

Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank

Brian E. Smith^{1,*}, Jeremy S. Collie², Nicole L. Lengyel²

¹NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543, USA

²University of Rhode Island, Graduate School of Oceanography, 215 South Ferry Road, Narragansett, Rhode Island 02882, USA

ABSTRACT: Feeding by demersal fishes on benthic invertebrates constitutes an important link between fishery resources and continental shelf habitats. However, concurrent sampling of demersal fish diets and benthic invertebrate prey fields has been limited, particularly in relation to chronic bottom fishing disturbance on continental shelves worldwide. Here, we quantified differences in the epibenthic invertebrate and fish communities between sites with contrasting levels of disturbance from mobile bottom fishing gear for 2 gravel regions of Georges Bank in the northwest Atlantic. The main objectives were to compare a suite of biological indices for epibenthic invertebrates, demersal fishes, and fish diets across year and level of fishing disturbance. The fishes selected for diet comparisons included winter skate *Leucoraja ocellata*, little skate *L. erinacea*, Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, winter flounder *Pseudopleuronectes americanus*, and longhorn sculpin *Myoxocephalus octodecemspinosus*. Three baseline benthic epifaunal indices, species richness, abundance (no. l⁻¹), and biomass (g l⁻¹), were lower in the heavily fished areas; however, evenness was higher in these areas. The lengths of haddock, Atlantic cod, and winter flounder tended to be larger at the undisturbed sites. Fish stomach contents differed significantly among habitats for 3 benthivores: haddock, winter flounder, and longhorn sculpin; diets were more highly correlated with the benthic fauna within than among sites, which indicated site-specific feeding. In several cases, prey that contributed to the diet dissimilarity between sites were benthic epifauna most sensitive to the impact of bottom fishing disturbance; thus, the availability of epibenthic prey was determined by this disturbance.

KEY WORDS: Trophic ecology · Anthropogenic impact · Benthic habitats · Marine protected area · Prey availability · Northwest Atlantic Ocean

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INTRODUCTION

Demersal fishes depend on benthic habitats for food and for protection from predation provided by emergent epifauna and abiotic structure (McCormick 1995, Tupper & Boutilier 1995, Gregory & Anderson 1997). In the USA, the Sustainable Fisheries Act of 1996 required essential fish habitat to be identified for all federally managed species. Despite the recognized importance of habitat, few studies

have quantified the functional importance of habitat for fish production (e.g. Lindholm et al. 1999, 2001). Quantifying these links is of practical importance because of the prevalence of anthropogenic disturbance to continental shelf habitats and concern over its effects on ecosystem function particularly for the benthos (Hiddink et al. 2006, Allen & Clarke 2007, Olgsgard et al. 2008).

Disturbance from mobile bottom-fishing gear (i.e. scallop dredges and demersal fish trawls) has

*Email: brian.smith@noaa.gov

received considerable attention due to the physical effects on the substratum and ecological effects on benthic communities (e.g. Auster et al. 1996, Kaiser & Spencer 1996, Jennings et al. 2001). In particular, bottom fishing has been shown to have immediate environmental consequences, including the displacement of physical structures (e.g. boulders and cobble), and the damage or removal of benthic biota (Jones 1992, Freese et al. 1999). Disturbance to benthic fauna depends strongly on substrate type (Auster & Langton 1999, Collie et al. 2000b, Kaiser et al. 2006) and taxonomic identity (e.g. pagurids, Ramsay et al. 1996). Additional effects also include increased scavenging by fishes and invertebrates on local trawl-induced carrion, although these occurrences generally tend to be short in duration (Kaiser & Spencer 1994, Ramsay et al. 1998). By comparison, long-term effects of bottom fishing on continental shelves can cause reductions in benthic biodiversity, abundance, and biomass, and changes in species composition (Tillin et al. 2006, Hinz et al. 2009, Svane et al. 2009).

Despite extensive efforts to quantify the direct effects of persistent bottom fishing on the benthic epifaunal community, few studies worldwide have examined the secondary effects, such as altered predator-prey dynamics, by concurrently sampling the available prey, predator, and diet fields (de Juan et al. 2007, Fanelli et al. 2009). Nevertheless, declines in

benthic epifaunal production in response to bottom fishing have been demonstrated (e.g. North Sea, Jennings et al. 2001), and there is evidence of fish growth rates and condition being altered by fishing disturbance (Choi et al. 2004, Shephard et al. 2010, Hiddink et al. 2011).

On Georges Bank in the northwest Atlantic Ocean, studies have documented the effects of bottom fishing on benthic communities. These effects include reductions in abundance, biomass and species richness (Collie et al. 1997), reduced epifaunal cover (Collie et al. 2000a), and reduced benthic production (Hermesen et al. 2003). Spatial comparisons have been made between the benthic communities in areas open and closed to fishing (Collie et al. 2005, Asch & Collie 2008). Work that has addressed the secondary effects of bottom fishing on the fish communities of Georges Bank has been limited (Link et al. 2005). The present study is one of the first to survey the benthic epifauna, demersal fish communities and fish diet compositions in areas with contrasting levels of bottom fishing disturbance.

Georges Bank is a shallow submarine plateau of the northeast US continental shelf that occupies an area of approximately 40 000 km² inside the 100 m isobath (Fig. 1). This area has been subjected to commercial fishing pressures spanning 4 centuries (German 1987), and the effects of overfishing on demersal fish assemblages are well documented (e.g. Fogarty

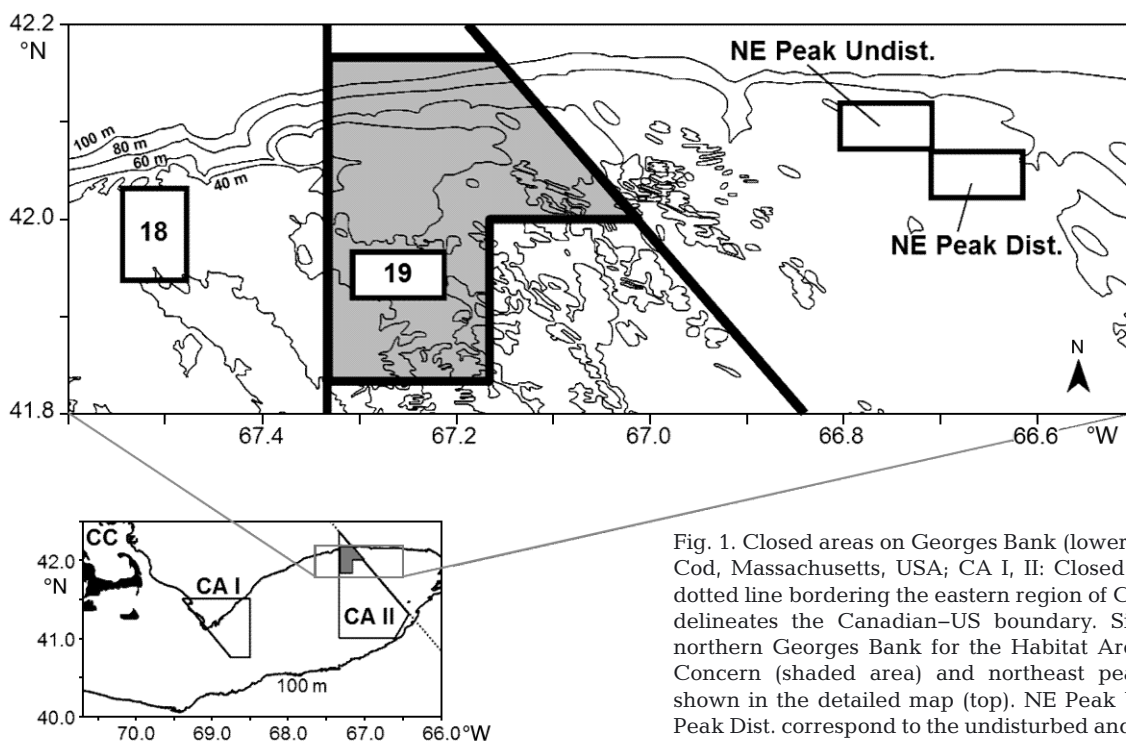


Fig. 1. Closed areas on Georges Bank (lower left). CC: Cape Cod, Massachusetts, USA; CA I, II: Closed Area I, II. The dotted line bordering the eastern region of CA II in the inset delineates the Canadian-US boundary. Site locations of northern Georges Bank for the Habitat Area of Particular Concern (shaded area) and northeast peak regions are shown in the detailed map (top). NE Peak Undist. and NE Peak Dist. correspond to the undisturbed and disturbed sites of the northeast peak, respectively

& Murawski 1998, Link et al. 2002). The sediment on Georges Bank is generally composed of sand, although regions of gravel and mixed gravel–sand substrates are distributed throughout the Bank (Twichell et al. 1987). Notably, the seafloor of the northeastern region of Georges Bank consists of gravel pavements exceeding 3000 km² in area (Valentine & Lough 1991). These extensive gravel areas provide ideal places for attachment by sessile benthic epifauna (e.g. bryozoans, hydroids, and various tube-building polychaetes; Collie et al. 2000a). Furthermore, Lough et al. (1989) demonstrated a positive association between juvenile gadids (i.e. Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*) and these gravel deposits, suggesting their importance as a nursery habitat for food and protection. Attached epifauna contribute to the structural complexity available in areas undisturbed by chronic bottom fishing; this structure is in sharp contrast with highly disturbed areas in this northern region of the Bank (Asch & Collie 2008).

In December 1994, the New England Fishery Management Council established 2 closed areas on Georges Bank (Closed Area I and Closed Area II) protecting approximately 25% (10 900 km²) of the total area of Georges Bank (Fig. 1). A Habitat Area of Particular Concern (HAPC) was also introduced within Closed Area II of northern Georges Bank to protect gravel habitat for juvenile Atlantic cod and haddock. The HAPC implementation was in direct response to specific concerns for habitat protection contained within the Sustainable Fisheries Act of 1996. The area closures prevented the use of all gears capable of retaining groundfish (trawls, scallop dredges, gill nets, and hook gear) and protect a diverse array of habitat types across the Bank (Murawski et al. 2000). Closed Area II has a southern region occupied by a generally smooth, sandy seafloor, and a northern region with extensive gravel pavement which includes the HAPC region (Valentine & Lough 1991, Theroux & Wigley 1998). The sediment of the northeastern region of Georges Bank (i.e. northeast peak) is an eastward extension of the gravel pavement from the HAPC, but additionally contains fields of glacial erratics which discourage bottom fishing (Valentine & Lough 1991).

The overall objective of this study was to investigate links between fish feeding and benthic habitats at spatial scales relevant to marine spatial planning (e.g. 50 km²). Specifically, we tested for differences in community composition of non-colonial benthic epifauna, and the length and diet composition of demersal fishes for 2 separate regions of Georges Bank with

sites subjected to contrasting levels of bottom fishing pressure. The hypothesis was that differences in benthic epifaunal composition between sites caused by bottom fishing are reflected in fish diets. We also hypothesized that fish length distributions are not equal between sites with contrasting levels of bottom fishing pressure.

MATERIALS AND METHODS

Data collection

Sampling occurred from 2004 to 2008 within 2 regions on Georges Bank: the northeast peak in Canadian waters, and the Habitat Area of Particular Concern (HAPC) of Closed Area II and surrounding US waters (Table 1, Fig. 1). Within these 2 regions, sites were selected to compare areas with contrasting levels of bottom fishing disturbance while controlling the natural variability of benthic epifaunal community composition due to substrate type, depth, and presence of the invasive ascidian *Didemnum vexillum* (see Valentine et al. 2007). Site designations within these gravel pavement regions were generally based on a continuation of work by Collie et al. (1997, 2005). In brief, 4 study sites (Table 1, Fig. 1; approximately 5 × 10 km) were chosen based on sediment maps (Valentine et al. 1993), evidence of chronic bottom fishing disturbance (i.e. trawl door and scallop dredge marks) from side-scan sonar surveys, and fishing effort data. The depth ranges of sampling sites were approximately 45 to 55 m for the HAPC and 70 to 78 m for the northeast peak region.

Table 1. Detailed summary of community sampling (benthic epifauna, demersal fish, and fish diet) for northeast peak and Habitat Area of Particular Concern (HAPC) regions of Georges Bank by sampling date. BF: sampling of the benthic epifaunal and demersal fish communities. Dist.: disturbed; Undist.: undisturbed. See Fig. 1 for site locations

Sampling dates	Northeast peak		HAPC	
	Dist.	Undist.	Site 18 (Dist.)	Site 19 (Undist. ^a)
Nov 2004			BF	
Aug/Sept 2005			BF	BF
Aug/Sept 2006	BF	BF	BF	BF
July 2007	BF	BF	BF	BF
Aug 2008	BF	BF	BF	BF

^aSite 19 closed to groundfishing as of December 1994

Fishing effort data for the northeast peak region (Canadian waters) were derived from logbook reports provided by the Canada Department of Fisheries and Oceans for the years 1992 to 2001 (Collie et al. 2005). These data helped categorize sites as either undisturbed (0 to 1 d yr⁻¹ of scallop dredge effort) or disturbed (0 to 10 d, i.e. averaging ≥ 3 d yr⁻¹ of scallop dredge effort). The extensive and continuous presence of colonial epifauna (e.g. hydrozoans and bryozoans) in benthic samples from the undisturbed site of the northeast peak region served as a secondary observation, confirming contrasting levels of fishing disturbance as shown recently for this region of Georges Bank (Asch & Collie 2008).

When sampling within US waters, Site 19, inside the closed area, was classified as undisturbed. Sampling stations within this area were at least 3.7 km (2 nautical miles) from the boundary to ensure minimal disturbance from illegal fishing. Site 18, outside of the closed area, was classified as disturbed. Scallop effort data from 1998 to 2005 were used to confirm disturbance-level designations: undisturbed (sites with an average of <10 h fished yr⁻¹) and disturbed (sites with an average of >120 h fished yr⁻¹).

Two to 3 benthic epifaunal samples were taken at one location at each site per year. A 1 m wide Naturalists' dredge with a 6.4 mm mesh liner was deployed at each station to sample the benthic epifauna. Tow duration was approximately 30 to 180 s to avoid overfilling the catch liner (i.e. loss of sample). The sample was brought on deck and organisms were manually sorted from the substrate. Sub-sampling was employed for gravel samples with large volumes (i.e. >100 l). After sorting for organisms, substrate volume was estimated by shoveling the gravel into 9 l buckets. One 9 l bucket of substrate from each sample was sieved through a 5 mm screen to collect any organisms neglected during the initial sort and later scaled to the total volume sampled. The biological samples were preserved with 5% buffered formalin and filtered seawater.

In the laboratory, benthic epifaunal samples were sorted and identified to the lowest taxon feasible (generally to species). The wet mass (± 1 mg) of each taxon was measured after blotting, and the numerical abundance of free-living species was recorded as appropriate (e.g. whole organisms, ophiuroid discs, and polychaete heads). Colonial fauna (e.g. ascidians, hydroids, and bryozoans) and solitary benthos too small to be sampled by the dredge mesh (e.g. caprellids and other amphipods) were removed prior to each analysis.

Concurrent with the benthic epifaunal sampling at each site, a standardized National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC) #36 Yankee otter trawl equipped with 41 cm diameter rollers was deployed at 1 to 4 stations per site for 15 min in 2004 to 2006 and 30 min in 2007 with a towing speed of 6.5 km h⁻¹ (3.5 knots). In 2008, a standardized NMFS, NEFSC 4-seam otter trawl with 41 and 36 cm diameter rollers was used at 2 to 3 stations at each site for 15 min and a speed of 5.6 km h⁻¹ (3.0 knots). The catches were sorted to species and all fishes were weighed (wet mass; 0.01 kg). Species selected for diet sampling included winter skate *Leucoraja ocellata*, little skate *L. erinacea*, Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, winter flounder *Pseudopleuronectes americanus*, and longhorn sculpin *Myoxocephalus octodecemspinosus*. Species were selected because of their abundance in the trawls and because they were known benthivores (Smith & Link 2010). These species were enumerated and individually weighed (wet mass; 0.001 kg). Biological sampling consisted of length–frequency data, total mass, and stomach content analysis. Stomach samples were examined at sea volumetrically and converted to mass following the methods described by Link & Almeida (2000) or individually preserved in 10% formalin and filtered seawater for laboratory processing. In the laboratory, preserved stomachs were emptied and their contents rinsed in fresh water and identified to the lowest taxon feasible. Wet masses (± 0.01 g) were recorded for each taxon.

Data analysis

Data from the northeast peak and HAPC regions were analyzed separately, because of the regional differences in depth and habitat management plans previously noted. This analytical approach was adhered to for the various datasets (e.g. benthic epifauna, demersal fish, and fish diet).

Baseline benthic epifauna

A suite of ecological indices was used to compare the benthic epifauna between sites disturbed and undisturbed by chronic bottom fishing within each region of Georges Bank. Numerical abundances and biomasses (standardized per unit volume of substrate sampled) for the total amount (species combined) and the 10 most abundant species of benthic epifauna, and the diversity indices species richness (S)

and evenness ($e^{H'}S^{-1}$, Buzas & Gibson 1969) were estimated; exponentiated indices were calculated from base 2 logarithms. A 2-way analysis of variance (ANOVA) was used to test for statistical differences ($\alpha = 0.05$) between means across the fixed effects: year and fishing disturbance level. Tests of homogeneity of variance (Bartlett's method, Sokal & Rohlf 1995) and residual normality (Shapiro-Wilks, Dean & Voss 1999) were applied with SAS, version 9.1 (SAS Institute). In general, log transformations were used to satisfy the model assumptions previously described. If unequal variances among factors were detected following transformation, Satterthwaite's approximation (PROC MIXED in SAS, Dean & Voss 1999) was performed to test for mean differences in ecological indices while effects remained fixed.

Demersal fish

Differences in demersal fish length–frequency distributions were assessed between sites, within years (2005 to 2008), and independently for each sampling region for the 6 species with a 2-sample Kolmogorov-Smirnov test. This method determines if the maximum vertical distance of the empirical distribution functions between the 2 samples is significant ($\alpha = 0.05$) (Conover 1999). Medians are represented by 50% of the cumulative distribution function. Species with <10 individual lengths for each species–site per year contrast were removed prior to analysis as suggested by Sokal & Rohlf (1995).

Fish diet

Prior to evaluating stomach sample size sufficiency (Ferry & Caillet 1996, Cortés 1997), a 2-sample Kolmogorov-Smirnov test was used to compare predator length distributions for individuals with diet data available across sites within each region. When statistical differences in length distributions were discovered ($\alpha = 0.05$), individuals were removed until a length-matched sample of fish was found to eliminate any bias associated with ontogenetic diet shifts.

The adequacy of stomach sample sizes was assessed with trophic diversity curves by estimating the mean cumulative Shannon-Wiener diversity of stomach contents plotted as a function of stomach number. The order of stomachs sampled was randomized 100 times, and cumulative diversity curves were constructed separately for each species–site combination considered for analysis. The criteria for

asymptotic diversity was met when the slope of the 5 preceding mean cumulative values relative to the total mean cumulative Shannon-Wiener diversity was ≤ 0.02 , which was similar to, albeit more conservative than, recent fish trophic studies (e.g. Koen Alonso et al. 2002, Belleggia et al. 2008, Braccini 2008). Approximately 20 to 40 fish stomachs for each species–site combination were required to reach asymptotic diversity. In order to preserve necessary stomach sample sizes per species group, data were pooled across years by species and site.

Fish diets were compared across fishing disturbance level independently by species and region. The total stomach content index used in this study, total stomach content (g) standardized by body mass (g), is similar to the gut fullness index used by Hall et al. (1995). To test for statistical differences in total stomach content between sites ($\alpha = 0.05$), a Kruskal-Wallis test was applied following transformation (arcsine square root) to stabilize variance between fishing disturbance levels (Cortés 1997).

The effect of fishing disturbance level on fish diet compositions within each sampling region was tested with the multivariate techniques in the PRIMER statistical package (version 6.1.11, Clarke & Gorley 2006). Prey data were taken as a proportion of individual total stomach content. Dissimilarities in diet compositions by mass for dominant prey items (i.e. $\geq 85\%$ of total fish diet by mass represented for each region) were assessed with 1-way analysis of similarities (ANOSIM; 9999 permutations; $\alpha = 0.05$). Similarity indices were based on the Bray-Curtis similarity index following arcsine square root data transformation for these proportional data (Sokal & Rohlf 1995). The SIMPER (SIMilarity PERcentages) routine was performed when the ANOSIM global R statistic was significant, identifying those prey taxa that contributed the most to the dissimilarity between species groups.

Given the benthic epifaunal (i.e. prey availability) and fish diet sampling, the correlation between fish diet and benthic epifauna within-site versus across-sites (e.g. Fish diet/Site 18–Benthic epifauna/Site 18 versus Fish diet/Site 18–Benthic epifauna/Site 19) was examined with Spearman's rank correlation coefficient (ρ). First, biomass data for the benthic epifauna were screened to eliminate species not adequately sampled by the Naturalists' dredge as previously reported. Additionally, rare species in the environment (i.e. frequency of occurrence <2 per site throughout the time series) were removed prior to analysis. To facilitate taxa comparisons between fish diet and benthic epifauna, species were combined

where appropriate to create taxonomic groupings that complemented the lower resolution prey data (e.g. *Pandalus montagui* and *Dichelopandalus leptocerus* to Family Pandalidae). Diet and benthic epifauna data were taken as proportions per individual stomach and per station respectively.

The selection of taxa for correlating the multivariate datasets followed the methods outlined for ANOSIM/SIMPER above. To eliminate known taxa that would have confounded the analysis due to their 'coarse' taxonomic level, Decapoda crab, and other taxa contributing <7% to the overall diet dissimilarity between sites were excluded. However, a minimum of 5 taxa were included for each predator to provide statistical power, so for haddock diet, taxa contributing <3% to the diet dissimilarity and Decapoda crab were excluded. Winter flounder diet posed an exception to this rule whereby the limited number of overlapping taxa between the Naturalists' dredge and diet permitted only 4 taxa for the analysis. Randomization tests were developed with the R statistical package (version 2.12.2, R Development Core Team 2011) to evaluate the significance of the difference between the original correlation coefficient (within-site fish diet and benthic epifauna) and zero ($\alpha = 0.05$). The diet datasets for each species–site combination were correlated with a randomly drawn sample without replacement from the 2 benthic datasets (i.e. Sites 18/19 or northeast peak undisturbed/disturbed; 9999 iterations). Similarity matrices were built from the Bray-Curtis similarity index following arcsine square root data transformation. To minimize extraneous results, correlation coefficients and respective probabilities were only reported for those fish species–site combinations with significant differences in feeding habits due to a fishing disturbance effect.

RESULTS

Baseline benthic epifauna

Northeast peak region

Total abundance (no. l^{-1}) and biomass (g l^{-1}) of benthic epifauna were generally greater at the undisturbed site of the northeast peak region; however, the respective Year \times Disturbance level interaction terms were significant given increases in these indices over the 3 yr time series at the disturbed site (Table 2, Fig. 2A,B). The top 10 abundant benthic species examined for this region included *Asterias*

Table 2. Analysis of variance table for total abundance (no. l^{-1}), total biomass (g l^{-1}), species richness (S), and evenness ($e^{H^*} S^{-1}$) for the benthic epifauna of the northeast peak and Habitat Area of Particular Concern (HAPC) regions. Factors included Year, Disturbance level and Year \times Disturbance level; values were calculated from Type-III sums of squares

	df	Mean square	F	p
Northeast Peak				
Log (Abundance)				
Year	2	0.576	2.080	0.188
Disturbance level	1	25.635	92.390	< 0.001
Year \times Disturbance level	2	1.399	5.040	0.038
Residual	8	0.277		
Biomass				
Year	2	1428.080	1.430	0.294
Disturbance level	1	5429.885	5.450	0.048
Year \times Disturbance level	2	5104.281	5.120	0.037
Residual	8	996.298		
Species richness (S)				
Year	2	16.804	0.780	0.489
Disturbance level	1	326.344	15.220	0.005
Year \times Disturbance level	2	8.304	0.390	0.691
Residual	8	21.438		
Evenness ($e^{H^*} S^{-1}$)				
Year	2	0.017	10.770	0.005
Disturbance level	1	0.063	41.250	< 0.001
Year \times Disturbance level	2	0.037	24.270	< 0.001
Residual	8	0.002		
HAPC				
Log (Abundance)				
Year	3	0.592	3.820	0.028
Disturbance level	1	0.287	1.850	0.190
Year \times Disturbance level	3	0.031	0.200	0.897
Residual	18	0.155		
Log (Biomass)				
Year	3	0.802	3.210	0.048
Disturbance level	1	1.236	4.950	0.039
Year \times Disturbance level	3	0.402	1.610	0.223
Residual	18	0.250		
Species richness (S)				
Year	3	72.697	3.440	0.039
Disturbance level	1	61.669	2.920	0.105
Year \times Disturbance level	3	86.837	4.110	0.022
Residual	18	21.135		
Evenness ($e^{H^*} S^{-1}$)				
Year	3	0.016	4.090	0.022
Disturbance level	1	0.047	11.840	0.003
Year \times Disturbance level	3	0.003	0.800	0.512
Residual	18	0.004		

vulgaris (northern sea star), *Buccinum undatum* (waved whelk), *Neptunea decemcostata* (ten-ridge whelk), *Pagurus acadianus* (Acadian hermit crab), *P. pubescens* (pagurid hermit crab), *Dichelopandalus leptocerus* (pandalid shrimp), *Eualus pusiulus* (hippolyte shrimp), *Hyas coarctatus* (decorator crab), *Ophiopholis aculeata* (brittle star), and *Thelepus cincinnatus* (tube-dwelling polychaete). Trends in

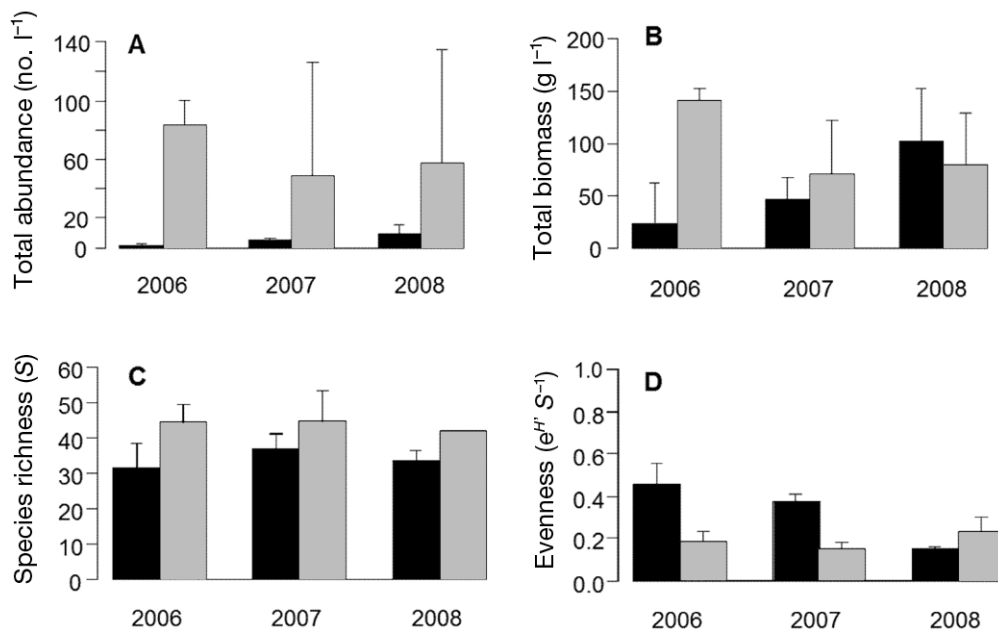


Fig. 2. (A) Total abundance (no. l⁻¹), (B) total biomass (g l⁻¹), (C) species richness (S), and (D) evenness ($e^{H'} S^{-1}$) of benthic epifauna for the northeast peak region, contrasting sites disturbed (black bars) and undisturbed (gray bars) for the years 2006 to 2008. Values represent means \pm 2 SE

the top 10 abundant benthic species generally followed the total abundance and biomass previously shown (Fig. 2) with markedly higher mean abundances (2-way ANOVA statistics for the disturbance effect provided) and, to a lesser degree, increased biomasses at the undisturbed site for *D. leptocerus* ($F_{1,4.7} = 8.61$, $p = 0.035$), *E. pusiolus* ($F_{1,8} = 42.06$, $p < 0.001$), *H. coarctatus* ($F_{1,8} = 73.56$, $p < 0.001$), *O. aculeata* ($F_{1,3.12} = 105.20$, $p = 0.002$), and *T. cincinnatus* ($F_{1,2.64} = 203.48$, $p = 0.001$). For *A. vulgaris* ($F_{1,8} = 10.31$, $p = 0.012$) and *B. undatum* ($F_{1,8} = 9.63$, $p = 0.015$), mean abundances and more noticeably mean biomasses were also consistently greater within the undisturbed site. Two exceptions to these trends were *P. adrianus* and *N. decemcostata*, which had no detectible differences in species abundance or biomass between sites. For each of the above indices, a significant year effect was only present for *D. leptocerus* given the Year \times Disturbance level effects aforementioned (abundance: $F_{2,4.70} = 28.24$, $p = 0.013$; biomass: $F_{2,8} = 8.69$, $p = 0.010$).

A statistically greater number of benthic species was observed in the undisturbed area of the northeast peak region (Table 2, Fig. 2C). Evenness had a significant Year \times Disturbance level effect: evenness at the disturbed site was greater than at the undisturbed site in 2006 and 2007 but lower in 2008 (Fig. 2D). Here, *Thelepus cincinnatus* dominated the samples in the undisturbed site, composing >40%

(often >50%) of the total abundance (no. l⁻¹). In the disturbed site, this species composed <5% of the total abundance per sample. Although the abundance of *Placopecten magellanicus* was low at the northeast peak sites (generally <0.8 l⁻¹), the significant Year \times Disturbance level effect for evenness in this region was likely caused by a 2008 dominance of this bivalve in the disturbed area (>40% of the total abundance per sample).

HAPC region

Given the contrast of Sites 18 and 19, the effect of fishing disturbance on the total abundance (no. l⁻¹) of benthic epifauna was non-significant (Table 2, Fig. 3A). In contrast, biomass tended to be higher at the undisturbed site (19) than the disturbed site (18), and this difference was significant (Table 2, Fig. 3B). The 10 most abundant epibenthic invertebrates for this region included *Asterias vulgaris* (northern sea star), *Crepidula plana* (flat slippersnail), *Pagurus acadianus* (Acadian hermit crab), *Placopecten magellanicus* (sea scallop), *Cancer irroratus* (Atlantic rock crab), *Crangon septemspinosa* (sand shrimp), *Dichelopandalus leptocerus* (pandalid shrimp), *Harmothoe* spp. (errant polychaete), *Nereis zonata* (errant polychaete), and *Strongylocentrotus droebachiensis* (green sea urchin). Sites 18 and 19 had significant

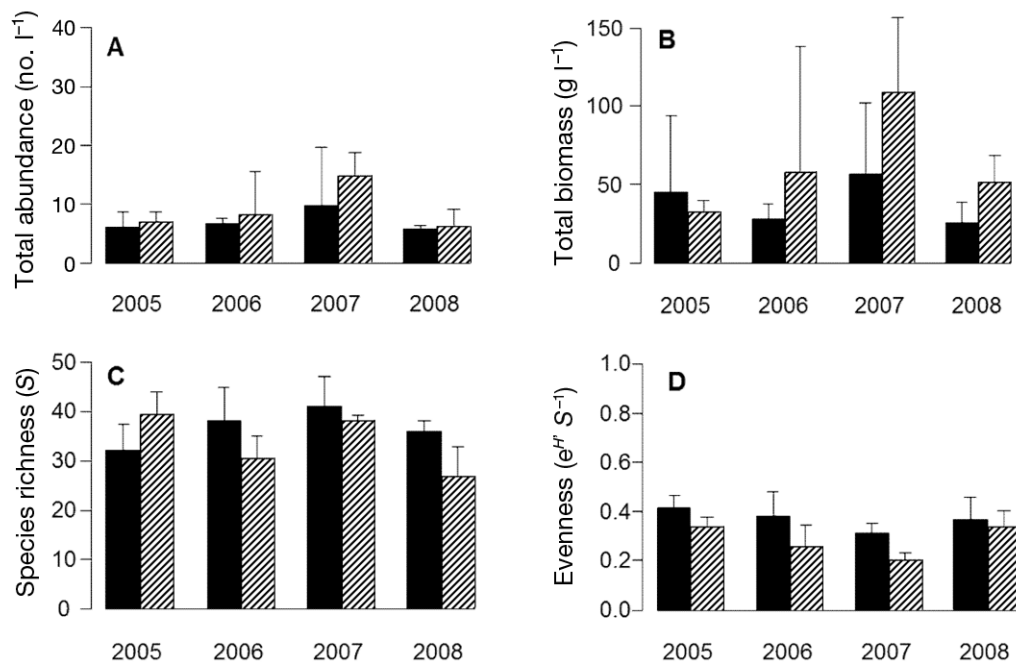


Fig. 3. (A) Total abundance (no. l⁻¹), (B) total biomass (g l⁻¹), (C) species richness (S), and (D) evenness (e^{H'} S⁻¹) of benthic epifauna for the Habitat Area of Particular Concern region, contrasting the disturbed Site 18 (black bars) and undisturbed Site 19 (diagonal lines) for the years 2005 to 2008. Values represent means ± 2 SE

disturbance level effects for 2 species, *A. vulgaris* and *S. droebachiensis*, according to 2-way ANOVA. *A. vulgaris* had a higher mean abundance in the undisturbed area (Site 19; $F_{1,18} = 9.56$, $p = 0.006$), but the difference in biomass was insignificant. *S. droebachiensis* had a larger mean abundance in the disturbed area (Site 18; $F_{1,17} = 9.60$, $p = 0.007$); for *S. droebachiensis* biomass, the Year × Disturbance level interaction was significant ($F_{3,17} = 3.39$, $p = 0.042$). Only one species, *C. septemspinosa*, had a statistically larger mean biomass at the undisturbed site (0.033 g l⁻¹ vs. 0.010 g l⁻¹ at the disturbed site; $F_{1,16} = 17.95$, $p = 0.001$). Significant year effects with observed trends in abundance or biomass at Sites 18 and 19 were seen for the following species: *C. septemspinosa* (decreasing biomass), and *Cancer irroratus*, *D. leptocerus*, and *Placopecten magellanicus* (increasing abundance and biomass). In summary, a significant fishing disturbance effect was detected for the abundance or biomass of only 3 benthic epifaunal species in this region.

Benthic epifaunal evenness and species richness exhibited significant disturbance level or interaction effects for Sites 18 and 19 (tested with 2-way ANOVA). Evenness diversity was higher at the disturbed Site 18 with the effect of disturbance level being significant (Table 2, Fig. 3D). A significant Year × Disturbance level interaction resulted for species

richness (Table 2). The variability of species richness was considerable among years, such that at Site 19, values were >37 species for the years 2005 and 2007, while in 2006 and 2008, <31 species were identified at this site (Fig. 3C). At Site 18, mean species richness ranged from a low of 32 in 2005 to >40 in 2007.

Demersal fish

Northeast peak region

Fishes sampled at the undisturbed site tended to be longer than at the disturbed site, although these differences were not significant every year (Fig. 4). In 2007, haddock and longhorn sculpin collected in the undisturbed area were significantly larger than those in the disturbed area (Fig. 4E,H). This trend in fish length distributions was also exhibited by Atlantic cod and haddock in 2008 (Fig. 4C,F). None of the species had larger individuals in the disturbed site of this region.

HAPC region

Some differences in the cumulative length–frequency distributions were detected across fishing

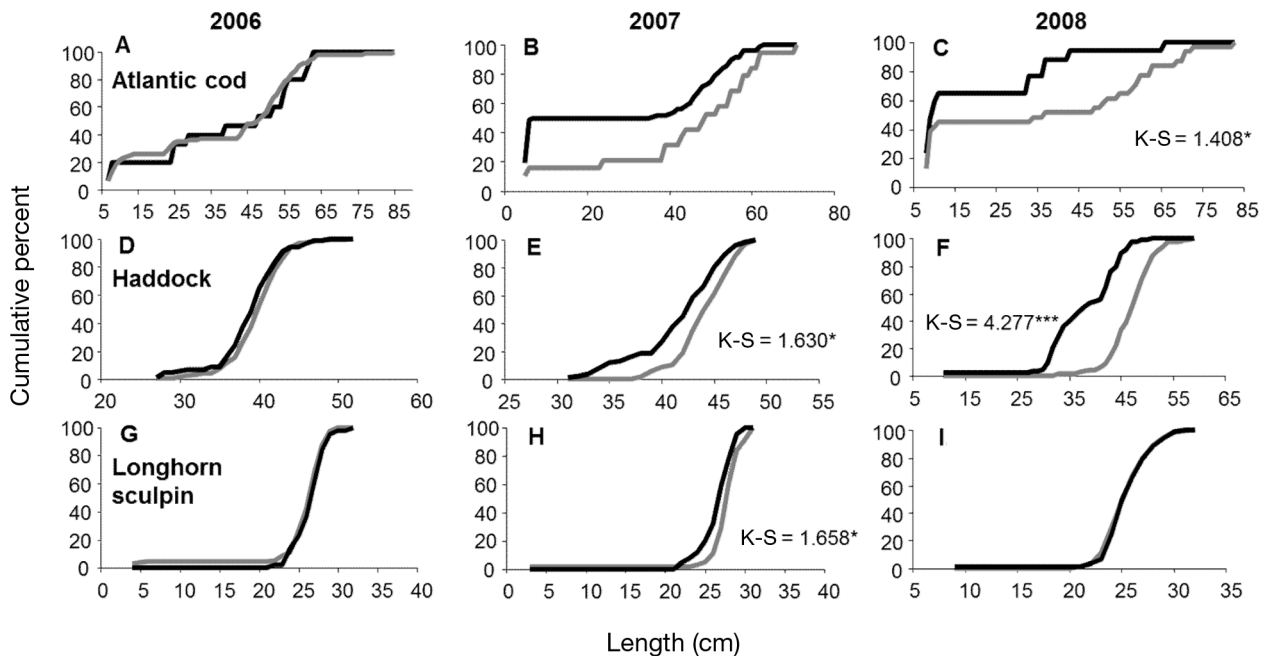


Fig. 4. Cumulative length–frequency distributions for (A,B,C) Atlantic cod *Gadus morhua*, (D,E,F) haddock *Melanogrammus aeglefinus*, and (G,H,I) longhorn sculpin *Myoxocephalus octodecemspinosus* for the years 2006 to 2008 in the northeast peak region. Black (disturbed) and gray (undisturbed) lines differentiate sites. The Kolmogorov-Smirnov (K-S) statistic denotes significance: * $p < 0.05$ and *** $p < 0.001$. Non-significant K-S statistics were excluded

disturbance level for the 5 demersal fishes of the HAPC region (Fig. 5). In 2005, larger haddock were observed in the undisturbed Site 19 (Fig. 5E). In 2008, winter flounder were also larger at Site 19 (Fig. 5H). In contrast, little skate length distributions in 2007 had a greater median length in the disturbed area (Site 18), although length differences were marginally significant (Fig. 5C). Longhorn sculpin collected in 2008 also showed a larger median length for individuals in the disturbed site (Fig. 5K). Despite these results, differences in fish length distributions between disturbance levels were sporadic for the HAPC.

Fish diet

Northeast peak region

Prey diversity curves for the 3 fishes sampled in the northeast peak were all asymptotically related to the numbers of stomachs sampled (Fig. 6A,B,C). Haddock and longhorn sculpin diets had higher cumulative diversities in the undisturbed area, although the opposite was true for Atlantic cod.

All 3 of the fish species examined in the northeast peak region ingested more food per stomach in the

area disturbed by bottom fishing when data were standardized by fish body mass. However, this difference was significant only for haddock (Kruskal-Wallis: $\chi^2 = 10.171$, $df = 1$, $p = 0.001$).

One-way ANOSIM revealed distinct differences in fish diet across fishing disturbance level for 2 of the 3 species studied in the northeast peak region (haddock: Global $R = 0.019$, $p = 0.022$; longhorn sculpin: Global $R = 0.094$, $p = 0.0005$). Trophic differences attributed to fishing disturbance were marginally insignificant for Atlantic cod (Global $R = 0.055$, $p = 0.052$). The SIMPER routine indicated an average dissimilarity between sites of 86% for haddock and 82% for longhorn sculpin. The predominant prey accounting for and contributing to >70% of this dissimilarity in haddock were *Ammodytes* spp., Gammaridea, and *Placopecten magellanicus* viscera (more abundant at the disturbed site); and Polychaeta, *Hyas* spp. crabs, and Ophiuroidea (more abundant at undisturbed site; Table 3). Similarly, larger prey contributions by epibenthic invertebrates in the undisturbed area were also demonstrated for longhorn sculpin, such that the major prey items contributing to the average site dissimilarity (>70%) were *Hyas* spp. crabs (more abundant at the undisturbed site); *Ammodytes* spp., and Pandalidae (more abundant at the disturbed site; Table 3).

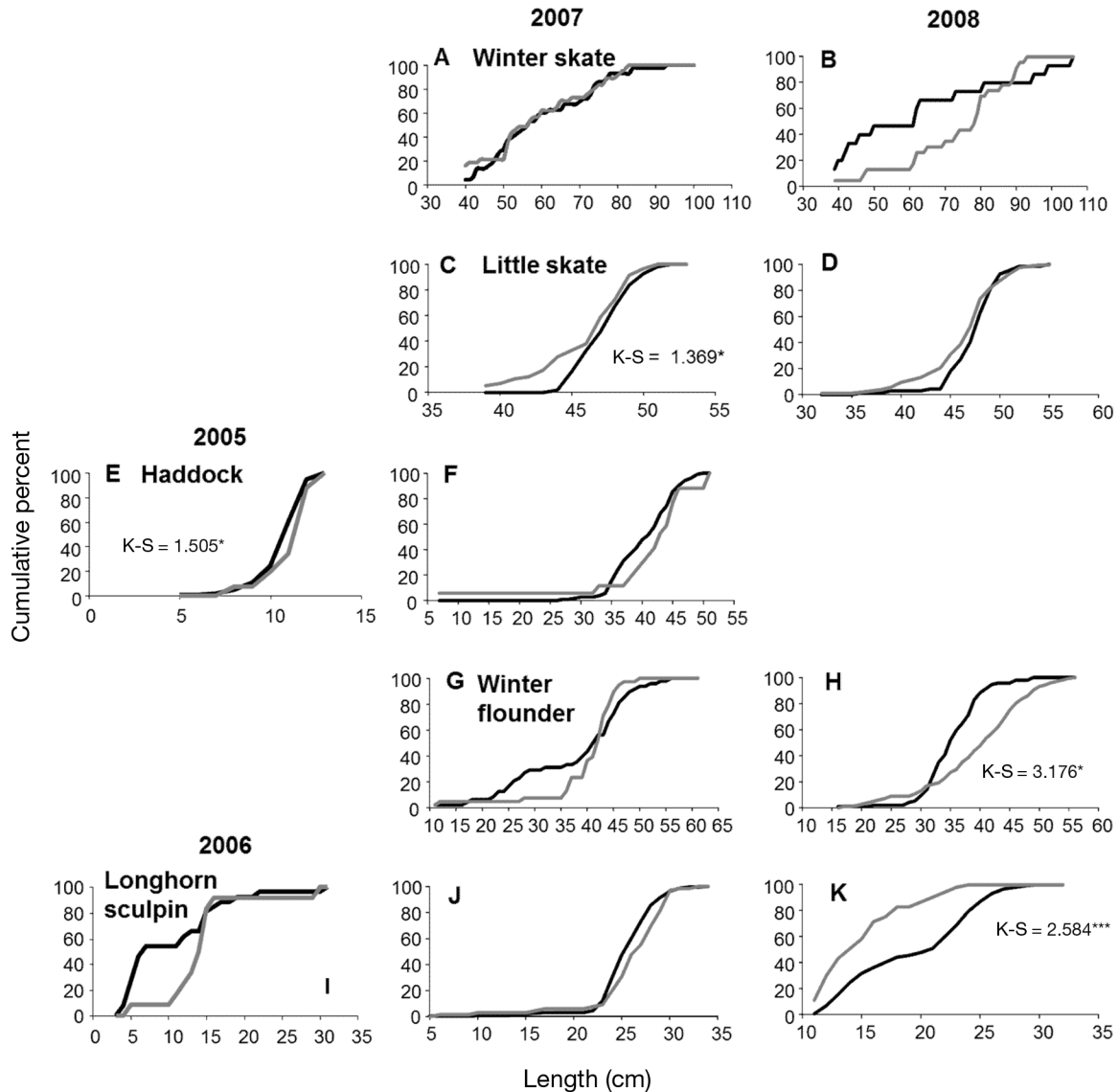


Fig. 5. Cumulative length–frequency distributions for (A,B) winter skate *Leucoraja ocellata*, (C,D) little skate *L. erinacea*, (E,F) haddock *Melanogrammus aeglefinus*, (G,H) winter flounder *Pseudopleuronectes americanus*, and (I,J,K) longhorn sculpin *Myoxocephalus octodecemspinosus* for the years 2005 to 2008 in the Habitat Area of Particular Concern region. Black (Site 18; disturbed) and gray (Site 19; undisturbed) lines differentiate sites. The Kolmogorov-Smirnov (K-S) statistic denotes significance level: * $p < 0.05$ and *** $p < 0.001$. Non-significant K-S statistics were excluded

Correlation coefficients for the fish diet and benthic epifaunal datasets demonstrated greater similarity within versus across sites for haddock (undisturbed site only) and longhorn sculpin (Table 4). These correlations suggest that the diets better reflected the benthos where sampling occurred in comparison to across sites, with the exception of haddock diet at the disturbed site. Interestingly, only the correlation coefficients for haddock diet and benthos within the undisturbed site, and haddock diet from the disturbed site and benthos from the undisturbed site were statistically different from zero. This suggests haddock

prefer benthic invertebrates in these locales. The reason for the lack of significant correlation between the Naturalists' dredge and longhorn sculpin stomachs is not entirely known. This may be due to differences in sampling efficiencies for particular benthic epifauna, but will require further investigation.

HAPC region

Similar to the northeast peak region, prey diversity curves for the 5 fishes of the HAPC region

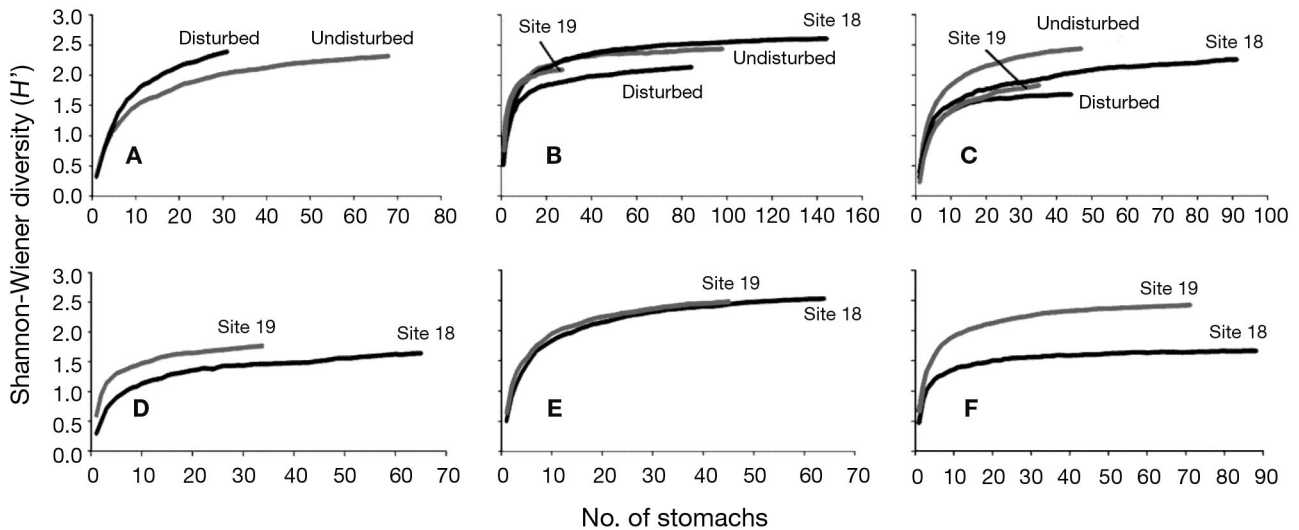


Fig. 6. Cumulative trophic diversity curves for (A) Atlantic cod *Gadus morhua*, (B) haddock *Melanogrammus aeglefinus*, (C) longhorn sculpin *Myoxocephalus octodecemspinosus*, (D) winter skate *Leucoraja ocellata*, (E) little skate *L. erinacea*, and (F) winter flounder *Pseudopleuronectes americanus* at each site (labeled). Lines represent mean Shannon-Wiener (H') diversity as a function of sample size. Gray and black lines designate undisturbed and disturbed sites, respectively, in all panels. Lines labeled 'Undisturbed' and 'Disturbed' correspond to sites of the northeast peak region

were asymptotic given the numbers of stomachs sampled per species–site combination (Fig. 6B–F). The diet diversity of winter skate and winter flounder was greater at the undisturbed site (19), but for haddock, diets were more species-rich at the disturbed site (18).

Two of the 5 species–site contrasts were significant when testing the effect of fishing disturbance level on the total amount of food eaten per stomach by the 5 fishes of the HAPC. These significant differences (Kruskal-Wallis statistics provided) were for haddock ($\chi^2 = 16.33$, $df = 1$, $p < 0.0001$) and longhorn sculpin ($\chi^2 = 8.49$, $df = 1$, $p = 0.004$). In each case, greater amounts of prey per stomach were found in fishes from the undisturbed area (Site 19).

The effect of fishing disturbance on fish diet was generally non-significant according to 1-way ANOSIM. There was one exception, winter flounder diet compositions were statistically different between disturbed and undisturbed areas (Global $R = 0.182$, $p = 0.0001$). The average dissimilarity between Sites 18 and 19 reported from the SIMPER routine was 85% for winter flounder. The primary prey components contributing 77% of this dissimilarity were Anthozoa (more abundant in the disturbed site), and *Cancer* spp. crabs, Polychaeta, Gammaridea, and well-digested prey (WDP) (more abundant in the undisturbed site) (Table 5).

The correlation of fish diet and benthic epifaunal data was strongest within each site for winter floun-

der at Sites 18 and 19 (Table 6). The prey considered for these correlations were limited to Anthozoa, *Cancer* spp. crabs, Polychaeta, and Mollusca, given the overlap in selectivity of benthic epifauna by winter flounder stomachs and the Naturalists' dredge. Although the diets of winter flounder at Sites 18 and 19 were more similar to the benthos at the same sites, analogous to the northeast peak, only the relationship between data from the undisturbed Site 19 was statistically significant.

DISCUSSION

This study documented significant spatial patterns in benthic epifaunal communities and demersal fish diets over 10 km scales on northern Georges Bank. Spatial differences in benthic epifaunal communities were attributable to bottom fishing disturbance, though other ecological factors may have contributed (e.g. *Didemnum vexillum* in the HAPC region). In general, undisturbed sites had higher abundance, biomass and species richness, and lower evenness due to a dominance of abundant species. As seen in prior studies (Collie et al. 2005), fragile species (e.g. tube-building polychaetes, pandalid shrimp, and *Hyas coarctatus*) were more abundant at sites without chronic bottom fishing disturbance. There was evidence of larger fishes at undisturbed sites, but this difference was inconsis-

Table 3. *Melanogrammus aeglefinus* and *Myoxocephalus octodecemspinosus*. Diet and diet dissimilarity of haddock (top 10 major prey items) and longhorn sculpin (all major prey items) of the disturbed (Dist.) and undisturbed (Undist.) sites of the northeast peak region. %M is the percent diet composition by mass and %F by frequency of occurrence for each taxon pooled across stomachs by site. SD: standard deviation. Dissimilarity is based on the Bray-Curtis similarity index. Taxa ordered by percent contribution to dissimilarity

Taxon	%M		%F		Dissimilarity		Percent	
	Dist.	Undist.	Dist.	Undist.	Mean	Mean SD ⁻¹	Contribution	Cumulative
Haddock								
<i>Ammodytes</i> spp.	35.33	28.70	34.52	26.53	18.40	0.85	21.43	21.43
Gammaridea	3.04	3.65	45.24	42.86	11.96	0.78	13.92	35.35
<i>Placopecten magellanicus</i> viscera	27.10	25.85	17.86	10.20	10.66	0.55	12.41	47.76
Polychaeta	2.44	4.91	19.05	27.55	8.33	0.58	9.70	57.46
<i>Hyas</i> spp. crab	1.81	6.46	8.33	19.39	6.50	0.48	7.57	65.03
Ophiuroidea	5.98	3.55	13.10	19.39	6.47	0.50	7.54	72.57
Decapoda crab	0.60	0.06	16.67	3.06	4.54	0.39	5.28	77.85
Gastropoda	0.07	0.73	4.76	17.35	3.06	0.37	3.57	81.42
Rock	1.04	1.53	26.19	19.39	3.03	0.64	3.53	84.95
<i>Placopecten magellanicus</i>	5.69	2.29	4.76	7.14	2.55	0.29	2.97	87.92
Longhorn sculpin								
<i>Hyas</i> spp. crabs	13.52	36.82	18.42	50.00	21.15	0.98	25.66	25.66
<i>Ammodytes</i> spp.	52.52	15.51	47.37	34.21	20.29	1.00	24.61	50.27
Pandalidae	12.92	5.72	44.74	23.68	18.99	0.85	23.04	73.31
<i>Pagurus acadianus</i>	2.17	19.44	2.63	15.79	6.90	0.45	8.37	81.68
Paguroidea	0.52	7.35	7.89	13.16	6.25	0.42	7.58	89.26
Decapoda crab	1.32	1.78	7.89	10.53	5.23	0.37	6.34	95.60
<i>Cancer</i> spp. crabs	12.02	0.00	18.42	0.00	3.63	0.36	4.40	100.00

Table 4. *Melanogrammus aeglefinus* and *Myoxocephalus octodecemspinosus*. Rank correlations between fish diet and benthos available in the environment for haddock and longhorn sculpin of the northeast peak region. X: usage of dataset (diet or benthos) for estimating Spearman's ρ correlation coefficient. Dist.: disturbed site; Undist.: undisturbed site. Taxa included: *Ammodytes* spp., Polychaeta, *Hyas* spp. crabs, Ophiuroidea, and Gastropoda for haddock; *Hyas* spp. crabs, *Ammodytes* spp., Pandalidae, *Pagurus acadianus*, and Paguroidea for longhorn sculpin. Probability of ρ coefficient < 0.05 denotes significance (shown in bold)

Combination	ρ		Probability
	Dist. Diet	Undist. Benthos	
Haddock			
X	X		0.394 0.254
X		X	0.680 0.036
		X	0.725 0.020
	X	X	0.467 0.182
Longhorn sculpin			
X	X		-0.300 0.390
X		X	-0.345 0.309
		X	-0.342 0.325
	X	X	-0.632 0.064

tent over time. Spatial differences in fish diet were observed, especially for species that feed primarily on benthic invertebrates throughout their entire life history. The diets of these species were more

strongly correlated with the benthic species composition within the areas where the fish were sampled than with the benthos in other areas, particularly at the undisturbed sites. This indicates that fishes were likely feeding within the sites where they were caught. Several prey taxa that accounted for the diet differences included the same fragile species that were more abundant in the undisturbed sites.

Similar to other comparative studies with regard to fishing effects and benthic communities, caveats in the sampling design were present (Hall 1999). Sampling was conducted somewhat opportunistically over 5 yr, which limited the numbers of Naturalists' dredge and trawl samples that could be made in each area. Trawling was conducted at night between sunset and sunrise, without controlling for feeding variability within this time period. In the case of fish stomach samples, data were pooled across years by species and site to achieve adequate numbers for diet estimates; thus, interannual feeding variability was not examined. Additionally, the fishes were not tagged; thus, their exact origins of feeding were not entirely known. Spatial comparisons were made between areas with known fishing histories, but the actual levels of fishing disturbance were not controlled. In addition to the effects of bottom-fishing disturbance, *Didemnum vexillum* was present at

Table 5. *Pseudopleuronectes americanus*. Diet and diet dissimilarity of winter flounder for the top 10 major prey items of Sites 18 and 19 of the Habitat Area of Particular Concern region. %M is the percent diet composition by mass and %F by frequency of occurrence for each taxon pooled across stomachs by site. SD: standard deviation; prey taxon WDP: well-digested prey. Dissimilarity is based on the Bray-Curtis similarity index. Taxa ordered by percent contribution to dissimilarity

Taxon	%M		%F		Dissimilarity		Percent	
	Site 18	Site 19	Site 18	Site 19	Mean	Mean SD ⁻¹	Contribution	Cumulative
Anthozoa	63.11	1.57	46.59	7.04	16.90	0.90	19.96	19.96
<i>Cancer</i> spp. crabs	2.54	26.15	30.68	71.83	15.56	1.01	18.38	38.34
Polychaeta	3.64	23.28	43.18	56.34	13.39	0.95	15.82	54.16
Gammaridea	8.72	2.38	29.55	40.85	11.65	0.73	13.76	67.92
WDP	1.38	8.91	19.32	30.99	8.00	0.60	9.45	77.37
<i>Didemnum</i> spp.	6.64	4.54	26.14	15.49	7.09	0.59	8.37	85.74
Sand	0.29	14.57	5.68	19.72	4.13	0.41	4.88	90.62
Hydroids (Hydrozoa)	2.67	1.09	27.27	18.31	3.25	0.52	3.84	94.46
Rock	0.64	1.70	19.32	29.58	2.65	0.69	3.13	97.59
Mollusca	1.26	0.45	12.50	8.45	1.42	0.30	1.67	99.26

Table 6. *Pseudopleuronectes americanus*. Rank correlations between fish diet and benthos available in the environment for winter flounder at Sites 18 and 19 of the Habitat Area of Particular Concern region. X: usage of dataset (diet or benthos) for estimating Spearman's ρ correlation coefficient. Taxa used for analysis included: Anthozoa, *Cancer* spp. crabs, Polychaeta, and Mollusca. Probability of ρ coefficient < 0.05 denotes significance (shown in bold)

Combination	ρ		Probability	
	Site 18 Diet	Site 19 Benthos	Site 18 Diet	Site 19 Benthos
Winter flounder				
X	X		0.429	0.347
X		X	-0.314	0.563
	X	X	0.943	0.003
	X	X	0.429	0.346

both sites in the HAPC region, but the actual levels of this effect remained uncontrolled. Despite these caveats, sampling for this study was conducted systematically over 5 yr and similar trends were observed across the 2 regions.

Baseline benthic epifauna

On the northeast peak of Georges Bank there were dramatic differences in benthic epifauna between sites disturbed and undisturbed by mobile bottom-fishing gear. Abundances and biomasses were greater where bottom fishing effort was minimal. This difference was particularly noticeable for those species that were highly vulnerable to mobile gear such as *Dichelopandalus leptocerus* (pandalid shrimp), *Eualus pusiolus* (hippolyte shrimp), *Hyas*

coarctatus (decorator crab), *Ophiopholis aculeata* (brittle star), and *Thelepus cincinnatus* (tube-building polychaete), thus confirming and extending the work of Collie et al. (2005) for this region. Mean abundances of these species were between 5 and 250 times greater at the undisturbed site in 2006 to 2008. In contrast, a few 'hard-bodied' benthic species, considered less susceptible to bottom fishing, had no detectable difference in abundance between sites, i.e. *Pagurus acadianus* (Acadian hermit crab) and *Neptunea decemcostata* (ten-ridge whelk). Akin to other systems, variable patterns of pagurid and whelk distributions in response to fishing effects have been exhibited (e.g. scavenging by select pagurids in the Irish Sea, Ramsay et al. 1996; increased whelk abundance attributed to fishing in Saldanha Bay, South Africa, Kruger et al. 2005). Within the northeast peak region, it may be that *P. acadianus* and *N. decemcostata* actively scavenge on damaged benthos in response to bottom fishing activity or are simply less sensitive to mobile bottom fishing gear, as previously suggested for *P. acadianus* by Collie et al. (1997).

Effects of mobile bottom fishing gear on the benthic epifauna of the HAPC region were less apparent. Here, the presence of the invasive ascidian *Didemnum vexillum* at Sites 18 and 19 provided an opportunity to test the effect of fishing on the benthic community inside versus outside of the closed area. Either no difference or marginally significant year and bottom fishing effects were detected for total abundance and total biomass indices between Sites 18 and 19. Furthermore, only 2 species responded negatively to fishing disturbance: *Asterias vulgaris* (northern sea star) and *Crangon septemspinosa*

(sand shrimp). Why the results from the HAPC region were less dramatic in comparison to the northeast peak is not entirely known. The invasive ascidian *D. vexillum* was broadly distributed within Sites 18 and 19 on both sides of the closed area boundary (Valentine et al. 2007). This species forms extensive 'mats' which cover the seafloor and has been documented to provide favorable conditions for several benthic epifauna (Lengyel et al. 2009). It may be that the presence of *D. vexillum* is dampening the effect of bottom fishing disturbance; however, we speculate that the physical disturbance from mobile bottom fishing gear would provide sufficient force to break apart these ascidian 'mats'. Either way, an examination of the effect of this invasive on benthic epifauna (and fish feeding) with and without the presence of bottom fishing disturbance is warranted.

Patterns of species diversity for the northeast peak and HAPC regions were largely consistent between undisturbed and disturbed sites. Higher evenness was observed for the disturbed areas of both regions (northeast peak 2006 to 2007 and HAPC Site 18), in agreement with previous work for these general locales (Collie et al. 1997, 2005). Patterns of evenness can be associated with the abundance of dominant species which are vulnerable to fishing disturbance. Accordingly, the total abundance of biota for the undisturbed site of the northeast peak was dominated by *Thelepus cincinnatus* (negatively affected by fishing disturbance), thus effectively decreasing evenness. In the HAPC region, samples at the undisturbed Site 19 were predominantly composed of *Nereis zonata* and this was most notable for years 2006 and 2007.

Species richness, by comparison, was greater in the undisturbed site of the northeast peak region. These findings confirm that chronic bottom fishing disturbance prevents species dominance within these benthic communities and limits biodiversity as measured by species richness (Collie et al. 1997, Watling & Norse 1998). Interestingly, the significant Year \times Disturbance level interaction on species richness for the HAPC region may have been a direct result of several factors. Again, the ascidian *Didemnum vexillum* may be responsible for this response at Sites 18 and 19 by producing benthic 'mats' that cover the substrate and harbor benthic epifauna. Lengyel et al. (2009) have shown that increases in benthic epifaunal abundance (e.g. 2 polychaetes: *Harmothoe extenuata* and *Nereis zonata*) can be attributed to the presence of *D. vexillum* on Georges Bank. Similar to the abundance/biomass indices of benthic epifauna, the absence of a disturbance effect on richness inside

versus outside the closed area was likely due to this ascidian. Additionally, frequent storm events on Georges Bank are suspected to cause high variability in benthic epifaunal indices (Collie et al. 2009).

Demersal fish

Differences in fish length–frequency distributions across disturbance levels were often insignificant, yet larger haddock, Atlantic cod, and winter flounder were collected exclusively in the undisturbed areas for multiple years. These results highlight a large degree of inter-annual variability in size distributions for the given locations on Georges Bank. The few differences observed for the fish length frequencies in relation to the effects of closed areas were generally in agreement with previous work on Georges Bank (Link et al. 2005) and elsewhere (southeastern USA; Sluka et al. 1994). The fishes selected by this study are mobile, yet depend heavily on benthic environments for large portions of their life histories as evidenced in their diets (Link & Almeida 2000, Smith & Link 2010). Furthermore, these fishes were not bound by the delineated undisturbed areas on an annual timescale. Murawski et al. (2000) suggested the Georges Bank closed areas mainly benefit less mobile species (i.e. flounders, skates, and sedentary invertebrates, e.g. sea scallop *Placopecten magellanicus*) and this work supports these conclusions. The results discussed are somewhat in contrast to other work on marine protected areas and marine reserves which have confirmed increases in fish size using these tools (Fisher & Frank 2002). Interestingly, Côté et al. (2001) did stress the variable effectiveness of area closures on fish assemblages, and given increased competition and predation within protected areas, potential negative effects have been reported although they more often pertain to non-target species (Micheli et al. 2004).

Fish diet

The fish species sampled were chosen for their known benthivorous feeding habits over broad (entire northeast US continental shelf; Link & Almeida 2000) and regional (Georges Bank; Smith & Link 2010) scales. These feeding classifications were strongly supported by the results of this work. In other studies, the effect of bottom fishing disturbance on the total amount of prey per stomach was

minimal (Jiang & Carbines 2002, Link et al. 2005, Fanelli et al. 2009 [juveniles only]). In our study, the results were mixed: on the northeast peak, the total stomach-content index was higher for haddock in the disturbed site; conversely, at the HAPC, the stomach-content index was higher in the closed (undisturbed) area for haddock and longhorn sculpin. It would appear that these fishes are not necessarily reducing their total food intake as a result of fishing disturbance as few differences were found overall. Many fishes of the northeast US shelf are documented opportunistic feeders (Smith & Link 2010), and this is true for benthivores as sampled in this study and other systems (e.g. haddock in the North Sea; Schücker et al. 2010). More importantly with regard to feeding, this work revealed differences in fish diet compositions in the presence of chronic bottom fishing.

Many demersal fishes in the northwest Atlantic also exhibit generalist feeding strategies (Garrison & Link 2000, Link 2002, Smith & Link 2010); therefore, moderately high dietary overlap across habitats is not surprising. In the northeast peak region, explicit dissimilarities in the diets of haddock and longhorn sculpin were documented between fishing disturbance levels. In the disturbed area, these predators consumed larger proportions of the fish Genus *Ammodytes*. In contrast, longhorn sculpin stomachs from the undisturbed area largely contained *Hyas* spp., and those from haddock had higher frequencies of Gammaridea, Polychaeta, and Ophiuroidea. Coincidentally, the dominant epibenthic invertebrates most sensitive to fishing disturbance revealed by this study were species of the taxa Polychaeta and Ophiuroidea, *Hyas* spp., and 2 shrimps. This indicates that the presence of chronic bottom fishing disturbance reduces the availability of benthic invertebrates in the environment, and these trends in benthic epifauna were also observed in the diets of 3 benthivores.

The absence of a fishing disturbance effect on Atlantic cod diet was not entirely unforeseen. Cod on the northeast US continental shelf undergo several ontogenetic diet shifts throughout their life history; notably, at ca. 50 cm total length, cod switch from benthivory to a more piscivorous diet (Link & Garrison 2002, Smith et al. 2007). Given this ontogenetic switch, it is possible that an increase in cod movement due to a reduced benthic affinity with size may have limited the detection of feeding differences. It would be of merit to examine cod within a finer size range (i.e. 10 to 40 cm total length) using the methods outlined by this study to address this concern.

Only winter flounder diets in the HAPC region were affected by chronic bottom fishing disturbance. Differences in diet between sites were clear in the results; notably, Anthozoa composed a large proportion of the diet within the disturbed area (Site 18) in contrast to *Cancer* spp. eaten at Site 19. However, from the dredge samples, no difference was observed between sites for *C. irroratus*, and the predominant anthozoan, *Urticina felina*, was excluded from analysis given its lesser abundance and uncertainty of adequate sampling by the dredge. Additionally, the percent diet composition by mass of Polychaeta to winter flounder diet was also 6 times greater at the undisturbed site (1.3 times greater by percent frequency of occurrence). Although the Year \times Disturbance level interactions were significant for 2 polychaetes (*Harmothoe* spp. and *Nereis zonata*) in the dredge samples, they generally had greater abundance and, to a lesser degree, larger biomass at Site 19. This suggests their dietary proportions were reflective of a bottom-fishing effect. As discussed previously, this dietary signal may have been dampened by the presence of *Didemnum vexillum*, but we cannot fully discount other factors as well (e.g. variable fishing intensity over time).

The correlation between fish diet and benthic epifauna in the environment was generally higher for communities from the same sampling site rather than across sites. This finding was consistent for the 2 major study regions of northern Georges Bank, suggesting that the fish diets from many sites reflected what was available in the immediate benthic epifaunal community where sampling occurred. However, only 2 of the 6 within-site correlation coefficients for the fish species-site combinations by region were significant. These results may be in direct response to caveats associated with the 2 sampling methods. Despite the documented benefits of using fish stomachs as samplers of the benthic community (Lilly & Parsons 1991, Fahrig et al. 1993, Link 2004), it is well known that the sampling efficiencies of the benthic samplers (i.e. Naturalists' dredge and fish stomachs) are not equal. The number of overlapping taxa that were sampled by both the dredge and fish stomachs may have limited the power of these correlation tests for some fishes. Interestingly, haddock and winter flounder, the 2 species with significant correlations between diet and benthos in the undisturbed areas, have notable dietary proportions of benthic invertebrates on Georges Bank when compared with the other species examined by this study, and this was also seen

by Smith & Link (2010). The correlation between haddock diet at the disturbed site and benthos from the undisturbed site further highlights the routine diet of this species as a benthic invertebrate feeder. Despite the contrasting contributions of benthic invertebrates and *Ammodytes* spp. to haddock diet at the undisturbed and disturbed sites, haddock appear to prefer benthic invertebrates regardless of their availability. It is not entirely clear why this correlation across sites was observed except that multiple prey taxa contributing >10% to the diet dissimilarity between sites for the northeast peak region had to be excluded from the analysis (i.e. Gammaridea and *Placopecten magellanicus* viscera). The possibility that haddock caught in the disturbed site were foraging in the undisturbed site (as would apply to the other fishes sampled, e.g. longhorn sculpin) should also not be discounted, yet this event could not be confirmed. However, for haddock and winter flounder sampled in the undisturbed sites we have proven this not to be the case as their diets represented the benthos available in the areas of collection; thus, altered in the presence of bottom fishing disturbance. Future efforts to conduct tagging experiments to address some of these issues are warranted but, nonetheless, may present additional sampling caveats similar to those previously discussed (e.g. achieving adequate sample sizes).

Previous studies have shown habitat-specific diets of demersal fish on Georges Bank over larger spatial scales (e.g. Collie 1987); this study is the first to establish a link between bottom fishing disturbance and fish feeding. For prey that are highly sensitive to disturbance, particularly in the gravel habitats of Georges Bank, an evaluation of their use as indicators to infer fishing disturbance through fish diet is of merit (Fanelli et al. 2009). Further, the relative benefits of particular prey items should be considered independently for each predator based on life history characteristics. Even though epibenthic fauna (e.g. ophiuroids, *Hyas* spp., and polychaetes) may not possess exceptionally high energy densities per mass of prey relative to other prey items (e.g. *Ammodytes* spp.; Steimle & Terranova 1985), they still constitute a major food source for many fishes during sub-adult stages or for entire life histories, particularly on Georges Bank. In areas undisturbed by mobile bottom-fishing gear, where benthic production exceeds that of disturbed areas (e.g. northern Georges Bank; Hermsen et al. 2003), the greater availability of these prey would require less effort for detection and exposure to predation,

thus conserving predator energy and aiding in survival. Further examination of such community interactions and bioenergetic relationships on Georges Bank are essential given the dietary inferences presented here.

CONCLUSION

The extensive knowledge surrounding habitat disturbance by bottom fishing gear has been expanded for Georges Bank (Collie et al. 1997, 2005, Hermsen et al. 2003). Additionally, the feeding habits of economically valuable (haddock and winter flounder) and ecologically valuable (longhorn sculpin) fishes were altered in response to bottom-fishing intensity. Haddock and winter flounder diet compositions depended on the epibenthos in the immediate environment, most notably for the undisturbed areas, suggesting that mobile bottom-fishing gear disturbance determines prey availability. It follows that fish population parameters could be affected indirectly by bottom fishing, as has been observed for plaice *Pleuronectes platessa* on gravel habitats in the Celtic Sea (growth rate; Shephard et al. 2010) and fine sand/mud sediments of the Irish Sea (condition; Hiddink et al. 2011). These findings will provide further support to fishery managers for implementing area closures, promoting the use of other fishery management tools such as low-impact mobile bottom-fishing gears, but additionally support the inclusion of habitat science in fish stock assessments, and aid in marine spatial planning for protection of benthic prey resources. Indeed, an emphasis on gear technology to advance ecosystem approaches to fisheries management has been proposed (Jennings & Revill 2007), and examples of such lower-impact bottom fishing gear have been tested (Shephard et al. 2009), but they have yet to be made a priority. Collie et al. (2005, 2009) have shown that the closure of gravel habitats on Georges Bank to bottom-fishing disturbance resulted in measureable increases in abundance and biomass of epibenthos. Therefore, increases in these sensitive fauna, which have been directly linked to fish feeding habits in this study, exemplify the benefits of area closures as fishery management tools.

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