow. Thus, abundance had only one value per tow. Stomach contents were removed from each monkfish and stored in 10% formalin. Individual dietary items were identified to species (where possible), counted, and weighed (after removing excess water) in the laboratory. Stomach content calculations were conducted separately for juveniles and adults. Information on monkfish diet from Armstrong *et al.* (1996) and size at maturity from Steimle *et al.* (1999) suggests that monkfish experience an ontogenetic diet shift around $\sim$250 mm total length (L_T), along with a physiological shift towards reproductive maturity at $\sim$320 mm L_T for males and $\sim$360 mm L_T for females. For this study, monkfish $\leq$300 mm L_T were considered juveniles and those $\geq$301 mm L_T as adults.

Two stomach content indices were utilized to assess how season, closure status, and habitat impact the feeding rate of juvenile and adult monkfish in the western Gulf of Maine: (i) feeding intensity was calculated by quantifying the percentage of monkfish stomachs with food present; (ii) the cumulative weight (g) of prey consumed by each monkfish was divided by its length (mm L_T) cubed, and this value was multiplied by 10^7 to create a length-standardized index of stomach fullness.

Frequency of occurrence (FO), percentage gravimetric contribution (P), partial fullness index (PFI), and total fullness index (TFI) were used to examine how the relative importance of major prey groups in the diet of juvenile and adult monkfish differs as a function of habitat type and closure status (Hyslop, 1980; Bowering and Lilly, 1992; Sherwood *et al.*, 2002). Prey items were partitioned into the six prey groups, which collectively explain >99.9% of the diet composition by weight of monkfish sampled in this study: (i) unidentified animal tissue; (ii) pelagic fish (clupeids); (iii) demersal fish (largely gadoids and pleuronectids); (iv) zooplankton (mysids); (v) shrimp (*Pandalus borealis*); (vi) cephalopods (squid). The FO of each major prey group was calculated by dividing the total number of stomachs with prey$_i$ (where i is each prey group found in the stomach of monkfish) by the total number of stomachs examined for both juvenile and adult monkfish in vs. out of the closure and on the edge vs. the mud habitat, then multiplying these proportions by 100. P was calculated for each prey category by dividing the total weight of prey$_i$ by the total weight of all prey consumed by juvenile and adult monkfish separately in each treatment, and multiplying these proportions by 100. PFI was calculated by dividing the total weight (g) of prey$_i$ in each monkfish by the length (mm L_T) of that fish cubed, and multiplying this proportion by 10^7. TFI, which is a length-standardized measure of gut fullness, was calculated for each monkfish by summing all PFI values for each fish.

Condition factor has been used effectively to compare the condition of fish stocks and to examine how factors such as habitat quality and ecosystem perturbations impact fish (Sherwood *et al.*, 2002; Ratz and Lloret, 2003). A length-standardized measure of fish condition (K_{adj}) was calculated to examine the effects of season, habitat type, and closure status on monkfish

condition:

$$K_{adj} = \frac{W_G}{L_T^b} \tag{1}$$

where W_G is the gutted fish weight (g), L_T the total length (mm), and the scaling coefficient (b) is derived from the length–weight relationship equation: weight is equal to a coefficient (a) multiplied by the fish length to the power b, which was estimated for this study.

Statistical analyses

The effects of closure and habitat on monkfish abundance and mean size (L_T) were analysed using separate three-way ANOVAs. When the effect of season was highly non-significant (i.e. $p > 0.25$), it was removed from the model and the data were reanalysed using a two-way ANOVA. Replication for all dependent variables other than abundance (i.e. size, TFI, and condition factor) depended on the number of monkfish sampled (i.e. an unbalanced design). A length–weight relationship equation was derived for all *L. americanus* caught in the study. Size–frequency relationships were generated to explore how the WGMCA influences the distribution and abundance of monkfish in the western Gulf of Maine. In particular, the frequencies of four non-overlapping 200 mm (L_T) size classes were used to determine which length classes of monkfish differ with closure status. Differences in abundance of monkfish in vs. out of the closure for each size category were assessed using Student's *t*-tests. The *t*-tests are not intended to include the overall variance of both size and abundance, but instead are meant to examine subsets of the data (i.e. specific size classes) individually without inflating our values of *n*.

Separate *t*-tests were used to analyse the individual effects of season, closure status, and habitat on the length-standardized index of stomach fullness of juvenile and adult monkfish. The effects of closure status and habitat on the PFI of the three most common prey groups for juvenile and adult (demersal fish, pelagic fish, and shrimp) monkfish were analysed using separate two-way ANOVAs. The effect of season was not included in these analyses because we did not catch monkfish in every season–closure status–habitat combination. The effects of season, closure, and habitat on monkfish condition (K_{adj}) were analysed using a three-way ANOVA. To determine whether stomach fullness is a good indicator of monkfish condition, the relationship between monkfish TFI and K_{adj} was analysed using linear regression. We also examined whether the amounts of demersal and pelagic fish when present in the diet of monkfish are related to fish condition by regressing each of these factors with K_{adj}.

Results

Abundance and distribution

In all, 122 monkfish ranging in size from 65 to 775 mm L_T were caught during the spring and autumn sampling trips (Table 1). The equation $W_G = 0.00002 L_T^{3.0092}$ explained >98% of the variation between length and weight of monkfish captured in this study (Figure 2). The distribution and abundance of monkfish were influenced primarily by closure status rather than by season (which was subsequently removed from both abundance and size analyses) or habitat configuration. Monkfish were significantly more abundant ($F_{[1,28]} = 9.6$, $p = 0.005$) and smaller ($F_{[1,118]} = 7.7$, $p = 0.006$) outside than in the closure. Careful examination

Table 1. Monkfish sample sizes (*n*) collected from bottom-trawl surveys conducted in autumn 2004 and spring 2005 inside and outside the northern portions of the WGMCA.

Season	Habitat	In			Out		
		A	G	S	A	G	S
Autumn	Mud	4	6	6	4	17	17
	Edge	4	3	3	4	21	21
Spring	Mud	4	15	15	4	25	25
	Edge	4	13	13	4	22	22

Response variables that were quantified included monkfish abundance (*A*), gut contents (*G*), and size (*S*).
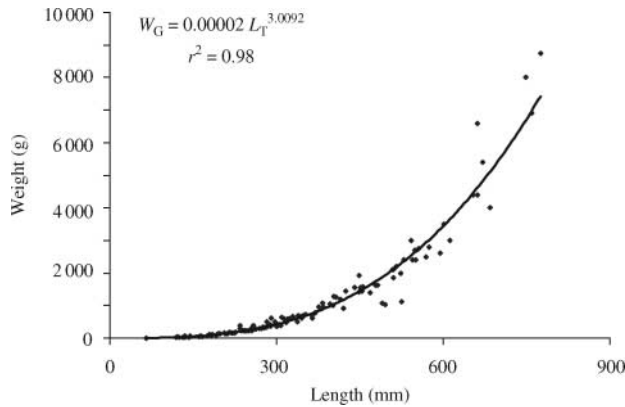

Figure 2. Length–weight relationship for fish caught in bottom-trawl surveys conducted in the northern portions of the WGMCA.
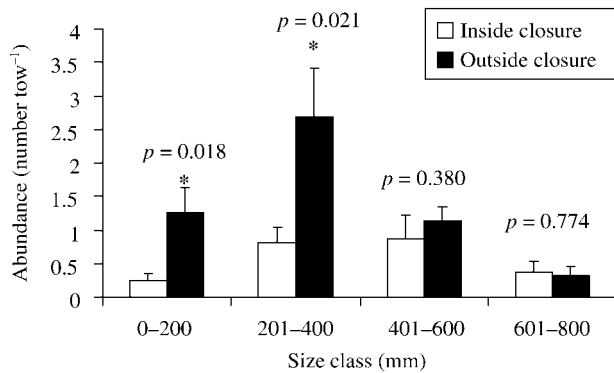

Figure 3. The effect of closure on the length–weight relationship of monkfish caught in bottom-trawl surveys conducted in the Gulf of Maine. Error bars represent +1 s.e.

of each size class of monkfish in vs. out of the closure revealed that the abundance of smaller monkfish is very low inside the closure (<200 mm L_T: $t_{[30]} = 6.3$, $p = 0.018$; 201–400 mm L_T: $t_{[30]} = 5.9$, $p = 0.021$; Figure 3), whereas closure status did not affect the abundance of larger monkfish (401–600 mm L_T: $t_{[30]} = 0.4$, $p = 0.54$; 601–800 mm L_T: $t_{[30]} = 0.03$, $p = 0.77$).

Diet composition

Juveniles (≤300 mm L_T)

Season, closure status, and habitat each influenced the feeding patterns of juvenile monkfish (Table 2). Juvenile monkfish

feeding intensity was greater in autumn than in spring, and outside than in the WGMCA. Feeding intensity was also slightly greater on the edge of structured seabed than on mud habitat. The effects of closure status and habitat on stomach fullness were not significant (*t*-tests, $p > 0.25$; Table 2).

Demersal fish were the most important component (i.e. greatest mean PFI) of the diet of juvenile monkfish in habitats inside and outside the WGMCA (Table 3, Figure 4a). Juvenile monkfish generally consumed more demersal fish outside the closure than in it, especially on muddy habitats. Juvenile monkfish consumed a variety of demersal fish species. Four-bearded rockling (*Enchelyopus cimbrius*) was present in the diet of monkfish caught inside the closure, but was most commonly consumed by monkfish outside the closure. Juvenile monkfish consumed other gadoids less frequently, including silver hake (*Merluccius bilinearis*) and the true hakes (*Urophycis* spp.). Demersal species other than gadoids consumed by monkfish included Acadian redfish (*Sebastes fasciatus*), ocean pout (*Macrozoarces americanus*), and American plaice (*Hippoglossoides platessoides*).

Closure status and habitat also influenced the diet composition of juvenile monkfish. Only juvenile monkfish outside the WGMCA consumed zooplankton (mysids) and shrimp (*P. borealis*; Table 3). Zooplankton and shrimp were also more prevalent in the diet of monkfish located at the edge of than actually in the mud habitat.

Adults (≥301 mm L_T)

In all, 65 adult monkfish stomachs were analysed; 11 were empty (15.9%). Adult monkfish generally consumed less prey biomass than juveniles (Table 2). Feeding intensity of adult monkfish was twice as high in spring than in autumn ($t_{[53]} = 2.3$, $p = 0.023$). Adult monkfish consumed almost twice as much prey biomass inside the WGMCA ($t_{[53]} = 2.0$, $p = 0.046$), but habitat did not significantly affect feeding intensity and stomach fullness ($t_{[53]} = 0.8$, $p = 0.40$).

Adult monkfish consumed a wider variety of fish species than juveniles, including clupeids, which were completely absent from the diet of juvenile monkfish. Pelagic and demersal fish were the two greatest contributors to the diet of adult monkfish, although the relative proportion of these two prey groups varied as a function of both closure status and habitat type (Table 4, Figure 4b).

Clupeids were more than an order of magnitude more prevalent in the diet of adult monkfish in spring than in autumn. The interaction between habitat and closure also significantly affected clupeid PFI in adult monkfish ($F_{[1,61]} = 5.9$, $p = 0.018$). Clupeids contributed more substantially to the adult monkfish diet on the edge habitat inside the WGMCA, but were less important in the edge habitat outside the closure (Figure 4b). The frequency of occurrence of clupeids in the diet of adult monkfish ranged from 18 to 78% (Table 4).

Counter to our findings for pelagic fish prey, closure status, and habitat type did not affect adult monkfish consumption of demersal fish ($p > 0.25$ for all effects). Adult *L. americanus* preyed on several demersal fish species, including Gadiformes (*E. cimbrius*, *M. bilinearis*, and *Urophycis* spp.), Pleuronectidae, and *S. fasciatus*. Zooplankton (mysids) were found in the stomach of one adult monkfish, whereas shrimp (*P. borealis*) were present in as much as 43% of their stomachs (Table 4). There was a non-significant trend of slightly higher shrimp PFI in the stomach of adult monkfish located on the edge of structured bottom than on mud ($F_{[1,61]} = 2.9$, $p = 0.092$; Table 4, Figure 4b).

Table 2. Feeding intensity and stomach fullness results for juvenile ($\leq$300 mm L_T) and adult ($\geq$301 mm L_T) monkfish captured (top panel) in spring and autumn, (middle panel) inside vs. outside the WGMCA, and (bottom panel) on mud bottom vs. at the edge of structured habitat.

Season	Juvenile monkfish ($L_T \leq 300$ mm)		Adult monkfish ($L_T \geq 301$ mm)	
	Spring	Autumn	Spring	Autumn
Total number of stomachs analysed (n_{tot})	32	25	43	22
Total number of stomachs with food (n_{full})	23	23	38	16
Feeding intensity (n_{full}:n_{tot} × 100)	71.9%	92.0%	88.4%	72.7%
Standardized stomach fullness (g mm^{-3})[a]	9.7 (2.4)	13.0 (3.3)	**9.1 (1.5)**	**4.0 (1.2)**
Reserve status	**Inside**	**Outside**	**Inside**	**Outside**
Total number of stomachs analysed (n_{tot})	9	48	28	37
Total number of stomachs with food (n_{full})	5	41	24	30
Feeding intensity (n_{full}:n_{tot} × 100)	55.6%	85.4%	85.7%	81.1%
Standardized stomach fullness (g mm^{-3})[a]	8.3 (4.4)	11.7 (2.2)	**9.9 (2.0)**	**5.5 (1.1)**
Habitat type	**Mud**	**Edge**	**Mud**	**Edge**
Total number of stomachs analysed (n_{tot})	26	31	38	27
Total number of stomachs with food (n_{full})	20	26	30	24
Feeding intensity (n_{full}:n_{tot} × 100)	76.9%	83.9%	78.9%	88.9%
Standardized stomach fullness (g mm^{-3})[a]	10.1 (3.0)	12.0 (2.6)	6.6 (1.2)	8.5 (2.1)

Significant results for monkfish TFI are emboldened (significant *t*-tests, $p < 0.05$).
[a]Standardized stomach fullness was calculated using the equation (total prey weight$_{(g)}$/L_T^3) × 10^7. Standard errors (+1 s.e.) are provided in parentheses.

Table 3. Contribution of six major prey groups to the diet of juvenile ($\leq$300 mm L_T) monkfish caught in trawl surveys conducted in vs. out of the WGMCA on mud bottom and at the edge of structured habitat.

Prey group	In						Out					
	Mud			Edge			Mud			Edge		
	FO (%)	P (%)	PFI	FO (%)	P (%)	PFI	FO (%)	P (%)	PFI	FO (%)	P (%)	PFI
Animal tissue (unidentified)	0.0	0.0	0.00	33.3	3.1	0.41	15.0	3.7	**0.27**	7.1	0.9	0.14
Pelagic fish	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00
Demersal fish	50.0	100.0	**6.20**	66.7	83.1	**10.17**	75.0	93.3	**10.81**	60.7	95.5	**10.98**
Zooplankton	0.0	0.0	0.00	0.0	0.0	0.00	5.0	0.0	0.01	17.9	0.1	0.06
Shrimp	0.0	0.0	0.00	0.0	0.0	0.00	20.0	3.0	0.19	17.9	3.5	**0.78**
Cephalopods	0.0	0.0	0.00	33.3	13.8	**1.83**	0.0	0.0	0.00	0.0	0.0	0.00
Total number of stomachs analysed (n_{tot})		6			3			20			28	
Total number of stomachs with food (n_{full})		3			2			17			24	
Feeding intensity (n_{full}:n_{tot} × 100)		50.0%			66.7%			85.0%			85.7%	
Mean TFI (g mm^{-3})		6.20			12.41			11.28			11.97	

FO, P, and mean PFI of each major prey group are provided. Emboldened values indicate the two most important prey groups based on mean PFI to the diet of monkfish. Feeding intensity and mean TFI results are also provided.

Condition factor

In contrast to monkfish abundance and size patterns, closure status did not affect the condition of monkfish. However, both season and habitat, but not their interaction, significantly affected monkfish condition (season: $F_{[1,113]} = 9.8$, $p = 0.002$; habitat: $F_{[1,113]} = 5.1$, $p = 0.026$). Monkfish condition was greater in spring than in autumn (Figure 5a). Meanwhile, the condition of monkfish caught at the edge of rock bottom was greater than that of those caught in the mud (Figure 5b). Prey consumption (as measured by TFI) by monkfish was weakly correlated with their condition (Figure 6a; $r^2 = 0.16$, $p < 0.0001$). For the 71 monkfish that consumed demersal fish, demersal fish PFI

explained even less of the variation in condition (Figure 6b; $r^2 = 0.08$, $p = 0.015$). Pelagic fish PFI was not significantly correlated with monkfish condition (Figure 6c; $r^2 = 0.14$, $p = 0.15$). However, a limited sample size (just 15 monkfish consumed pelagic fish) inhibited our ability to explore this relationship.

Discussion

Marine closures can effectively reduce human activities such as trawling and dredging, which disturb habitat. However, whether they also achieve the goal of promoting populations of harvested species by providing EFH for critical stock components remains the central question governing the efficacy of this widely used
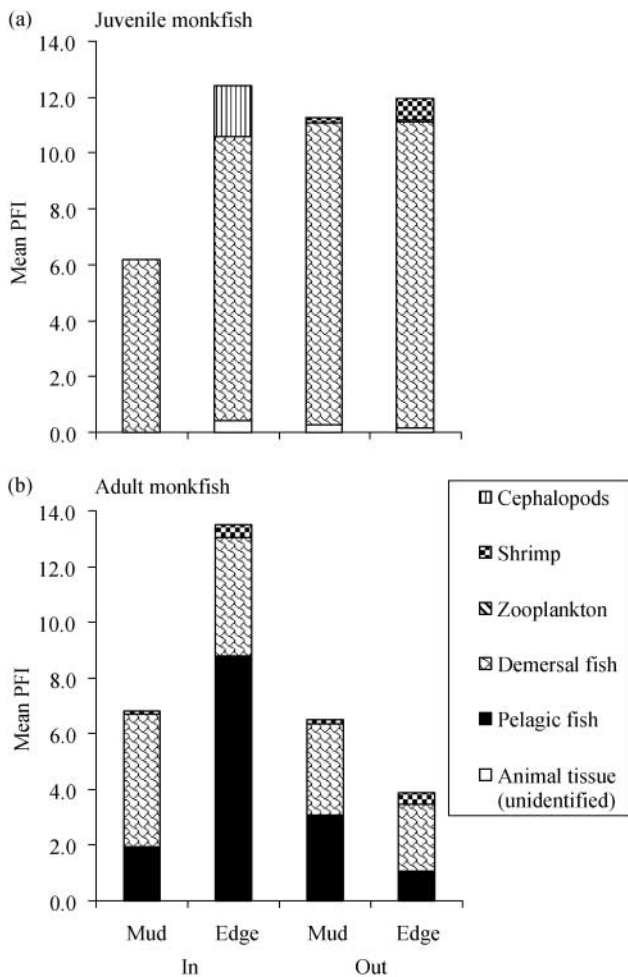
Figure 4. Contribution of six major prey groups to the diet of (a) juvenile and (b) adult monkfish captured in vs. out of the WGMCA on mud bottom and bottom along the edges of boulder fields and rock ledges.

fisheries management tool. The WGMCA is the single largest closure in the Gulf of Maine. Yet, understanding of whether the WGMCA is important habitat for monkfish remains limited even though monkfish are currently the most valuable groundfish species landed in New England.

We found unexpectedly that juvenile monkfish were far more abundant outside the closure (Figure 3) than in it. This suggests that the northern portion of the WGMCA may not be important nursery habitat for this species, despite its having been closed for 8 years when this study was conducted. The greater abundance of juvenile monkfish outside the closure suggests that prey may be concentrated outside the WGMCA in trawled areas. This hypothesis is supported by the fact that juvenile monkfish feeding intensity was much higher outside the closure (Table 3) than inside. Juvenile monkfish caught outside the closure consumed far more crustaceans and demersal fish such as four-bearded rockling than those captured inside the reserve. Whether dietary differences in juvenile monkfish caught in vs. out of the closure are a function of (i) trawling activity disturbing the bottom and increasing the availability of prey resources or (ii) site-specific differences in prey resources independent of the closure remains unknown. Therefore, further investigation of the impact of the closure and the removal of trawling activity on monkfish prey resources is merited.

The closure did not affect juvenile monkfish condition, suggesting that the influence of closure status on their diet is not substantial. This apparent disconnect between diet and condition could also be a consequence of a density-dependent response to greater food availability that eventually results in increased competition for food outside the closure. However, the few juvenile monkfish caught inside the closure (nine in total) may have limited our ability to explore the effects of the closure on the link between diet and condition of juvenile monkfish.

Although fisheries managers have largely reduced fishing mortality from commercial fishing activities inside the WGMCA, adult monkfish did not differ in abundance in vs. out of the closure. Counter to the situation for juveniles, adult monkfish consumed

Table 4. Contribution of six major prey groups to the diet of adult ($\geq$301 mm L_T) monkfish caught in trawl surveys conducted in vs. out of the WGMCA on mud bottom and at the edge of structured habitat.

Prey group	In						Out					
	Mud			Edge			Mud			Edge		
	FO (%)	P (%)	PFI	FO (%)	P (%)	PFI	FO (%)	P (%)	PFI	FO (%)	P (%)	PFI
Animal tissue (unidentified)	6.7	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00
Pelagic fish	13.3	18.1	**1.92**	46.2	74.1	**8.79**	21.7	53.0	**3.10**	14.3	15.2	**1.05**
Demersal fish	53.3	79.3	**4.75**	61.5	23.3	**4.25**	47.8	45.0	**3.27**	57.1	78.2	**2.43**
Zooplankton	0.0	0.0	0.00	0.0	0.0	0.00	4.3	0.0	0.00	0.0	0.0	0.00
Shrimp	26.7	2.5	0.15	30.8	2.6	0.47	17.4	2.0	0.15	42.9	6.6	0.40
Cephalopods	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00
Total number of stomachs analysed (n_{tot})		15			13			23			14	
Total number of stomachs with food (n_{full})		12			12			18			12	
Feeding intensity (n_{full}:n_{tot} × 100)		80.0%			92.3%			78.3%			85.7%	
Mean TFI (g mm^{-3})		6.83			13.52			6.52			3.88	

FO, P, and mean PFI of each major prey group are provided. Emboldened values indicate the two most important prey groups based on mean PFI to the diet of monkfish. Feeding intensity and mean TFI results are also provided.
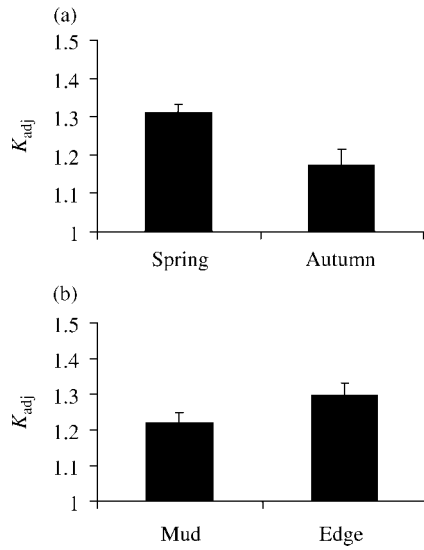
Figure 5. The effects of (a) season and (b) habitat on the condition factor (K_{adj}, length-corrected) of monkfish caught in bottom-trawl surveys in the western portions of the Gulf of Maine. Error bars represent +1 s.e.

more prey inside the closure, and this effect was most pronounced on the edge of structured habitat. Once again, the closure did not affect monkfish condition, suggesting that these dietary differences are ephemeral.

Monkfish are a slow-growing demersal fish species which may not respond quickly to management actions such as the implementation of marine closures. Closures may contain important foraging grounds for juvenile and adult groundfish, including monkfish. With fewer disturbances inside the WGMCA, benthic community structure should be more complex than habitats that are trawled routinely (Collie, 1998; Watling and Norse, 1998). This study found that adult monkfish consumed more prey inside the WGMCA when located on the edges of structured habitat, which have responded to the absence of bottom-disturbing mobile gear inside the closure (R. Grizzle, unpublished data). However, it is still unclear whether habitat recovery in the WGMCA benefits local monkfish populations, because monkfish abundance was lower (juveniles) or equal (adults) inside than out of the closure, and closure status did not affect monkfish condition.

By focusing this study in the northern portions of the WGMCA, we cannot fully address whether these results are germane to the entire WGMCA. However, the habitats (mud, cobble, and rock ledge) and bottom depths that characterize the northern portions of the WGMCA are common farther south in the closure, and monkfish are ubiquitous throughout it. Investigations of the effects of more southern portions of the WGMCA on monkfish would assist coastal regulators determine whether any part of the closure benefits monkfish populations in the Gulf of Maine. A second possible limitation of this study is that it was conducted over only one annual cycle, so by design is incapable of detecting interannual variability. Additional investigations of the effects of the WGMCA and key habitats on the distribution, abundance, and feeding ecology of monkfish will be useful in verifying whether the trends detected in this study are consistent through time. Sampling was conducted along the edges rather than within boulder and rock-ledge habitat, which
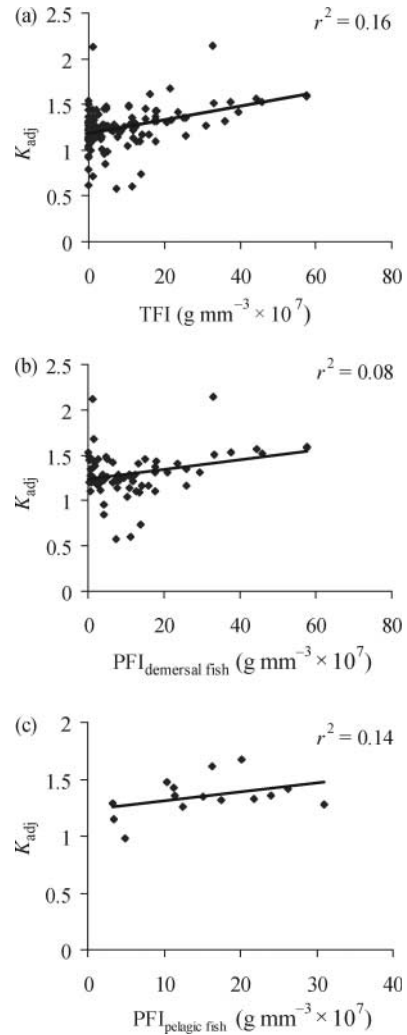

Figure 6. The relationships between condition factor (K_{adj}) and (a) TFI, (b) $PFI_{demersal\ fish}$, and (c) $PFI_{pelagic\ fish}$ for monkfish living in the western portions of the Gulf of Maine.

potentially limited our ability to detect responses. It is possible that differences in the diet and condition of adult monkfish are more pronounced within these complex habitats inside the closure. However, it seems unlikely that we would have detected positive closure effects on juvenile monkfish had we sampled in these habitats, because we found that mud bottom next to boulder and ledge bottom had positive effects on monkfish diet and growth, and these effects were independent of closure status. Further investigation regarding how these habitats affect the diet, growth, and mortality of monkfish is merited given the extremely high value of the fishery coupled with the paucity of information currently available on essential monkfish habitat.

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