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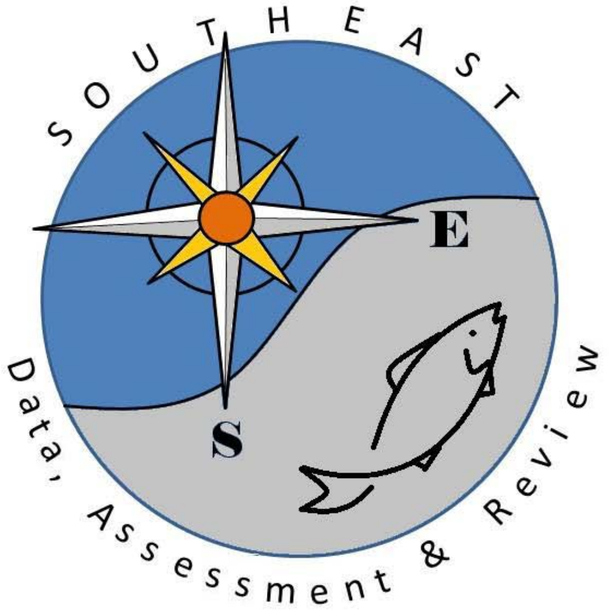

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The goals of this study were to characterize habitat-specific fish and invertebrate community structure over sand, shell-rubble, and natural reef substrata, and to assess the effects of trawling on the sand and shell-rubble habitats and their associated communities during quarterly trawl surveys over a 2-year period. Fish and invertebrate communities differed significantly among habitat types [analysis of similarities (ANOSIM); Global $R = 0.436$, $p < 0.001$), and with respect to trawling exposure (ANOSIM; Global $R = 0.128$, $p < 0.001$). Habitat characteristics were quantified from video transects sampled with a remotely operated vehicle, and included percentage coverage of tubeworms, bryozoans, anemones, corals, and algae, significantly affecting fish community structure. Diversity indices differed among habitats, with the highest Shannon diversity (H') and Pielou's evenness (J') over shell-rubble, specifically non-trawled shell-rubble. In addition, higher values of H' and J' were found over trawled sand relative to non-trawled sand habitats. Length frequency distributions of several abundant fish species showed truncated size distributions over trawled and non-trawled habitats and were both habitat- and species-specific. The study describes habitat-specific differences in community structure, highlighting the differences between trawled and non-trawled areas on the northern Gulf of Mexico continental shelf.

Keywords: community structure, habitat, ROV, species diversity, trawling.

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Introduction

Habitat disturbance by trawling affects marine ecosystems through substratum modifications such as the reduction of habitat complexity, benthic community disturbance, and the removal of non-target species (Auster and Langton, 1998; Jennings *et al.*, 2001; NRC, 2002). The physical damage caused by trawls alters biogenic and sedimentary habitat structure, and potentially can alter the structure of habitat-specific, biological communities (Auster *et al.*, 1996; Freese *et al.*, 1999). In addition, there can be indirect impacts to species that use either the habitat created by infaunal and epifaunal organisms (e.g. ecosystem engineers) or depend on these species as food resources (Auster *et al.*, 1996; Auster, 1998; Coleman and Williams, 2002).

The Gulf of Mexico (GOM) trawl fishery targets penaeid shrimps mostly on soft-bottom sediments that are assumed to be of low structural and species diversity. However, these habitats play an important role in transferring carbon to higher trophic levels, as well as serving as important nursery areas for many species (Snelgrove, 1999; Thrush *et al.*, 2001; Patterson *et al.*, 2005). Moreover, trawling in the northern GOM is not confined solely to soft sediments, but also takes place over such habitat types as low relief shell-rubble. Auster (1998) identified biogenic structures and shell aggregates as some of the most susceptible to the adverse impacts by trawling.

Shrimp trawling in the GOM directly affects many fish and invertebrate species via bycatch mortality. Harrington *et al.* (2005) stated that the highest discard-to-landings ratio in US marine fisheries was in the GOM shrimp-trawl fishery. Population declines experienced by commercially and recreationally important finfish, elasmobranchs, and endangered sea turtles, as well as impacts on the benthic ecosystem, have been attributed to the shrimp-trawl fishery (Henwood and Stuntz, 1987; Martinez *et al.*, 1996; Shephard and Myers, 2005). In an attempt to reduce excessive bycatch of fish and invertebrates, bycatch reduction devices (BRDs) in shrimp trawls were required in western GOM federal waters by 1998. However, recent estimates have indicated that just 16.5% of fish species are successfully excluded by the currently approved BRDs (Foster and Scott-Denton, 2004). Therefore, a technological solution to bycatch reduction may not exist, and the addition of shrimp no-trawl areas or time closures may be needed to supplement the BRD programme (Gallaway *et al.*, 1999; Patterson *et al.*, 2005). Before these ecosystem-based management strategies can be implemented to protect communities and exploited species over multiple habitat types, species-specific habitat-use patterns, as well as the effects of trawling on benthic ecosystems, need to be quantified. Aside from simply characterizing the bycatch, alterations of seabed habitats by trawling and the resulting effects on post-settlement processes of fish and invertebrates in the GOM have received little attention.

The goals of this study were to characterize the habitat use patterns and to assess the effects of trawling on demersal fish and invertebrate communities on the northern GOM continental shelf. Specifically, sand, shell-rubble, and natural hard-bottom reef habitats were selected for habitat-specific community comparisons. In addition, sand and shell-rubble habitats were compared inside and outside an extensive artificial-reef permit area off Alabama, which served as a *de facto* non-trawling area, to assess the impacts of shrimp trawling on habitat characteristics and the associated biological communities. Our trawl comparisons were limited to sand and shell-rubble habitats, because trawling does not occur directly on hard-bottom reef sites.

Material and methods

Sampling sites

Sampling was conducted on the continental shelf in the northern GOM (Figure 1). The largest artificial-reef permit area in the USA, which covers more than 3000 km^2, exists there. The reef zones serve as *de facto* non-trawl areas (Link, 1997; NRC, 2002), and they are in proximity to sampling locations exposed to trawling (Figure 1). Seabed characterization of the region inside and outside the permit areas was recently performed with digital side-scan sonar along with the analysis of boxcore sediment samples taken during previous studies (Dufrene, 2005; Patterson *et al.*, 2005). The results indicate that similar habitat types inside and outside the permit areas have similar geotechnical properties (e.g. sand: mud ratio, percentage $CaCO_3$, organic carbon content; Dufrene, 2005; Patterson *et al.*, 2005). Habitat types identified include sand sites with interspersed mud, low-relief, shell-rubble sites ($<$1 m vertical relief; $<$40% $CaCO_3$), high-relief shell-rubble sites (1–3 m vertical relief; $>$40% $CaCO_3$), and high-relief ($>$2 m vertical relief) reef sites (Figure 1).

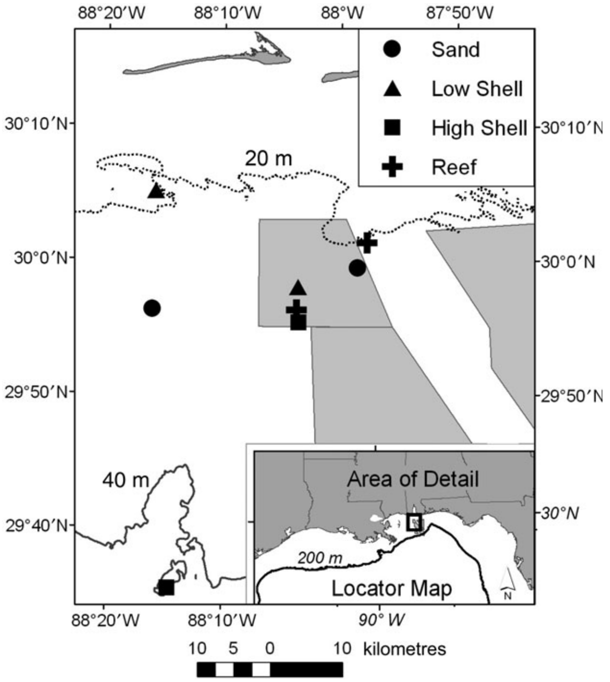

Figure 1. Map of the study-site locations in the north-central GOM. The 20- and 40-m depth contours are shown, with the 200-m depth contour representing the shelf edge. Shaded regions indicate the Alabama artificial-reef permit areas used as *de facto* non-trawl areas.

Sampling methodology

Trawl sampling was conducted quarterly in 2004 and 2005. Three sampling stations were randomly selected for trawling over each habitat type, both exposed and not exposed to trawling; stations were fixed for the duration of the study. Sampling was conducted with the standard trawl gear used on National Marine Fisheries Service (NMFS) Fall Groundfish Surveys (FGS: SEAMAP Information System, NMFS, Pascagoula, MS, USA), which included a single otter trawl 12.8 m wide, with 4-cm mesh. A 0.7-cm codend lining was added to the gear to increase capture efficiencies for smaller individuals. Trawl sampling was only during daylight (30 min after sunrise to the same period before sunset), and trawls were towed at $\sim$4.6 km h^{-1} per 10-min sample along the edges of the reefs, to avoid damaging the habitat or hanging the net.

All fish and invertebrates from the trawls were weighed, sorted, and identified to the lowest possible taxon. The entire catch was first weighed to the nearest 0.1 kg, then each fish was measured and weighed to the nearest millimetre total length (TL) and total weight (g), respectively. Each invertebrate was measured to the nearest millimetre in a manner consistent with body shape.

Water-mass characteristics (salinity, temperature, depth, dissolved oxygen, and optical backscatter) were measured at each site with a SeaBird SBE-25 conductivity–temperature–depth (CTD) instrument. Habitat characteristics were quantified by analysing the video collected with a VideoRay Pro II remotely operated vehicle (ROV). Two fixed, 50-m video transects were randomly chosen on similar habitat types near each trawl-survey area, but not directly along trawl transects. Each of the two ROV transects started at the same point of origin and ran in opposite directions, to prevent re-sampling transect survey areas. The ROV was equipped with a short baseline, acoustic-navigational system that was integrated with the ship's differential GPS system, and used to provide real-time ROV position information to the pilot and to determine the transect length sampled by the ROV. Analysis of the ROV video was performed in the laboratory by estimating the percentage coverage of habitat categories (see below) from 25 squares of equal size (9 × 9 cm) overlain on digital images of individual video frames. One digital image (frame) was analysed every 10 m per transect, resulting in ten observations per site. The nearfield half of each observation was first enumerated, then forwarded to view the farfield half, to preclude bias of the percentage cover attributable to the oblique angle of the camera (Auster *et al.*, 1996). Percentage cover was divided among the five categories including: (i) sessile biological features (e.g. alga, anemone, bryozoan, coral, sponge, worm tube); (ii) mobile biota (e.g. fish, invertebrate); (iii) sediment type (e.g. sand and mud, sandstone, shell, rock); (iv) sediment characteristics by sediment type (e.g. flat, hole, mound, ridge, ripple); and (v) miscellaneous features (e.g. wood). In addition, a maximum vertical-relief estimate, the maximum height (cm) of any geological or biological structure within view, was made at each observation, based on the 10 cm width between the ROV arms.

Data analysis

Fish and invertebrate community data were analysed with the Plymouth Routines in the Multivariate Ecological Research (PRIMER) statistical package (Clarke and Warwick, 2001). The densities of fish and invertebrates were transformed by using $\ln(x+1)$ to downweight the abundant species and to retain information regarding some of the less abundant species. A Bray–Curtis similarity matrix then was computed with density data among all samples. A stepwise data-reduction procedure in PRIMER, BV-STEP, was performed with a Spearman rank correlation coefficient of 0.95 as the threshold, to determine which group of species together explained most of the variability in the fish and invertebrate communities (Clarke and Warwick, 2001). Two-factor, non-metric, multidimensional scaling (MDS) models were computed for each sampling season to visualize similarities and dissimilarities among habitats and areas exposed to trawling vs. those that were not. Stress (residual modelling error) coefficients of 0.2 were treated as critical values to test the goodness-of-fit of a given MDS model in two dimensions (Clarke and Warwick, 2001).

The analysis-of-similarities (ANOSIM) permutation procedure was used to test for differences in fish and invertebrate communities among habitats, seasons, and exposure to trawling (Clarke and Warwick, 2001). A percentage-habitat-distinctness value for each habitat type in trawled and non-trawled areas was calculated by taking the number of significant pairwise differences divided by the total number of pairwise comparisons possible, then multiplying by 100. To assess species-specific contributions, similarity percentage (SIMPER) values were used in a *post hoc* analysis to indicate the contribution of a particular species to the overall fish and invertebrate community similarity and dissimilarity among seasons and habitats (Clarke and Warwick, 2001).

The total number of species (S), the total number of individuals, and Pielou's evenness (J') and Shannon diversity (H') indices were calculated and analysed individually with a three-factor, randomized, block analysis of variance (ANOVA) in SAS (SAS Institute Inc., 2006), with habitat type, exposure to trawling, and seasonal main effects blocked by year. The equal-variance assumption of ANOVA was assessed by examining the plot of the residuals vs. the predicted values, and normality was tested with a Shapiro–Wilk test.

The sizes of fish species that most contributed to community structure (based on SIMPER) were analysed by habitat and presence of trawling. Length frequency distributions were compared with Kolmogorov–Smirnov two-sample tests, and differences in location were tested with a median, linear rank test (Gibbons and Chakraborti, 1992).

Habitat characteristics from the ROV surveys were analysed with canonical correspondence analysis (CCA; ter Braak and Smilauer, 2002). They were also combined with near-bottom water mass characteristics in the CCA to determine if the environmental data were correlated with community structure. The same species selected for fish and invertebrate community analyses using the BV-STEP procedure were used in the CCA, to reduce bias associated with rare taxa. An alpha level of 0.05 was set for all statistical analyses.

Trawling exposure

Potential exposure to shrimp trawling in the study area was estimated using annual, commercial, shrimp-trawling effort data. Trawled sites were between 18 and 40 m deep within subareas 10 and 11 of the 21 NMFS statistical subareas used to calculate shrimp catch per unit effort. Shrimping-effort data between 18 and 55 m deep within subareas 10 and 11 during 2004 and 2005 were 4860.9 and 4570.8 days fished (24 h), respectively (J. Nance, pers. comm., NOAA/NMFS, Galveston, TX, USA), and Patella (1975) estimated the bottom surface area between 18 and 55 m within subareas 10 and 11 to be 10 444.7 km^2. Calculations of the area swept by a commercial shrimp vessel were based on standard NMFS gear specifications (12.8-m wide net, 4.6 km h^{-1} towing speed; FGS: SEAMAP Information System). A conservative estimate of two nets towed per fishing vessel was used, because most vessels tow between two and four nets at a time (NRC, 2002). Therefore, a total bottom area of 2.826 km^2 was swept by trawls per day fished, and estimated areas of 13 736.9 and 12 917.1 km^2 were swept during 2004 and 2005, respectively. These conservative calculations show that sufficient fishing effort was performed to cover the entire area at least once per year between 18 and 55 m within subareas 10 and 11.

Life-history strategy

The conceptual model proposed by Winemiller and Rose (1992) was used to ordinate the representative species collected from trawled vs. non-trawled habitats, using SIMPER, on a trivariate (fecundity, age at maturity, juvenile survivorship) plot of life-history traits. Winemiller and Rose (1992) defined opportunistic strategists as those with an early age-at-maturity, high fecundity, short generation time (T), high net replacement rate (R_0), and low juvenile survivorship. In contrast, periodic strategists have later ages-at-maturity, lower fecundity, longer T, lower R_0, and low juvenile survivorship. Finally, equilibrium strategists have the latest ages at maturity, lowest fecundity, longest T, lowest R_0, and highest juvenile survivorship. The intrinsic rate of natural increase (r) incorporates both generation time and replacement rate as $r = \ln R_0 \, T^{-1}$.

Results

Large numbers of species ($n = 214$; 144 fish and 70 invertebrates) and individuals ($n = 83\,226$) were collected in trawl samples over the GOM continental shelf during the 2-year study period. Species sampled represented 11 classes, 33 orders, and 90 families. Results from the BV-STEP procedure in PRIMER showed that 15 fish and 13 invertebrate (28 in total) species accounted for 95% of the variance in community structure (Table 1), so all statistical analyses of community structure were computed using data for these 28 species.

The community structure and habitat characteristics analysed with ANOSIM indicated no differences between the low shell-rubble and high shell-rubble content sites, within either the non-trawled or the trawled area (ANOSIM; Global $R = 0.076$, $p = 0.280$). These two shell-rubble levels were therefore collapsed into a single shell-rubble level for non-trawled area, and one for trawled area. Additionally, year differences (2004 and 2005) as a main effect were not significant (ANOSIM; Global $R = 0.073$, $p = 0.120$), so samples were combined across years to increase statistical power. The total numbers of trawls at each habitat × trawling exposure site over the 2-year study period were sand trawl ($n = 21$), sand non-trawl ($n = 24$), shell trawl ($n = 33$), shell non-trawl ($n = 48$), reef trawl ($n = 21$), and reef non-trawl ($n = 24$).

Habitat-specific communities

Significant differences existed in the fish and invertebrate community among habitat types (ANOSIM; Global $R = 0.436$, $p < 0.001$) and sampling seasons (ANOSIM; Global $R = 0.342$, $p < 0.001$), as well as between trawled and non-trawled areas (ANOSIM; Global $R = 0.128$, $p < 0.001$). Plots of MDS results

Table 1. Classification and catch characteristics of the 28 species (out of 214 total species) used for all analyses.

Class	Order	Family	Species	Total number	% Total composition	% Frequency of occurrence
Ascidiacea	Paxillosida	Luidiidae	*Luidia clathrata*	138	0.17	40.35
Asterozoa	Ophiurida	Ophiodermatidae	*Ophioderma appressum*	44	0.05	11.70
		Ophiolepididae	*Ophiolepis elegans*	1 748	2.10	46.78
Echinoidea	Arbacioida	Arbaciidae	*Arbacia punctulata*	123	0.15	20.47
Malacostraca	Decapoda	Dromiidae	*Dromidia antillensis*	25	0.03	12.28
		Inachidae	*Podochela sidneyi*	79	0.09	22.81
		Penaeidae	*Farfantepenaeus aztecus*	261	0.31	19.30
			Parapenaeus politus	217	0.26	4.09
		Parthenopidae	*Parthenope granulata*	55	0.07	17.54
		Portunidae	*Callinectes similis*	69	0.08	8.77
			Ovalipes floridanus	60	0.07	11.11
			Portunus spinimanus	127	0.15	27.49
		Sicyoniidae	*Sicyonia brevirostris*	224	0.27	29.24
Osteichthyes	Aulopiformes	Synodontidae	*Saurida brasiliensis*	5 570	6.69	63.16
			Synodus foetens	1 696	2.04	92.98
	Clupeiformes	Engraulidae	*Anchoa hepsetus*	9 357	11.24	9.94
	Perciformes	Haemulidae	*Orthopristis chrysoptera*	292	0.35	25.15
		Lutjanidae	*Lutjanus campechanus*	1 477	1.77	66.08
			Lutjanus synagris	191	0.23	35.67
		Sciaenidae	*Cynoscion nothus*	463	0.56	15.79
			Micropogonias undulatus	6 423	7.72	23.39
		Serranidae	*Centropristis ocyurus*	317	0.38	45.03
			Diplectrum bivittatum	859	1.03	60.82
		Sparidae	*Lagodon rhomboides*	813	0.98	42.11
			Stenotomus caprinus	38 407	46.15	84.80
		Stromateidae	*Peprilus burti*	2 128	2.56	26.32
	Pleuronectiformes	Paralichthyidae	*Syacium papillosum*	3 392	4.08	94.15
	Scorpaeniformes	Triglidae	*Prionotus roseus*	301	0.36	39.77

These 28 species explained 95% of the variance in community structure. Values of total number, percentage of the total composition, and percentage frequency of occurrence are derived from 171 trawls over the 2-year study period.

demonstrate similarities and dissimilarities among habitats and seasons in terms of exposure to trawling (Figure 2). The sand, shell, and reef communities within the trawled and non-trawled areas showed differences in community structure. Pairwise comparisons among the three habitat types within the trawled and non-trawled areas demonstrate that significant differences existed 50 and 67% of the time, respectively.

The community over the sand habitat was the most distinct when compared with the shell and reef communities in the trawled area. Results of the SIMPER analysis show that seven species contributed most to the community over the trawled sand habitat. In order of decreasing importance, these include longspine porgy (*Stenotomus caprinus*), large-scale lizardfish (*Saurida brasiliensis*), Atlantic croaker (*Micropogonias undulatus*), gulf butterfish (*Peprilus burti*), dwarf sand perch (*Diplectrum bivittatum*), inshore lizardfish (*Synodus foetens*), and dusky flounder (*Syacium papillosum*). In contrast, SIMPER analysis identified pinfish (*Lagodon rhomboides*) as an important member of the shell community, and striped anchovy (*Anchoa hepsetus*) as important to the reef community in the trawled area.

The shell and sand habitats supported the most distinct communities within the non-trawled area. Bank sea bass (*Centropristis ocyurus*) was the most important contributor to the shell community, and red snapper and dusky flounder to the reef community (based on SIMPER). The species that most contributed to the sand community in the non-trawled area, by order of importance, were striped anchovy, brittlestar (*Ophiolepis elegans*), and Atlantic croaker.

Trawl vs. non-trawl communities

The fish and invertebrate communities occupying the trawled and non-trawled sand and shell habitats differed in three of the four seasons (Figure 2). The sand-trawled and non-trawled communities differed significantly in winter, spring, and summer, and the shell-trawled and non-trawled communities were significantly different in winter, spring, and autumn ($p < 0.05$; Figure 2). Several species emerged as general representative species for trawled vs. non-trawled locations based on SIMPER analysis, regardless of habitat type. The species more commonly found in trawled areas included longspine porgy, Atlantic croaker, large-scale lizardfish, gulf butterfish, brown shrimp (*Farfantepenaeus aztecus*), and dwarf sand perch. In contrast, brittlestar, bank sea bass, red snapper, and dusky flounder were found over non-trawled shell habitats in greater abundance.

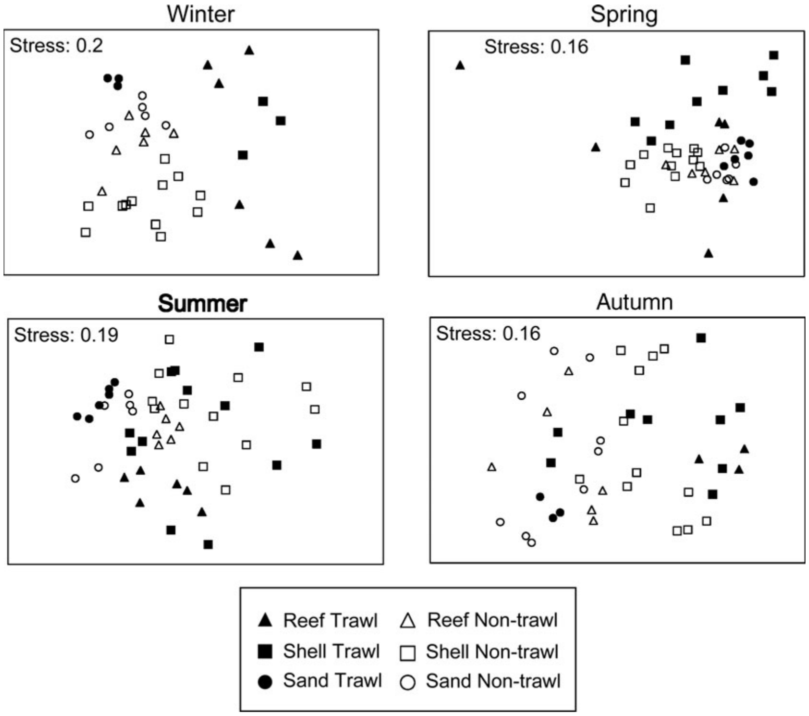

Figure 2. MDS plots of habitat-specific trawl samples by season over the 2-year study period. Each sample represents the 28 species analysed for the habitat-specific fish and invertebrate community. Stress coefficients represent goodness-of-fit criteria.

Life-history strategy

Several of the most common fish species collected from the trawled and non-trawled habitats had life-history traits typical of opportunistic and periodic life-history strategists, respectively (Table 2). Based on the criteria of Winemiller and Rose (1992), four species [longspine porgy, large-scale lizardfish, gulf butterfish, and silver seatrout (*Cynoscion nothus*)] abundant over trawled areas lie on the opportunistic-strategist side of the trivariate plot: attaining small size, early maturation, and high intrinsic rates of population increase. In contrast, the two species (bank sea bass and red snapper) more abundant over the non-trawled area (specifically the non-trawled shell) lie on the periodic-strategist side of the trivariate plot: attaining larger size, delayed maturation, and lower intrinsic rates of natural increase.

Faunal diversity

Diversity (H') and evenness (J') were highest for shell communities, and total abundance highest for sand communities (Table 3). Significant habitat × trawl × season interactions existed for all indices ($p < 0.05$), demonstrating that the magnitude of the differences varied over time relative to habitat type and exposure to trawling. Nevertheless, least-square means indicated similar trends of highest H' and J' for both non-trawled and trawled shell communities, followed by reef, then sand

Table 2. Life-history information of the most important fish species discriminating between trawled and non-trawled communities.

Common name	Scientific name	Size at maturity (mm)	Age at maturity	Maximum size (mm)	Maximum age	Intrinsic rate of increase (*r*)	Reference
Longspine porgy	*Stenotomus caprinus*	90–125	12 months	200	2.5–3 years	3.94 year^{-1}	Geoghegan and Chittenden (1982)
Large-scale lizardfish	*Saurida brasiliensis*	157	9 months	250	3 years	3.82 year^{-1}	Froese and Pauly (2006)
Gulf butterfish	*Peprilus burti*	134–215	9–16 months	269	2–2.5 years	4.90 year^{-1}	Murphy and Chittenden (1991)
Silver seatrout	*Cynoscion nothus*	162–197	12 months	220	2 years	2.04 year^{-1}	DeVries and Chittenden (1982)
Bank sea bass	*Centropristis ocyurus*	185	2 years	300	8 years	2.08 year^{-1}	Froese and Pauly (2006)
Red snapper	*Lutjanus campechanus*	295–482	2–5 years	1 039	59 years	1.06 year^{-1}	Wilson and Nieland (2001), Woods *et al.* (2003)

Lengths are in total length (TL). We used www.fishbase.org to obtain life-history information for two species because of limited information in the literature, and for all intrinsic rates of natural increase.

Table 3. Least-square-mean (± 1 s.e.) estimates of Shannon diversity (H'), Pielou's evenness (J'), richness (S), and total number of individuals collected from each habitat exposed and not exposed to trawling, over the 2-year study period.

Habitat	Trawl				Non-trawl			
	Diversity (H')	Evenness (J')	Richness (S)	Total number	Diversity (H')	Evenness (J')	Richness (S)	Total number
Sand	1.72 (0.10)+	0.52 (0.04)+	28.12 (1.46)*+	1 097 (174)*	1.03 (0.09)*+	0.39 (0.04)*+	17.25 (1.33)+	1 359 (156)*
Shell	1.85 (0.09)*+	0.69 (0.04)*	16.76 (1.01)+	185 (152)	2.07 (0.07)*+	0.73 (0.04)*	18.92 (1.03)+	128 (110)
Reef	1.77 (0.09)	0.65 (0.04)	16.51 (1.34)	245 (156)	1.64 (0.10)*	0.55 (0.04)*	19.79 (1.46)	382 (174)

Asterisks (*) indicate a significant habitat effect and plus signs (+) a significant trawl effect ($p < 0.05$). Note: reef trawl was not compared with reef non-trawl because trawling does not occur over natural hard bottom reef habitat.

communities (Table 3). Diversity indices also differed between sand and shell communities exposed and not exposed to trawling. Higher H' and S were observed for the non-trawled vs. trawled shell communities, whereas higher H', J', and S were observed for the trawled vs. non-trawled sand communities (Table 3).

Size structure

Truncated size distributions and smaller median sizes were observed for several fish species that most contributed to the community structure between trawled and non-trawled areas of similar habitat type (Table 4). Differences were habitat-specific, except for red snapper, which showed significantly truncated size distributions and smaller median sizes over trawled sand (Kolmogorov–Smirnov test, $p = 0.001$; median test, $p < 0.001$) and trawled shell (Kolmogorov–Smirnov test, $p < 0.001$; median test, $p < 0.001$), compared with similar non-trawled habitat types. Habitat-specific shell comparisons showed five species (out of the nine) with significantly smaller size over trawled shell habitats compared with non-trawled shell (Table 4). Similarly, habitat-specific sand comparisons revealed that four species were significantly smaller over trawled sand than over similar non-trawled sand (Table 4). In contrast, the inshore lizardfish and gulf butterfish were significantly larger over trawled sand than over non-trawled sand habitat (Table 4).

Fish and habitat associations

A mixture of habitat types, habitat characteristics, the presence of trawling, and water mass characteristics affected the structure of fish and invertebrate communities. The CCA biplot of species scores reveals the weighted average of a species with the corresponding water-mass variables and with the mean values of species within a habitat (as nominal variables). The most important variables for CCA axis 1 were the presence of trawling, temperature, sand habitat, and shell habitat (Figure 3). In addition, three of the same four variables (temperature, sand habitat, and shell habitat) were the most important variables for CCA axis 2 (Figure 3). The variables that loaded highly positive on CCA axis 1 are inversely related to those that loaded negatively on CCA axis 1. Therefore, the presence of trawling was inversely correlated with the estimates of habitat vertical relief and almost all the percentage composition differences among the structural habitat variables. These included, in order of their correlation coefficients relative to CCA axis 1, tubeworms, bryozoans, anemones, wood, rock, coral, sandstone, and algae. In addition, temperature and dissolved oxygen were important positive, and salinity and depth negative water-mass characteristics on axis 2.

Mobile, invertebrate species loaded positively on CCA axis 1 and were positively correlated with trawling. These include species such as the lesser blue crab (*Callinectes similis*), blotched swimming crab (*Portunus spinimanus*), and brown shrimp. In addition, fish species that were more abundant over trawled areas and sand habitats loaded positively on CCA axis 1. These included longspine porgy, Atlantic croaker, silver seatrout, gulf butterfish, and dwarf sand perch. In contrast, less mobile invertebrates such as the urchin (*Arbacia punctulata*), brittlestar (*Ophioderma appressum*), starfish (*Luidia clathrata*), sponge crab (*Dromidia antillensis*), and shortfinger neck crab (*Podochela sidneyi*) correlated with structural variables. Additionally, red snapper, lane snapper (*Lutjanus synagris*), and bank sea bass were more common over structured habitats and were correlated with shell, reef, and structural variables.

Table 4. Average size (mm TL $\pm$ 1 s.e.) of the nine most important fish species collected over sand and shell trawl and non-trawl habitats.

Species	Common name	Sand		Shell	
		Trawl	Non-trawl	Trawl	Non-trawl
Lutjanus campechanus	Red snapper	97.4 (2.6)	123.8 (5.7)*	125.2 (3.6)	143.8 (3.1)*
Stenotomus caprinus	Longspine porgy	84.9 (1.7)	83.5 (1.9)	99.8 (2.8)	114.1 (2.7)*
Synodus foetens	Inshore lizardfish	230.9 (4.8)*	216.0 (3.8)	239.1 (5.1)	254.1 (3.5)*
Saurida brasiliensis	Large-scale lizardfish	84.2 (1.9)	93.7 (1.6)*	82.2 (3.6)	92.8 (1.8)
Syacium papillosum	Dusky flounder	117.5 (2.3)	139.4 (3.8)*	155.3 (3.3)	151.7 (3.4)
Micropogonias undulatus	Atlantic croaker	166.1 (1.0)	167.5 (1.9)	178.7 (4.7)	186.0 (5.4)
Diplectrum bivittatum	Dwarf sand perch	106.5 (2.6)	117.3 (3.6)*	105.5 (3.1)	101.4 (5.7)
Peprilus burti	Gulf butterfish	155.5 (3.0)*	109.7 (8.3)	90.9 (7.9)	186.0 (2.9)*
Lagodon rhomboides	Pinfish	145.0 (2.2)	145.8 (1.8)	147.0 (2.8)	159.9 (2.1)*

Asterisks indicate a significant size distribution difference (Kolmogorov–Smirnov test) and median difference (median rank test) ($p < 0.05$).

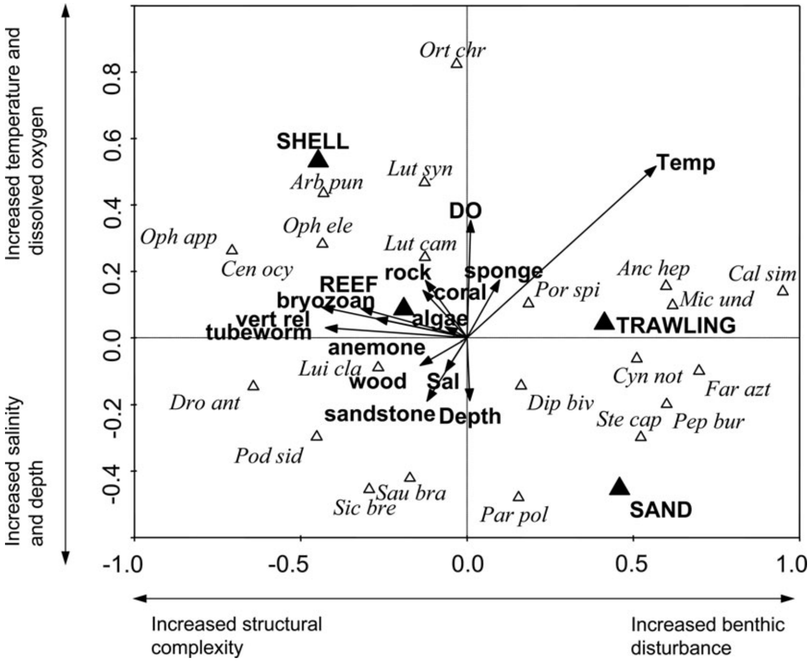

Figure 3. Biplot of axes 1 and 2 from CCA of the abundant fish and invertebrate species (italics), habitat characteristics (bold), and water-mass variables (bold). Nominal variables (Trawling, Sand, Shell, and Reef) are emboldened and capitalized. Only 22 of the 28 species are included for visual simplification, the six excluded species loading weakly on both CCA axes. Species codes: *Anc hep*, *Anchoa hepsetus* (striped anchovy), *Arb pun*, *Arbacia punctulata* (urchin), *Cal sim*, *Callinectes similus* (lesser blue crab), *Cen ocy*, *Centropristis ocyurus* (bank sea bass), *Cyn not*, *Cynoscion nothus* (silver sea trout), *Dip biv*, *Diplectrum bivittatum* (dwarf sand perch), *Dro ant*, *Dromidia antillensis* (hairy sponge crab), *Far azt*, *Farfantepenaeus aztecus* (brown shrimp), *Lui cla*, *Luidia clathrata* (sea star), *Lut cam*, *Lutjanus campechanus* (red snapper), *Lut syn*, *Lutjanus synagris* (lane snapper), *Mic und*, *Micropogonias undulatus* (atlantic croaker), *Oph app*, *Ophioderma appressum* (brittlestar), *Oph ele*, *Ophiolepis elegans* (brittlestar), *Ort chr*, *Orthopristis chrysoptera* (pigfish), *Par pol*, *Parapenaeus politus* (rose shrimp), *Pep bur*, *Peprilus burti* (gulf butterfish), *Pod sid*, *Podochela sidneyi* (shortfinger neck crab), *Por spi*, *Portunus spinimanus* (blotched swimming crab), *Sau bra*, *Saurida brasiliensis* (large-scale lizardfish), *Sic bre*, *Sicyonia brevirostris* (brown rock shrimp), *Ste cap*, *Stenotomus caprinus* (longspine porgy).

Discussion

The results of this study identify differences in community structure among sand, shell, and reef habitats over the inner continental shelf of the GOM. Moreover, differences in biotic community structure and habitat characteristics between similar habitats in trawled and non-trawled areas suggest that the presence of trawling may impact the benthic ecosystem. Nevertheless, we recognize that this study was limited to one trawl area and one non-trawl area, so the results need to be interpreted with caution, because similar findings may not be widespread over the entire shelf of the GOM.

Differences in habitat use by fish and invertebrates over sand, shell, and reef habitats show that these habitats provide unique qualities to their associated communities. Several species showed consistent habitat-use patterns, regardless of exposure to trawling. Longspine porgy, dwarf sand perch, and Atlantic croaker were more abundant over sand habitat, both outside and within the non-trawled area. Longspine porgy and Atlantic croaker have been characterized previously as the most abundant demersal fish species over sand and mud habitats on the northern GOM continental shelf (Moore *et al*., 1970; Chittenden and McEachran, 1976; Chittenden and Moore, 1977). Additionally, dwarf sand perch have been shown to occupy sand and mud habitats (Bortone *et al*., 1981). Pinfish and bank sea bass displayed an affinity towards shell habitats in both trawled and non-trawled areas. Juvenile pinfish are primarily estuarine, but larger adults are found offshore (Nelson, 2002). Information pertaining to the habitat preferences of pinfish on the continental shelf is limited, but Jordan *et al*. (1996) found habitat selection by pinfish of structurally complex seagrass beds to be a function of behaviourally mediated predator avoidance. Therefore, structural complexity of shell-rubble may explain the abundance of pinfish on the shallow GOM shelf. This may also be true of bank sea bass, which have a preference for hard bottom habitats such as shell-rubble (Hoese and Moore, 1998). Numerically, red snapper displayed an affinity for reef habitats both outside and within non-trawled areas, consistent with Bradley and Bryan (1975), providing further support for the view that red snapper have an affinity for structured habitats over the sizes found in this study (mean TL ± s.e. = 155.1 ± 2.0 mm).

Diversity estimates similar to those found in this study have been found in other studies investigating benthic communities in the northern GOM. Chittenden and McEachran (1976) found diversity and evenness values over sand habitats on the NW GOM inner shelf ranging from 0.892 to 2.586, and 0.293 to 0.937, respectively, and Chittenden and Moore (1977) found an average diversity of 2.616 over the 110-m bathymetric contour of the NW GOM. The higher end of these diversity indices could be a function of time, because our diversity estimates nearly 30 years later may be influenced by the cumulative impact of trawling over time. In addition, diversity estimates from this study are probably a function of gear type, because reef habitat had the highest diversity, evenness, and richness in the same areas studied using an underwater, video-camera array (Wells and Cowan, 2007). Other studies characterizing offshore-reef fish communities in the GOM have reported higher values than the indices reported here (Dennis and Bright, 1988; Rooker *et al*., 1997; Gledhill, 2001). The use of otter trawls to sample a reef community influenced our results, because we sampled along the edges of the reef structure in an attempt to minimize trawling impacts on sensitive members of the reef community, such as corals and sponges. Therefore, a combination of multiple gear types, such as underwater video and otter trawls, to identify the large mobile species as well as the small cryptic species, may provide the best estimate of species diversity.

The patterns we observed were only partly consistent with conceptual models that contend that fishing disturbance reduces species diversity, evenness, and richness, and leads to an increase in one or a few numerically dominant small, fast-growing species (Hall, 1999). These patterns were found over more complex shell-rubble habitat type, whereas the sand habitat showed opposite trends in diversity indices. Our results suggest that more complex habitats may be more sensitive to the effects of fishing activities and cause reductions in habitat complexity, which can lead to increased predation on species relying on the structure, or indirectly on other organisms that create the structures (e.g. ecosystem engineers; Auster *et al*., 1996; Auster, 1998; Coleman and Williams, 2002; NRC, 2002). Sainsbury *et al*. (1997) found that a loss of the structural epibenthic community resulted in a shift from snappers (Lutjanidae) and emperors (Lethrinidae) towards one dominated by lizardfish (Synodontidae) and bream (Nemipteridae). The reduction in bryozoans, tubeworms, and the shell-ridge features in the trawled shell area in this study may have contributed to the community differences observed between trawled and non-trawled shell habitats. In contrast to the shell habitat, our study found higher diversity indices associated with the trawled sand habitat than with non-trawled sand. Collie *et al*. (2000) reported that sandy bottom communities were much more resilient to disturbance events, and concluded that two or three physical disturbances annually could take place without any major changes in community composition. Based on our trawling-effort calculations, at least one disturbance event annually was possible over the study sites, which may explain the high diversity of the trawled-sand community.

Several representative species consistently abundant over trawled areas share similar life-history characteristics of small size, short life, high mortality, and rapid biomass turnover (DeVries and Chittenden, 1982; Geoghegan and Chittenden, 1982; Murphy and Chittenden, 1991; McEachran and Fechhelm, 1998). These species included longspine porgy, silver seatrout, large-scale lizardfish, and gulf butterfish. Findings here are consistent with Chittenden (1977) in that these abundant species found over brown and white shrimp grounds in the GOM exhibit life-history characteristics typical of species adapted to environments experiencing frequent perturbations. In addition, disturbance theory predicts that short-lived, highly motile species with high rates of reproduction will recover faster than long-lived, sessile, low-dispersal species (Pickett and White, 1995). However, these species were also found over similar non-trawled habitats, though in different numbers, and could merely be an artefact of our sampling design or movement among habitats.

Several of the invertebrate species frequently collected over shell and reef habitat with more structural complexity were sedentary and sessile species relative to those collected over trawled sand areas. Two brittlestars (*O. appressum* and *O. elegans*), a sea star (*L. clathrata*), an urchin (*A. punctulata*), a hairy sponge crab (*D. antillensis*), the shortfinger neck crab (*P. sidneyi*), and brown rock shrimp (*Sicyonia brevirostris*) were more abundant over the structurally complex, non-trawled areas. The hairy sponge crab is common in offshore-reef habitat, with sponges attached to the carapace, the shortfinger neck crab is found in association with reefs and rocky outcroppings, and the rock shrimp is found over shell-bottom habitats (Williams, 1984). In contrast, two portunid crabs (*C. similis* and *P. spinimanus*) and the brown shrimp (*F. aztecus*) were more common on sand habitat exposed to trawling. It is difficult to discern whether they were directly impacted by trawling activities because the observed habitat-use patterns were most likely associated with both habitat type and the associated structural complexity provided.

Several fish species showed truncated size distributions and reduced median sizes in this study, but these trends were habitat- and species-specific. Our results showed truncated size distributions for several species over trawled habitats, several species that showed no difference in size, and two species that were larger over trawled habitats. The species analysed are among the most abundant species collected as bycatch in the shrimp trawl fishery in the GOM (Chittenden and McEachran, 1976). Decreases in the biomass and average size of demersal fish and invertebrate fauna have been attributed to trawling and dredging in other studies (Bianchi *et al*., 2000; Zwanenburg, 2000; Duplisea *et al*., 2002). However, our study results were too inconsistent relative to each species and habitat type to draw any conclusions regarding the impact of trawling activity on fish size.

The Atlantic croaker was the only species that did not show a size difference between trawled and non-trawled areas, regardless of habitat. These results are consistent with those of Diamond *et al*. (1999), who demonstrated severe declines in the abundance of GOM Atlantic croaker since the 1930s, but no changes in life-history parameters such as size distribution, maximum size, and size-at-maturity. In contrast, the abundance of Atlantic croaker has declined in the Atlantic and there have been life-history parameter changes, including reductions in maximum size, size-at-maturity, and size distribution. These changes were attributed by Diamond *et al*. (1999) to the effects of bycatch on juveniles and intense fishing pressure on adults. Currently, there are no directed commercial or recreational fisheries for Atlantic croaker in the GOM, although they are landed in small numbers by recreational anglers targeting other species.

The use of an artificial-reef permit area as a *de facto* non-trawl area required several assumptions. The first is that trawling did not occur within this area, an assumption supported by Link (1997), who suggested that these reef permit areas added a significant amount of untrawlable area to the northern GOM shelf, and by the distribution of shrimp-trawl effort data, which shows the extensive effort outside the artificial-reef permit zone and the absence of trawling within it (NRC, 2002). The second is that the presence of artificial reefs did not directly affect the fish and invertebrate communities in this study. To minimize any potential effect of artificial reefs, we selected study areas in which sonar surveys indicated an absence of artificial reefs (Dufrene, 2005). Additionally, few of the 28 species analysed for community comparisons have life histories of reef dependence, so it is unlikely that these species were affected by the presence of artificial reefs in our study area. The third assumption is that differences in predation pressure between sites exposed and not exposed to trawling were not significant. Although we cannot be sure that this assumption was met, several community indices in trawled areas were negative, suggesting that differences in predation may be negligible compared with the presence of trawling. The final assumption is that depth differences among study sites did not influence our results. However, trawled sand was deeper than non-trawled sand, but trawled shell and reef sites were shallower than non-trawled shell and reef. Moreover, mean depth differences between similar habitat types located inside and outside the non-trawl area were minimal (mean range 5–8 m).

Our study was limited to a single artificial-reef permit area, so the results may not be broadly representative given the limited spatial replication. Unfortunately, as was the case in this study, limited spatial closures exist on the northern GOM shelf, which limited our ability to cover a large spatial area. Future studies should aim at better replication over a larger area of the shelf to test for the effects of fishing activities on benthic ecosystems. To date, no habitats exposed to trawling have been closed in the GOM to assess the impacts on the benthic ecosystem. Studies in the North Atlantic, North Pacific, and the North Sea over closed areas have been valuable in quantifying the effects of fishing on benthic communities (Auster *et al*., 1996; Freese *et al*., 1999; Piet and Jennings, 2005). Similar studies over shell-rubble features and surrounding sand habitat in the GOM would prove beneficial to provide management with knowledge of the ecosystem effects of fishing, beyond single-species effects.

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