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CASCADING OF HABITAT DEGRADATION: OYSTER REEFS INVADED BY REFUGEE FISHES ESCAPING STRESS

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Abstract. Mobile consumers have potential to cause a cascading of habitat degradation beyond the region that is directly stressed, by concentrating in refuges where they intensify biological interactions and can deplete prey resources. We tested this hypothesis on structurally complex, species-rich biogenic reefs created by the eastern oyster, *Crassostrea virginica,* in the Neuse River estuary, North Carolina, USA. We (1) sampled fishes and invertebrates on natural and restored reefs and on sand bottom to compare fish utilization of these different habitats and to characterize the trophic relations among large reef-associated fishes and benthic invertebrates, and (2) tested whether bottom-water hypoxia and fishery-caused degradation of reef habitat combine to induce mass emigration of fish that then modify community composition in refuges across an estuarine seascape. Experimentally restored oyster reefs of two heights (1 m tall "degraded" or 2 m tall "natural" reefs) were constructed at 3 and 6 m depths. We sampled hydrographic conditions within the estuary over the summer to monitor onset and duration of bottom-water hypoxia/anoxia, a disturbance resulting from density stratification and anthropogenic eutrophication. Reduction of reef height caused by oyster dredging exposed the reefs located in deep water to hypoxia/anoxia for >2 wk, killing reef-associated invertebrate prey and forcing mobile fishes into refuge habitats. Refugee fishes accumulated at high densities on reefs in oxygenated shallow water, where they depleted epibenthic crustacean prey populations. Thus, physical disturbances can impact remote, undisturbed refuge habitats through the movement and abnormal concentration of refugee organisms that have subsequent strong trophic impacts. These results have implications for the design of Marine Protected Areas (MPAs), showing that reserves placed in proximity to disturbed areas may be impacted indirectly but may serve a critical refuge function on a scale that matches the mobility of consumers.

Key words: cascading interactions; Crassostrea virginica; *ecosystem management; essential fish habitat; fish use of restored oyster reefs; habitat structure; hypoxia effects; Neuse River estuary, North Carolina, USA; oyster reefs; reef habitat, biogenic; refugee species; restored habitat.*

INTRODUCTION

There is widespread recognition that disturbances influence food webs (Polis and Winemiller 1996). In lakes, estuaries, and coastal marine ecosystems, human activities, especially fishing and nutrient loading, induce major changes in aquatic food webs (Carpenter and Kitchell 1993, Botsford et al. 1997, Micheli 1999). For example, exploitative harvesting often preferentially removes larger predators, thereby eliminating "top-down" controls in marine food webs (Simenstad et al. 1978, Jackson 1997, Pauly et al. 1998). Bottom-disturbing fishing gear also degrades or destroys bottom habitats (Dayton et al. 1995, Watling and Norse 1998, Hall 1999). In addition, anthropogenic nutrient loading modifies aquatic food webs through "bottom-up" processes, enhancing primary production (Ryther and Dunstan 1971, Micheli 1999) and inducing nuisance algal blooms and hypoxia/anoxia in coastal and estuarine waters (Dyer and Orth 1994, Turner and Rabalais 1994).

Sustainable management of biological resources requires an ecosystem perspective that includes recognition of the effects of natural and anthropogenic disturbances on supporting food webs (Crowder et al. 1996). Studies of human impacts on marine food webs typically rely on bioenergetic modeling (Christensen and Pauly 1993), mesocosm experiments (Grice and Reeve 1982, Paerl et al. 1990), or statistical analyses of fishery and ocean monitoring data (Micheli 1999, NRC 1999). Recent conceptual development emphasizes the need for consideration of spatially explicit ecological processes (Tilman and Kareiva 1997), especially in metapopulation dynamics (Peterson et al. 1996, Hanski 1999, McCarthy and Lindenmayer 1999)

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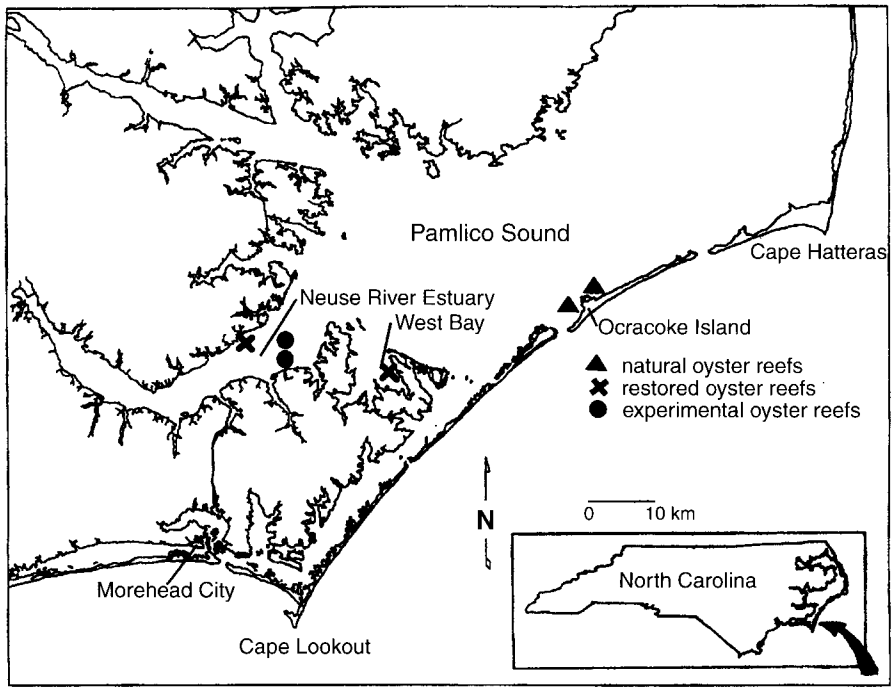

FIG. 1. Map of study sites (Ocracoke Island, West Bay, and the Neuse River estuary) located within Pamlico Sound, North Carolina. The dotted line in the Neuse River estuary represents the transect along which hydrographic measurements (temperature, salinity, and dissolved oxygen concentration) were taken (oxygen data shown in Fig. 5).

and community succession (He and Mladenoff 1999, Petraitis and Latham 1999). Surprisingly little attention has been given to how the effects of disturbances propagate through space beyond the immediate area of direct influence (but see Bonsdorff [1992], Estes et al. [1998]). Here we report the results of a mesoscale manipulative field experiment designed to test how anthropogenic disturbances occurring in one area propagate through space via the mobility of top consumers to affect populations in an adjacent, undisturbed area.

We chose to conduct our test of how mobility of fishes can transport effects of disturbance to areas outside the zone of direct impact by designing a set of observations of changes in food webs on experimentally restored oyster reefs. This study represents an important test case because oyster reefs have been widely degraded by human disturbances (Hargis and Haven 1988, Rothschild et al. 1994, Lenihan and Peterson 1998) and there is growing appreciation of the need to quantify the value of this habitat for estuarine fishes (Zimmerman et al. 1989, Harding and Mann 1999). We test the hypotheses (1) that natural and restored oyster reefs experience greater utilization by large mobile fishes of commercial and recreational value than sand-bottom habitat and (2) that fishery degradation of reef habitat and bottom-water hypoxia/anoxia combine to cause the movement of predatory fishes and to decrease the abundance of invertebrate prey on oyster reefs located in both stressed and nearby undisturbed refuge areas. As tests, we (1) sampled fishes and epibenthic invertebrates on natural and restored oyster reefs and on nearby sand bottom to compare these habitats and to establish trophic relationships (i.e., to depict the top levels of the local oyster-reef food web) and (2) conducted a large-scale field experiment to track changes in the abundance of predatory fishes and their prey on experimental oyster reefs located across a seascape experiencing different levels of stress from hypoxia/anoxia.

METHODS

Study site

Coastal North Carolina contains many large marine lagoons and estuaries, including Pamlico Sound, the second largest estuary in the USA. Like seagrass beds and salt marshes, oyster reefs are a conspicuous biogenic habitat in North Carolina estuaries. Oyster reefs occur both intertidally and subtidally. The Neuse River estuary (Fig. 1) is typical mesohaline [5–30 practical salinity units (psu)] habitat where oysters form subtidal reefs (Lenihan 1999). Production and harvests of oysters have been historically high in the Neuse River but have declined by nearly two orders of magnitude over the last 50 yr because of reef habitat destruction, degraded water quality, and oyster disease (Lenihan and Peterson 1998, Lenihan et al. 1999). The estuary is subjected to prolonged periods of severe hypoxia/anoxia during warm months when meteorological conditions are conducive. Meteorological conditions can

TABLE 1. Number of mobile fishes (per fish trap or gill net) on natural and restored oyster reefs in three areas of Pamlico Sound, North Carolina, and on sand bottom in one of these areas in September 1997 (mean ± 1 SD).

			Fish traps			
			Natural reefs	Restored reefs		Sand bottom
Species †	Common name	Information codes‡	Ocracoke Island	West Bay	Neuse River estuary	Neuse River estuary
Anguilla rostrata	American eel	c, j	0	0.5 ± 0.6	0	0
Archosargus probatochephalus	sheepshead	c, r, j, m	0.9 ± 0.8	0.5 ± 0.5	0.6 ± 0.5	0
Bairdiella chrysoura	silver perch	r, j, x	1.2 ± 0.5	2.0 ± 1.6	2.5 ± 1.3	0
Balistes capriscus	gray triggerfish	c, r, j, x	0.7 ± 0.5	0	1.0 ± 1.1	0
Brevoortia tyrannus	menhaden	c	0	0	0	0
Centropristis striata	black seabass	c, r, j, x	0	0	0	0
Chaetodipterus faber	spadefish	c, r, j, x	0	1.0 ± 1.1	1.2 ± 0.5	0
Cynoscion nebulosus	speckled seatrout	c, r, p	0	0	0	0
Cynoscion regalis	weakfish	c, r, p	0	0	0	0
Lagodon rhomboides	pinfish	r, j, x	1.2 ± 0.5	1.0 ± 1.1	1.0 ± 1.1	0
Lutjanus griseus	gray snapper	c, r, j, x	0.7 ± 0.5	0.5 ± 0.6	0	0
Micropogonias undulatus	croaker	c, r, x	0.5 ± 0.6	1.0 ± 0.8	0.5 ± 0.6	0
Mycteroperca microlepis	gag grouper	c, r, j	0	0	0.5 ± 1.0	0
Opsanus tau	oyster toadfish	r, j, x, m	0.7 ± 0.5	0.7 ± 0.5	0.7 ± 0.5	0
Orthopristis chrysoptera	pigfish	c, r, j, x	0.7 ± 0.5	1.2 ± 0.5	1.25 ± 0.5	0
Paralichthys lethostigma	southern flounder	c, r, j, x, p	0	0.7 ± 0.5	0.2 ± 0.5	0.2 ± 0.5
Pogonias cromis	black drum	c, r, x	0	0.5 ± 0.6	0	0
Pomatomus saltatrix	bluefish	c, r, p	0	0	0	0
Rhinoptera bonasus	cownose ray		0	0	0	0
Scomberomorus maculatus	Spanish mackerel	c, r, p	0	0	0	0
Trachinotus carolinus	pompano	c, r, x	0.2 ± 0.5	0.5 ± 0.6	0.7 ± 0.5	0

† Other fish associated with oyster reefs targeted in fisheries within the Neuse River estuary (but not caught in sampling gear) are red drum (*Sciaenops ocellatus*), striped mullet (*Mugil cephalus*), and tarpon (*Megalops atlanticus*).

‡ Information codes: c = commercially caught in North Carolina; r = recreationally caught in North Carolina; j = found on reefs as juveniles as well as adults; x = reef crustaceans (pieces of amphipods, mud crabs, and grass shrimp) found in stomachs; m = reef molluscs; p = reef-associated fishes found in stomachs. Data based on four replicate reefs and four replicate sand bottom areas sampled on two dates.

drive a wedge of high-salinity bottom water up estuary, limit the depth of mixing by surface waves, and cap the water column with low-salinity runoff. Such conditions produce persistent vertical density stratification, which allows microbial degradation of organic matter, anthropogenically enhanced by eutrophication, to consume available dissolved oxygen (DO) in bottom waters (Lenihan and Peterson 1998, Paerl et al. 1998). Mass mortality of oysters, reef-associated sessile invertebrates, and small sedentary fishes, as well as alterations of food-web interactions, occurs during these severe hypoxic/anoxic events (Seliger et al. 1985, Pihl et al. 1992, Breitburg et al. 1997, Lenihan and Peterson 1998, Paerl et al. 1998). Recent increases in the frequency and duration of hypoxia/anoxia have been linked to nitrogen loading in the estuary (Paerl et al. 1998). In the Chesapeake Bay, an analogous mid-Atlantic estuary, Cooper and Brush (1993) collected stratigraphic evidence from cores covering 2500 yr to show that the stress of low DO was minimal or even absent before the local landscape was grossly modified by recent human land uses.

Natural oyster reefs in the Neuse River estuary reach ~1.5 ha in surface area and most (~80%) are located in water depths of ≥4 m (Lenihan and Peterson 1998). The height of oyster reefs located in deep portions of the estuary has declined from 1.8–2.4 m in 1868 to 0.3–0.9 m in 1993 (Lenihan and Peterson 1998). Reef-height reduction in the Neuse River estuary is a consequence of decades of destructive oyster dredge harvesting (Lenihan and Peterson 1998), as is the case in Chesapeake Bay (e.g., DeAlteris 1988, Hargis and Haven 1988, Rothschild et al. 1994). Oyster reefs in shallow water and the tops of tall oyster reefs located in deeper water provide spatial refuge for oysters and other sessile invertebrates from bottom-water hypoxia/anoxia (Lenihan and Peterson 1998). Oyster reefs of the Neuse River also represent habitat for commercially and recreationally important blue crabs (*Callinectes sapidus*), brown shrimp (*Penaeus aztecus*), and several finfishes (list in Table 1).

Sampling fish and invertebrate communities on oyster reef and sand bottom habitats

We sampled fishes and their potential prey on natural and restored oyster reefs within Pamlico Sound (Fig. 1) in September 1997 to describe the summer-season structure at the higher trophic levels in this oyster-reef food web. Four large (rectangular: 10–14 m long × 4–5 m wide × 0.5–0.8 m tall) natural reefs were sampled in the Pamlico Sound near Ocracoke Island. Four restored oyster reefs (hemispherical: ~8 m in diameter × 0.5–0.9 m tall) were sampled in both West Bay (located in the middle portion of the Pamlico Sound shore-

TABLE 1. Extended.

Gill nets			
Natural reefs	Restored reefs		Sand bottom
Ocracoke Island	West Bay	Neuse River estuary	Neuse River estuary
0.5 ± 0.5	0.9 ± 0.3	0.6 ± 0.5	0
0	0	0	0
0	0	0	0
0	0	0	0
0	0	0	4.3 ± 1.7
0.5 ± 0.6	0	0.5 ± 0.6	0
0	0	0	0
0.5 ± 0.6	0.5 ± 0.6	0.5 ± 0.6	0
0.7 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	0
0	0	0	0
0	0	0	0
0	0	0	0
0	0	0	0
0	0	0	0
0	0.1 ± 0.3	0.2 ± 0.5	0
0.6 ± 0.9	0.4 ± 0.5	0.6 ± 0.7	0.5 ± 0.5
0	0	0	0
0	0	0	0.7 ± 0.5
0	0	0	0.5 ± 0.6
0	0.5 ± 0.6	0	0
0	0	0	0

line in Carteret County) and the Neuse River estuary. We chose restored reefs at two sites because hydrographic differences exist between West Bay and the Neuse River (salinity was higher in West Bay than in the Neuse River). The hydrographic regime at West Bay restored reefs closely matched that of Ocracoke Island, where natural oyster reefs were sampled. We also sampled sand bottom areas 160–180 m distant from the restored reefs in the Neuse River estuary to compare fish communities on and off reefs. The hydrographic regime at the Neuse River sand bottom sites was identical to that at the Neuse River restored reefs. The restored reefs sampled in the Neuse River to describe trophic relationships were not the same reefs used in our experiment to determine the effects of disturbances on mobile fishes and their prey (see *Methods: Experimental reefs,* below). Reefs and sand-bottom control areas were located in 3.5–4.5 m water depth. The restored reefs had been created by the North Carolina Division of Marine Fisheries (NCDMF) in summers of 1990 and 1991.

Methods used to compare fish communities on oyster reefs and sand bottom involved use of gill nets and fish traps. Monofilament gill nets (10 m long × 1 m high) consisted of two 5 m long panels, one with 10-cm mesh (when stretched) and the other with 15-cm mesh, and were designed to catch large fish (>200 mm in standard length [SL]). Divers deployed one stretched gill net over the top of each of four replicate reefs and on four replicate sand-bottom areas for a 12-h period from dusk to early morning. Sampling with gill nets was conducted on each of two successive days. Fish traps consisted of steel rebar frames (box-shaped, 0.7 m long × 0.7 m wide × 0.5 m tall) fitted with 0.5-cm nylon mesh that contained a side-mounted entrance funnel designed to allow fish (ranging 10–200 mm in standard length) entry but inhibit escape (Munro 1974). Divers placed one unbaited trap on the top of each of four replicate reefs and on four sand-bottom sites at dusk and collected them 12 h later. Sampling with fish traps and gill nets was conducted simultaneously (i.e., on the same two successive days). Fishes caught in gill nets and traps were identified, counted, measured, and released alive at locations ≥1 km away from sample sites. Sampling efficiencies for these methods are not known, but we employed visual surveys along with fish traps in our subsequent experiment and demonstrated nearly identical patterns in the two data sets. Gill net catches would not be expected to differ between restored and natural reefs because all oyster reefs used in this contrast had similar topography. Gill nets deployed over sand bottom may experience different catch efficiency, but demersal fishes swimming across the seafloor would be expected to encounter the bottom-deployed nets in both cases.

Methods for sampling mobile epibenthic invertebrates and small (≤20 mm SL) benthic fishes involved use of habitat traps (1-mm wire mesh trays 0.25 m^2 × 12 cm high with an open top [Daniel 1988]). Habitat traps were filled with defaunated (i.e., soaked for >48 h in freshwater and then sun-dried for 7–10 d) oyster shells for the reef deployments, or sand for the traps placed in sand bottom, and were dug into the reef and seafloor by divers so that the top edges sat flush with the substrate surface. Habitat traps were deployed once in September 1997 on reefs and sand bottoms for 7 d before being retrieved from a boat by pulling them rapidly to the surface using an attached buoy line. Animals in traps were identified and counted on board the boat. Habitat traps typically attracted only species that could crawl or swim into them, and so provided no data on sessile invertebrate species, except for softshell clams and ribbed mussels, which recruited from the water column. Species caught by habitat traps included small benthic fishes (a goby, three blennies, and a clingfish), amphipods, shrimps, and small crabs that nestle into interstices of oyster shells. (Table 4 includes scientific names of these invertebrates and small benthic fishes.)

Stomach contents were collected from a subset of fishes caught in gill nets and fish traps to infer predator–prey relationships among reef-associated species. Stomach contents were collected by sacrificing 33–67% of each species of fish caught in traps on one of two sampling dates, and 100% of large piscivores caught in gill nets on one of the two sampling dates in September 1997 and fixing their stomachs with a 10% formalin solution. Organisms and body parts in stomach contents were identified to the lowest possible taxonomic level in the laboratory using a dissecting mi-

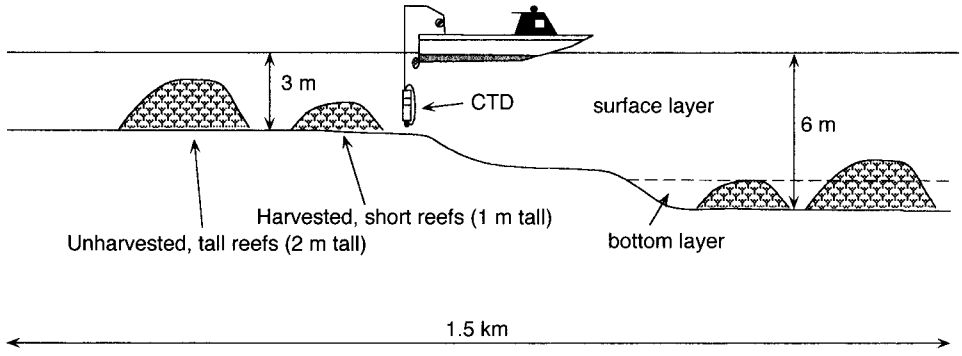

FIG. 2. Design of experimentally restored oyster reefs of two heights (2 m tall to mimic natural, undisturbed reefs and 1 m tall to mimic dredge-damaged reefs) created at 3 and 6 m water depths in the Neuse River estuary, North Carolina. Twelve reefs of each height were placed at each water depth to vary exposure to deep-water hypoxia/anoxia (i.e., below the surface mixed layer as indicated by the dashed line). CTD is a device that measures water conductivity, temperature, and depth.

croscope and their wet mass was measured with an electronic balance.

Experimental reefs

We tested the hypothesis that reef height reduction and hypoxia/anoxia combine to cause changes in the abundance and distribution of mobile fishes and epibenthic invertebrates on reefs by sampling communities occupying experimental oyster reefs in the Neuse River estuary. Our experimental oyster reefs were installed in a factorial design that varied reef height, as a proxy for effects of oyster dredging on physical habitat structure, and water depth, as a means of manipulating exposure to seasonal hypoxia/anoxia that occurs below the mixed zone during summer stratification. In June 1993, with help from the NCDMF, we constructed 12 replicate experimentally restored oyster-shell reefs of each of two heights (tall reefs [2 m height, 5 m diameter] and short reefs [1 m height, 6 m diameter]) at each of two water depths (3 and 6 m), for a total of 48 reefs (Fig. 2). Experimental reefs were located ~9 km away from the restored reefs that we sampled in September 1997 to assess fish and invertebrate community structure and to obtain trophic information.

Sampling fish and invertebrate communities on experimental oyster reefs

To test how sustained hypoxia/anoxia influenced the fish and epibenthic invertebrate communities across water depths and reef heights in the Neuse River estuary, we sampled fishes on experimental oyster reefs using fish traps (seven dates) and visual observations (six dates), and sampled invertebrates using habitat traps (five dates) from May to September 1997. Adjacent sand bottom was not sampled in this experiment. Fish and habitat traps were used to compare fish and invertebrate communities on sand bottoms and on natural and restored reefs. Fish traps were deployed on each of five (out of 12 total) randomly chosen experimental reefs of each height (1 and 2 m tall) at each water depth (3 and 6 m) on 30 May, 12 June, 5, 17, and 19 July, 4 August, and 2 September. Fish were also sampled visually by scuba divers, who swam systematically around and over reefs for 5-min periods counting and identifying fishes. Visual counts were made on each of five randomly selected reefs of each height at each depth on 30 May, 18 June, 9, 18, and 19 July, and 5 August. We also collected stomachs from 25–33% of each species of fish caught in traps in May, June, and July, except during hypoxia/anoxia, when stomach contents were collected from 100% of the fish. Fish not sacrificed for gut analyses were released alive at distant (>1 km away) locations. Habitat traps were deployed on 8 May, 3 June, and 1, 14, and 31 July. Gill net sampling was not used in this experiment.

Hydrographic sampling

Depth profiles of hydrographic conditions (temperature, salinity, and DO) in the Neuse River estuary were measured weekly or more frequently throughout spring and summer 1997 along a cross-river transect. Measurements were taken at 1 m depth intervals at stations located 200–500 m apart along a sampling transect across the estuary in the near vicinity of the experimental oyster reefs (Fig. 1). During stratification events, finer scale depth intervals (10–50 cm) were used to provide more detailed information about the two-dimensional extent of oxygen-depleted bottom water. All measurements were made with a Yellow Springs Instrument (YSI) 6000 CTD (an oceanographic instrument that measures conductivity, temperature, and depth) with an attached oxygen meter. The CTD was deployed on a cable by hand from a boat (see Lenihan et al. [1999] for details).

Statistical analyses

To test whether fish abundance (pooled over all species) and species richness differed among habitat types

(natural oyster reefs at Ocracoke Island vs. restored reefs in West Bay vs. restored reefs in the Neuse River estuary vs. sand bottom in the Neuse River estuary), we first used MANOVAs. MANOVAs were conducted before using separate univariate ANOVAs because the two response variables (fish abundance and species richness) are not independent. The two crossed (fixed) factors in the MANOVAs and subsequent ANOVAs were habitat type and date. All data were log-transformed prior to analysis and homogeneity of variances was tested using Cochran's method (all data passed tests at $\alpha = 0.05$). We conducted separate analyses for fish trap and gill net data.

To test whether total fish abundance (pooled over all species) in fish traps and in visual observations (separate analyses) varied on experimental reefs in the Neuse River estuary, we used three-way ANOVAs. The crossed (fixed) factors in the ANOVAs were date, water depth (3 m vs. 6 m), and reef height (short [1 m] vs. tall [2 m]). An analogous ANOVA analyzed the total abundance of crustacean prey species (pooling mud crabs, amphipods, and benthic shrimps) sampled in habitat traps. All data were log-transformed prior to analysis and homogeneity of variances was tested using Cochran's method (all data passed tests at $\alpha = 0.05$). During the experiment, a hypoxic/anoxic event occurred. To analyze the biological impacts of this hypoxic/anoxic event, we pooled observations made on different dates into three time periods: before, during, and after hypoxia/anoxia. We then compared differences among these time periods in Student-Newman-Keuls (SNK) post hoc tests. This poststratification of samples (Cochran 1963) provides a more efficient method of detecting the biological effects of hypoxia/anoxia than multiple comparisons between pairs of sampling dates. To avoid excessive Type I error in post hoc comparisons after ANOVAs, we calculated significance levels for SNK tests using Bonferroni's method, which adjusts the P value based on the number of pairwise comparisons conducted (Underwood 1997). All 66 possible pairwise comparisons of means for significant three-way interactions among the crossed factors in ANOVAs were tested with SNK.

To explore the fish community data to indicate which species contributed to the overall pattern in total fish abundance in response to hypoxia/anoxia, we analyzed both the fish-trap and visual-sampling data by sets of nonparametric orthogonal contrasts using Wilcoxon and Kruskal-Wallis methods. These analyses were similar in structure to the ANOVAs used for total fish abundance except that the available degrees of freedom in the time period factor were used to establish two a priori orthogonal contrasts: one contrast compared the period before hypoxia/anoxia to the period of hypoxia/anoxia, and the other compared the before and during periods to the period after hypoxia/anoxia. A set of these nonparametric contrasts was done for each species of fish. Nonparametric analyses were chosen because for most species, multiple zero entries violated assumptions of normality of distribution required for parametric analysis.

To test whether the concentration of predatory fishes on oyster reefs in refuge habitats during the stress of hypoxia/anoxia indicates a top-down control on abundance of their crustacean prey, we regressed the total abundance of crustaceans caught in habitat traps against the number of crustacean-eating fishes (based on stomach analyses) caught in fish traps using a least-squares linear regression model. We used data on epibenthic invertebrates (all were crustaceans) from habitat traps and data on fishes from fish traps on each of five dates from 31 May to 6 August. All fish–invertebrate (predator–prey) data pairs were closely matched in time except for those sampled in May (15 May for invertebrates and 31 May for fishes).

Results

Fish and invertebrate communities on oyster reef and sand bottom habitats

Natural and restored oyster reefs sampled in various locations in Pamlico Sound (Ocracoke Island, West Bay, and the Neuse River) in September 1997 were utilized by 18 species of mobile fishes (Table 1), not counting small, sedentary, reef-associated benthic fishes (a goby, three blennies, and a clingfish). All 18 species are fished commercially and/or recreationally in North Carolina, and 12 of the 18 species were found to utilize oyster reefs as juveniles (Table 1). All species of fish found on natural oyster reefs were also found on restored reefs. In contrast, five species (American eel, spadefish, gag grouper, black drum, and Spanish mackerel) were found only on restored reefs. Because restored reefs were sampled in two locations and natural reefs in only one, the sampling effort was twice as high on restored reefs. The six most abundant fishes in reef samples in September 1997 were, in order of declining abundance, silver perch, sheepshead, pigfish, pinfish, toadfish, and croaker (Table 1). Data from gill nets and fish traps are separated in Table 1. Menhaden, bluefish, and cownose rays were exclusively caught over sand bottom: the only other species caught on sand bottom, southern flounder, also occurred on reefs.

Statistical analyses using first MANOVA, followed by ANOVAs when the MANOVA proved significant, revealed strong patterns of differences in fish assemblages between oyster reef and sand-bottom habitats in both data sets, the fish traps and gill nets. In both MANOVAs, there was no significant interaction between habitat type and date in the total abundance or species richness of fishes (Tables 2 and 3). For both the fish trap and the gill net data sets, the total abundance and species richness of fishes varied significantly among natural oyster reefs, restored reefs, and sand bottom in the MANOVA that combined both these (nonindependent) response variables (Tables 2 and 3). In the sub-

TABLE 2. Tests of whether the abundance and species richness of fishes caught in traps varied with habitat type (natural oyster reefs at Ocracoke Island, restored oyster reefs in West Bay, restored reefs in the Neuse River estuary, and sand bottom in the Neuse River estuary), date (two successive sampling dates in September 1997 for each habitat type), and their interaction. Shown also are subsequently conducted univariate two-way ANOVAs for each response variable.

		Univariate ANOVAs								MANOVA		
		Abundance				Species richness						
Source	df	SS	MS	F	P	SS	MS	F	P	Wilk's Lambda	F	P
Habitat	3	144.34	48.11	46.70	0.0001	141.50	47.17	66.44	0.0001	0.06	22.45	0.0001
Date	1	0.28	0.28	0.27	0.61	0.12	0.12	0.17	0.68	0.98	0.23	0.79
Habitat × Date	3	4.09	1.36	1.32	0.29	1.37	0.46	0.65	0.59	0.80	0.90	0.51
Residual	24	24.75	1.03			17.00	0.71					

SNK results (A > B at $P = 0.01$)

Site	Ocracoke Island	West Bay	Neuse River	Neuse River
Habitat type	Natural reefs	Restored reefs	Restored reefs	Sand bottom
	A	A	A	B

Notes: F ratios and P values for MANOVA were generated by Wilks' Lambda test. Provided also are the results of SNK post hoc contrasts for abundance and species richness (using Bonferroni's adjustment to retain experiment-wise α). Both tests had the same result, so only one set of results are given.

sequent ANOVAs done on each separate response variable, the two fish data sets yielded identical results for both total fish abundance and species richness (Tables 2 and 3). In both fish trap and gill net analyses, neither fish abundance nor species richness differed among the natural and restored reefs or between restored reefs at the two sites (data means in Fig. 3; ANOVA and SNK results in Tables 2 and 3). In contrast, fish abundance and species richness were two to three times as high on oyster reefs as on sand-bottom habitat (Fig. 3).

Natural and restored oyster reefs in Pamlico Sound were utilized by eight species of epibenthic invertebrates (crustaceans) and five species of small, relatively sedentary benthic fishes (Table 4) in September 1997. The most abundant groups of mobile invertebrates collected in habitat traps were four species of amphipods, grass shrimp, and two species of mud crabs. The most abundant benthic fish was the naked goby. Only two of the 13 species of crustaceans and benthic fishes found on reefs also occurred in the sand-bottom habitat (Table 4). Oyster reefs were characterized by vastly higher densities of amphipods, benthic fishes, and decapods than sand-bottom habitat (Table 4). Reefs were also inhabited by many other sessile benthic invertebrate species not sampled in habitat traps but described elsewhere (Wells 1961, Bahr and Lanier 1981, Zimmerman et al. 1989). In addition to organisms sampled in September 1997, Table 4 also presents densities of recruits of the bivalve *Mya arenaria,* which recruited heavily to reefs during June 1997. The most abundant macroinvertebrate species on oyster reefs, excluding oysters, appeared to be the ribbed mussel. Several species of polychaete annelids, barnacles, bryozoans, tunicates, and hydroids were also present.

Stomach contents of fishes collected on natural and restored oyster reefs in September 1997 indicate that reefs were utilized by four species of relatively large (>250 mm SL) piscivores (speckled seatrout, weakfish,

TABLE 3. Tests of whether the abundance and species richness of fishes caught in gill nets varied with habitat type (natural oyster reefs at Ocracoke Island, restored oyster reefs in West Bay, restored reefs in the Neuse River estuary, and sand bottom in the Neuse River estuary), date (two successive sampling dates in September 1997 for each habitat type), and their interaction. Shown also are subsequently conducted univariate two-way ANOVAs for each response variable.

		Univariate ANOVAs								MANOVA		
		Abundadance				Species richness						
Source	df	SS	MS	F	P	SS	MS	F	P	Wilk's Lambda	F	P
Habitat	3	20.59	6.86	6.93	0.002	12.34	4.11	5.41	0.006	0.46	3.86	0.004
Date	1	0.28	0.28	0.28	0.60	0.28	0.28	0.37	0.55	0.96	0.45	0.64
Habitat × Date	3	0.84	0.28	0.28	0.84	1.09	0.36	0.48	0.70	0.92	0.32	0.92
Residual	24	23.75	0.99			18.25	0.76					

SNK results (A > B at $P = 0.01$)

Site	Ocracoke Island	West Bay	Neuse River	Neuse River
Habitat type	Natural reefs	Restored reefs	Restored reefs	Sand bottom
	A	A	A	B

Notes: F ratios and P values for MANOVA were generated by Wilks' Lambda tests. Provided also are the results of SNK post hoc contrasts for abundance and species richness (using Bonferroni's adjustment to retain experiment-wise α).

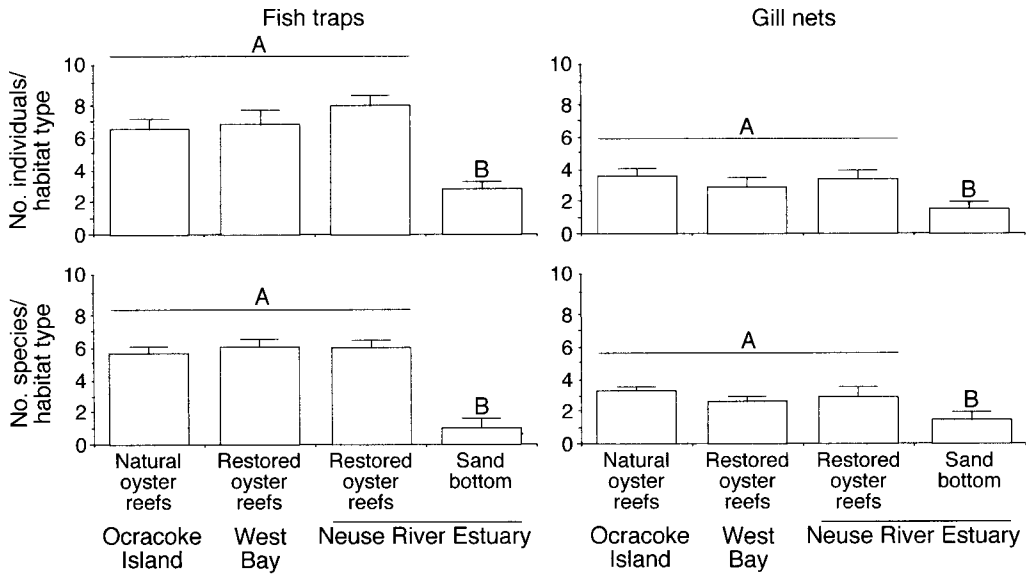

FIG. 3. Numbers of individuals and species of fish sampled on natural oyster reefs at one site, restored oyster reefs at two sites, and sand-bottom habitat at another site ($N = 4$ replicates of each habitat type at each site) using fish traps and gill nets in September 1997. One gill net and one fish trap were placed on each replicate habitat type at each site for each of two successive days. Letters over bars indicate means that differ significantly ($P < 0.05$) in SNK contrasts conducted after significant habitat effect was demonstrated in ANOVA (Tables 2 and 3). Error bars show 1 SE above treatment mean.

TABLE 4. Number of epibenthic invertebrates and sedentary benthic fishes (per 0.25-m^2 habitat trap) on natural and restored oyster reefs in three areas of Pamlico Sound, North Carolina, and on sand bottom in one of these areas in September 1997 (mean ± 1 SD).

Species	Common name	Descr.†	Natural reefs	Restored reefs		Sand bottom
			Oracoke Island	West Bay	Neuse River estuary	Neuse River estuary
Amphipods						
Dullichiata appendiculata	amphipod	p				
Elasmopus levis	amphipod	p				
Melita spp.	amphipod	p				
Micropodopus radii	amphipod	p				
Total amphipods:			53.5 ± 15.8	47.5 ± 12.7	88.0 ± 34.6	0
Decapods						
Callinectes sapidus	juvenile blue crab		1.5 ± 1.0	1.0 ± 0.8	0	1.2 ± 0.5
Eurypanopeus depressus	mud crab	p				
Panopeus herbstii	mud crab	p				
Total mud crabs:			3.7 ± 2.2	4.5 ± 1.9	0.2 ± 0.5	0
Palaemonetes vulgaris	grass shrimp	p	6.0 ± 1.1	6.7 ± 2.6	4.2 ± 1.5	1.2 ± 0.5
Fishes						
Chasmodes bosquianus	striped blenny		1.0 ± 0.8	1.5 ± 1.0	0	0
Gobiesox strumosus	skilletfish		4.5 ± 1.7	2.7 ± 1.2	2.53 ± 1.3	0
Gobiosoma bosci	naked goby		6.7 ± 2.6	6.0 ± 1.1	3.5 ± 0.6	0
Hypleurochilus geminatus	crested blenny		0	1.2 ± 0.5	1.1 ± 1.1	0
Hypsoblennius hentzi	feather blenny		1.0 ± 1.1	0.7 ± 0.5	0	0
Molluscs						
Mya arenaria	softshell clam	p	0	0	45.3 ± 12.3	44.2 ± 17.5
Guekensia demissa	ribbed mussel	p	many	many	many	none

Note: Data are based on four replicate reefs and four replicate sand bottom areas on one date.
† Description: p = found in fish stomachs (i.e., as prey).

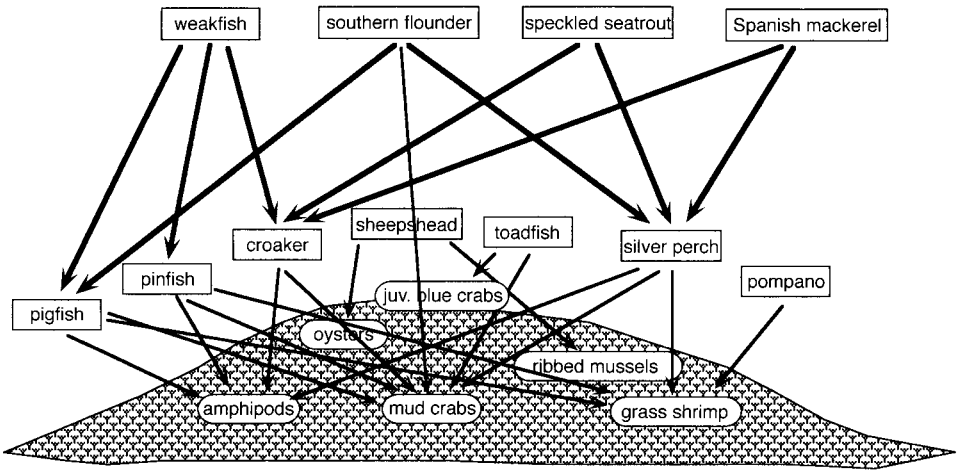

FIG. 4. A partial food web describing predator–prey interactions among large mobile fishes, benthic crustaceans, and other large invertebrates inhabiting experimental oyster reefs in the Neuse River estuary. Trophic interactions depicted are based solely on stomach contents of fishes sampled on reefs in this study in September 1997.

adult southern flounder, and Spanish mackerel) that eat reef-associated fishes, and 13 species (counting juvenile southern flounder that ate only reef crustaceans) of relatively small (<150 mm) fishes that eat reef-associated crustaceans (see Table 1). Stomachs of seven sheepshead contained only reef-associated ribbed mussels and barnacles. Speckled seatrout ate croakers and silver perch. Weakfish ate pinfish and croaker. Flounder ate juvenile pigfish, silver perch, and mud crabs. The one Spanish mackerel caught on reefs had eaten a silver perch. The 13 species of relatively small species caught in fish traps had remains of reef-associated amphipods, mud crabs, or grass shrimps in their stomachs (Table 1). Amphipods were the most abundant food item in stomachs of fishes on reefs, not counting the shells of ribbed mussels and tests of barnacles that were found in high quantities in stomachs of sheepshead. Fig. 4 depicts the food web for oyster reef fishes and invertebrates based solely on our stomach content analyses. From all our quantitative sampling, 88% of all fishes and crustaceans sampled were basal prey species (crustaceans eaten by fishes plus small benthic fishes), 9.8% were primary predators (i.e., those that ate reef invertebrates), and 1.5% were secondary predators that ate reef-associated fishes. This crude characterization places the benthic fishes at the basal prey level, even though we did not sample enough piscivorous fishes to demonstrate predation on the small benthic fishes, nor did we sample gut contents of the small benthic fishes to assess their prey, which could include crustaceans like amphipods. If the benthic fishes were moved from the basal prey level to the primary predator level, then 80% of the total individuals would be basal prey, 16% would be primary predators, and 1.5% secondary predators.

Community dynamics on experimental reefs and hydrography in the Neuse River estuary

Fourteen species of fish were collected in fish traps on experimental oyster reefs in the Neuse River estuary from May to September 1997. Six of these (silver perch, pinfish, pigfish, croaker, southern flounder, and oyster toadfish) were by far the most abundant. Only a few of each of the remaining eight species (black drum, black seabass, gag grouper, gray snapper, gray triggerfish, pompano, sheepshead, and spadefish) were caught in traps on experimental reefs. Most of the silver perch found on reefs in August were 0-yr-class recruits (15–30 mm in length). Only six fishes (southern flounder, silver perch, sheepshead, spadefish, pigfish, and oyster toadfish) were observed on reefs in visual counts.

During a prolonged period of vertical salinity stratification in the Neuse River estuary during July 1997, the water column below 5 m became hypoxic or anoxic, remaining so for ≥20 consecutive days (9–28 July; Fig. 5). Short reefs and the bases of tall reefs in deep (6-m) water (Fig. 2) were completely engulfed by hypoxic/anoxic waters for the 20-d period (Fig. 5). The tops of tall reefs in deep water, however, provided substrate that projected into the well-oxygenated surface layer. Neither short nor tall reefs in shallow (3 m deep) water were ever exposed to stress from low DO during our measurement periods, and severe hypoxia/anoxia never occurred in water >5 m depth.

Data from fish traps imply that the fishes escaping from short reefs in deep water during hypoxia/anoxia migrated to reef substrata that remained well oxygenated, primarily to reefs at 3 m depth and to a lesser degree to the tops of tall reefs in deep (6-m) water. During bottom-water hypoxia/anoxia in July, the abundance of fishes sampled in traps (Fig. 6) on short reefs at 6 m depth declined to zero. There were contemporaneous increases by 51–65% in the number of fishes on reefs at 3 m depth, and on the tops of tall reefs in deep (6 m) water. The ANOVA assessing variation in total numbers of fishes caught in fish traps on exper-

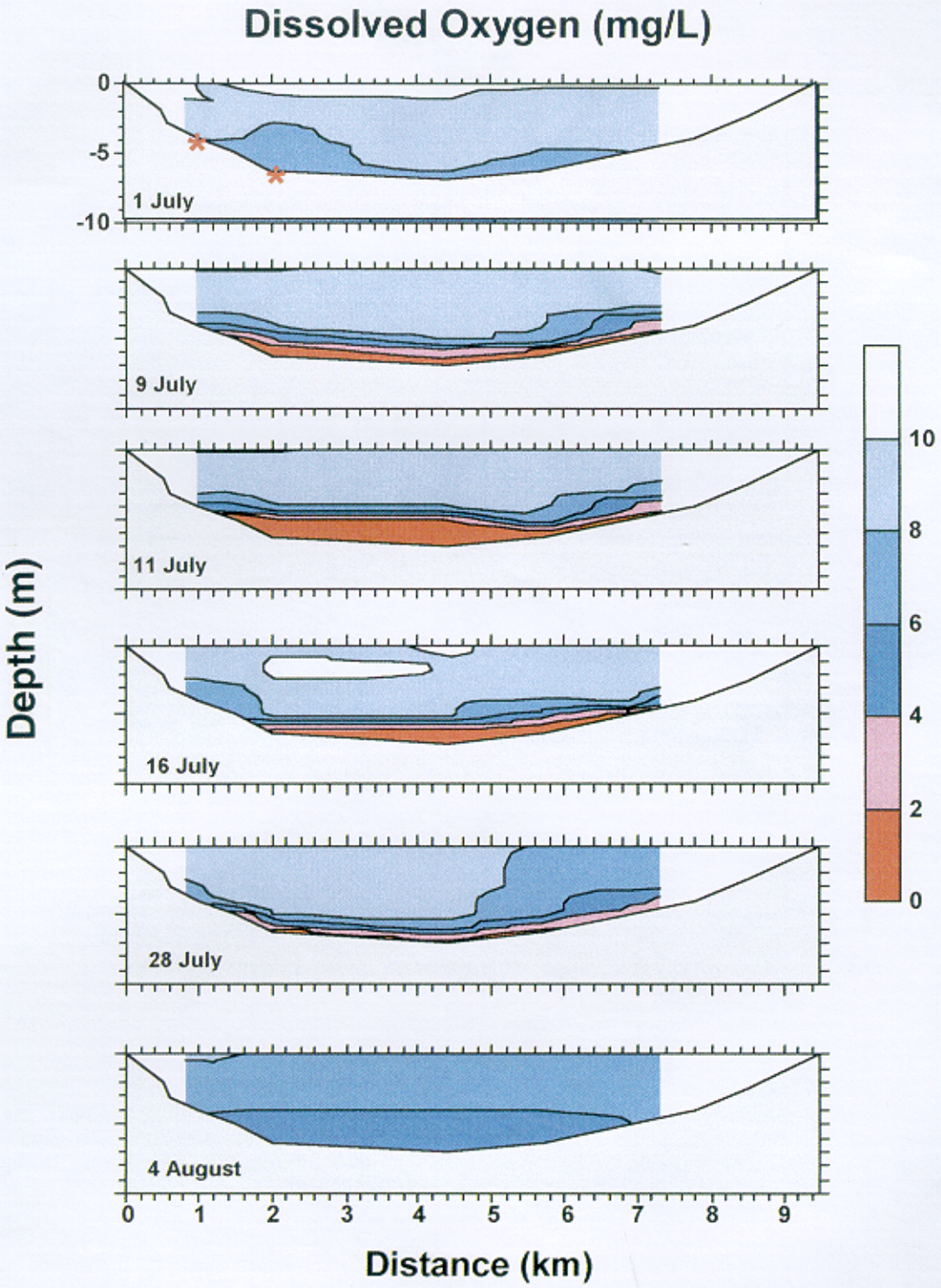

FIG. 5. Dissolved oxygen (DO) concentrations measured in 1997 along the transect of the Neuse River estuary shown in Fig. 1. The vertical shading scale to the right of the six estuary cross-section diagrams shows concentration of dissolved oxygen. Severe hypoxia/anoxia (DO = 0–2 mg/L) lasted at least from 9 to 28 July, engulfing the entire structure of short reefs and the bases of tall reefs at 6 m depth. Distance is measured from the south shore.

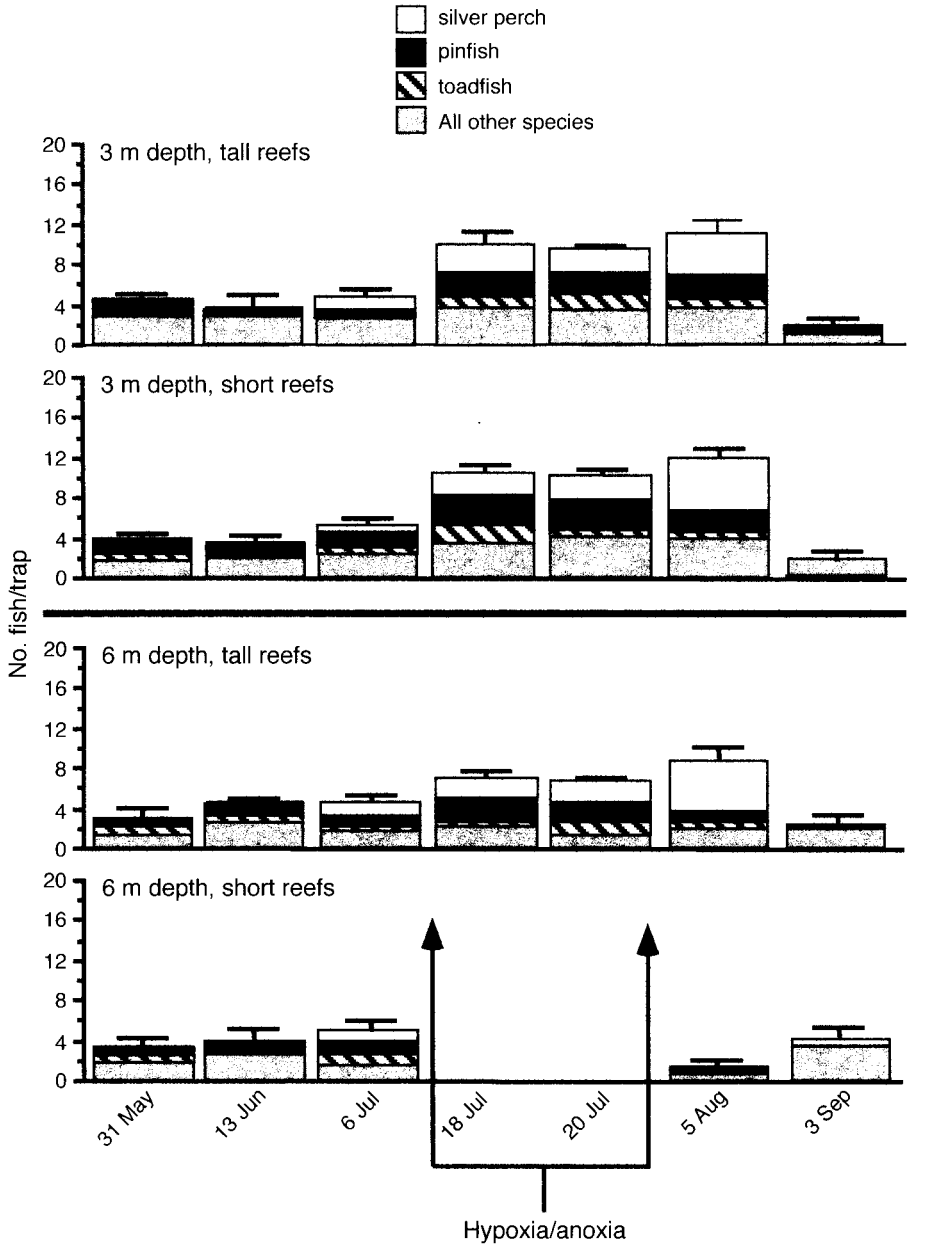

FIG. 6. Numbers of mobile predatory fishes caught in fish traps on the tops of experimental oyster reefs (N = 5 reefs) in the Neuse River estuary during spring–summer 1997. Error bars represent 1 SE above the total mean abundance of all fishes combined for each treatment. One trap was deployed on each replicate reef on each sampling date. The time and location of severe hypoxia/anoxia are represented by the goal-post figure. Results of orthogonal Wilcoxon and Kruskal-Wallis tests for each species showed that the significant period × water depth × reef height three-way interaction in total fish abundance (see Table 5) was driven by significant change from the before to the during hypoxia/anoxia periods in the abundances of three species: pinfish (P = 0.007), silver perch (P = 0.03), and toadfish (P = 0.04). The a priori contrasts revealed that for each of the three species abundance increased on tall reefs in deep water and on both short and tall reefs in shallow water and decreased on short reefs in deep water during hypoxia/anoxia.

imental reefs revealed a highly significant three-way interaction among sampling date, water depth, and reef height (Table 5). This interaction occurred because in the time period before hypoxia/anoxia (31 May, 13 June, and 6 July) fish abundance did not vary with water depth or reef height, whereas both during (18 July and 20 July) and after (5 August and 3 September) hypoxia/anoxia there were more fishes on tall reefs in deep water and on short and tall reefs in shallow water, than on short, deep reefs (SNK contrasts in Table 5;

TABLE 5. Results of a three-way crossed ANOVA testing whether the number of fishes caught in fish traps on experimental oyster reefs in the Neuse River estuary, North Carolina, varied with date (31 May, 13 June, 6, 18, and 20 July, 5 August, and 3 September 1997), water depth (3 m vs. 6 m), reef height (short vs. tall), and their interactions.

Source of variation	df	SS	MS	F	P
Date	6	1.84	0.31	12.14	0.0001
Water depth	1	1.60	1.60	63.17	0.0001
Reef height	1	0.70	0.70	27.64	0.0001
Date × water depth	6	3.00	0.50	19.77	0.0001
Date × reef height	6	0.82	0.14	5.40	0.0001
Water depth × reef height	1	0.92	0.92	36.48	0.0001
Date × water depth × reef height	6	0.98	0.16	6.47	0.0001
Residual	112	2.83	0.025		

Three-way interaction: date × water depth × reef height

	Shallow		Deep	
	Tall reefs	Short reefs	Tall reefs	Short reefs
Before	C	C	C	C
During	A	A	B	E
After	B	B	B	D
	A = B	B > C	C = D	D > E
	A > C	B > D	C = E	
	A > D	B > E		
	A > E			

Notes: One fish trap was deployed on the top of each of five replicate reefs of each treatment for 12 h during each sampling date. Provided also are results of SNK post hoc comparisons (using Bonferroni's adjustment to $P = 0.0008$ for multiple contrasts to retain experiment-wise α) for the three-way interaction of date × water depth × reef height. Means from dates occurring before (31 May, 13 June, and 6 July), during (18 July and 20 July), and after (5 August and 3 September) hypoxia/anoxia were pooled into three time periods (before, during, and after) for the SNK contrasts (see Fig. 5 for dates of hypoxia/anoxia).

data in Fig. 6). Results from Kruskal-Wallis tests on individual species demonstrated that three species of fish, silver perch, pinfish, and toadfish, were significant contributors to this pattern of change from the period before to that during hypoxia/anoxia (Fig. 6). During the period of 5 August–3 September, after the hypoxia/anoxia, total fish abundance declined dramatically on short and tall reefs in shallow water, and on tall reefs in deep water. During the same period, total fish abundance increased only slightly on the tops of tall reefs in deep water (Fig. 6).

Analysis of fish in visual counts revealed a pattern of results essentially identical to that derived from trap samples (Fig. 7). Again, fish disappeared during hypoxia/anoxia on short reefs at 6 m depth, while contemporaneously increasing by 60–70% on reefs at 3 m depth and by 20–30% on tall reefs at 6 m depth. As in the fish data set from traps, the visual counts revealed a lack of recovery on short, deep reefs by 5 August after relaxation of hypoxia/anoxia (Fig. 7). The ANOVA assessing variation in total visual counts of fishes on experimental reefs revealed a highly significant three-way interaction among sampling date, water depth, and reef height (Table 6). This interaction occurred because in the time period before hypoxia/anoxia (30 May and 18 June) fish counts did not differ with water depth or reef height, whereas during (9–19 July) and after (5 August) hypoxia/anoxia there were more fish on tall reefs in deep water and on short and tall reefs in shallow water than on short, deep reefs (SNK contrasts Table 6; data in Fig. 7). Results from Kruskal-Wallis tests on individual species demonstrated that four species of fish (sheepshead, southern flounder, toadfish, and spadefish) were significant contributors to this pattern of change from the period before to that after hypoxia/anoxia (Fig. 7). Unlike the trap sampling, the visual counts were not conducted on two dates in the period after hypoxia/anoxia, so we possess no ability in the visual counts to examine further temporal change into September.

In contrast to the mobile fishes, reef-associated crustaceans caught in habitat traps declined dramatically by 55–65% on short and tall reefs in well-oxygenated, shallow water during hypoxia/anoxia (Fig. 8). There was also a decline to zero in crustaceans on short reefs in 6 m depth, the reef treatment exposed in its entirety to low DO. Habitat traps on short, deep reefs during hypoxia/anoxia contained only dead crustaceans, thus indicating that this disturbance caused mortality of the benthic prey species. No such mortality was observed on shallow-water reefs. Carcasses of dead mud crabs and polychaetes littered the surfaces of short reefs in deep water during the hypoxic/anoxic event. Recovery of crustacean abundances on short reefs in deep water

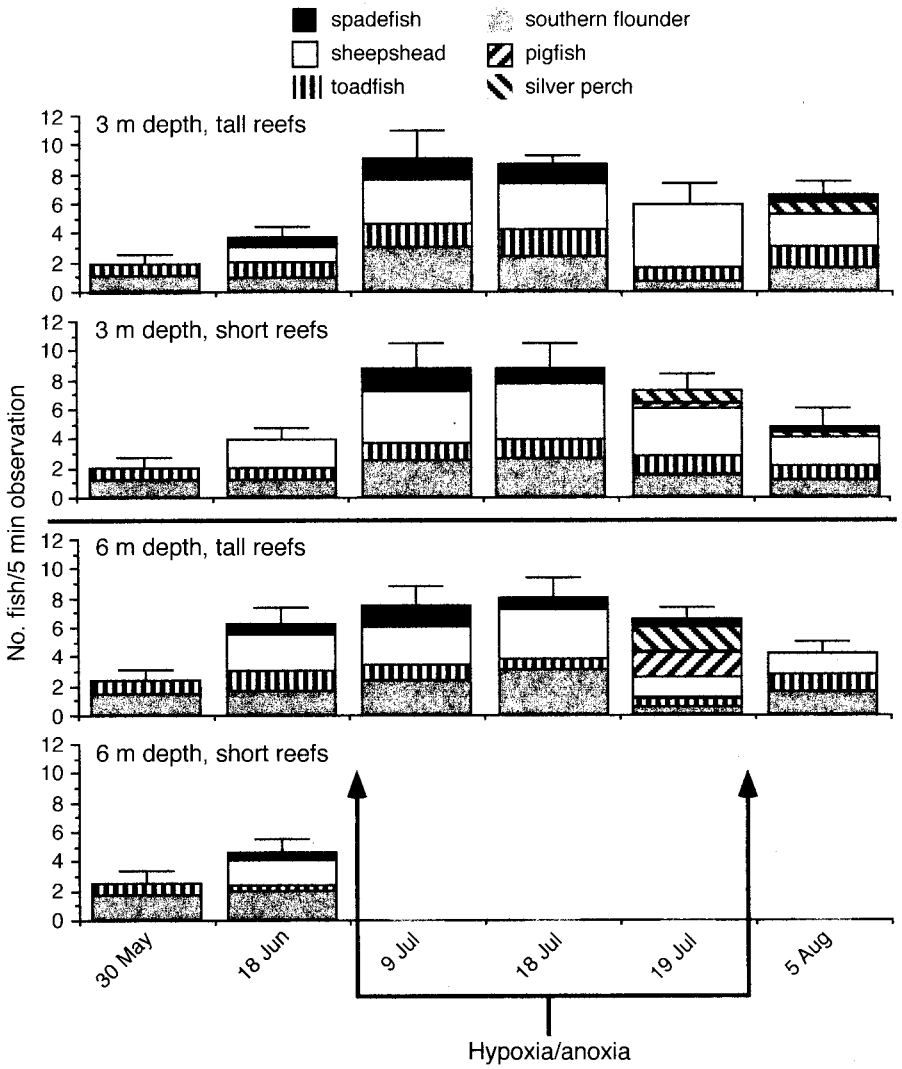

FIG. 7. Diver counts of mobile predatory fishes from 5-min visual surveys of the tops of experimental oyster reefs (N = 5 reefs) in the Neuse River estuary during spring–summer 1997. Error bars represent 1 SE above the total mean abundance of all fishes combined for each treatment. One visual observation survey was conducted on each replicate reef on each sampling date. The time and location of hypoxia/anoxia are represented by the goal-post figure. Results of orthogonal Wilcoxon and Kruskal-Wallis tests for each species showed that the significant period × water depth × reef height three-way interaction in total fish abundance (see Table 6) was driven by significant change from the before to the during hypoxia/anoxia periods in the abundances of four species: spadefish (P = 0.007), sheepshead (P = 0.04), oyster toadfish (P = 0.04), and southern flounder (P = 0.05). The a priori contrasts revealed that for each of the four species abundance increased on tall reefs in deep water and on both short and tall reefs in shallow water and decreased on short reefs in deep water during hypoxia/anoxia.

was not even initiated by 6 August, when DO had risen to 4–6 mg/L (Fig. 5). The three-way ANOVA revealed a significant three-way interaction among sampling date, water depth, and reef height (Table 7). This interaction occurred because in the time period before hypoxia/anoxia (15 May, 10 June, and 7 July) crustacean abundance did not vary with water depth or reef height, whereas during (21 July) and after (6 August) hypoxia/anoxia there were more crustaceans on tall reefs at 6 m depth and on short and tall reefs at 3 m than on short, deep reefs (SNK contrasts in Table 7; data in Fig. 8). In addition, during hypoxia/anoxia the crustaceans were more abundant on tall, deep reefs than on both reef types in shallow water (Fig. 8). Habitat traps sampled on 21 July on short reefs at 6 m depth contained densities of amphipods, shrimp, and small crabs similar to those found on 7 July, but all animals were dead. In addition, at 6 m depth all oysters were killed by hypoxia/anoxia (indicated by the goal-post figure) on bottoms and tops of short reefs and the bottoms of tall reefs.

Twelve of the 14 species of fishes caught in traps on

TABLE 6. Results of a three-way crossed ANOVA testing whether the number of fishes observed visually on experimental oyster reefs varied with date (30 May, 18 June, 9, 18, and 19 July, and 5 August 1997), water depth (3 m vs. 6 m), reef height (short vs. tall), and their interactions.

Source of variation	df	SS	MS	F	P
Date	5	258.44	51.69	35.82	0.0001
Water depth	1	138.67	138.67	96.19	0.0001
Reef height	1	114.07	114.07	79.13	0.0001
Date × water depth	5	137.17	27.43	19.03	0.0001
Date × reef height	5	139.57	27.91	19.36	0.0001
Water depth × reef height	1	95.41	95.41	66.18	0.0001
Date × water depth × reef height	5	61.84	12.37	8.58	0.0001
Residual	96	138.40	1.44		

Three-way interaction: date × water depth × reef height

	Shallow		Deep	
	Tall reefs	Short reefs	Tall reefs	Short reefs
Before	C	C	C	C
During	A	A	B	E
After	B	B	B	D
	A = B	B > C	C = D	D > E
	A > C	B > D	C = E	
	A > D	B > E		
	A > E			

Notes: Visual counts were made by divers on each of five replicate reefs of each treatment for 5-min periods. Provided also are results of SNK post hoc comparison (using Bonferroni's adjustment to $P = 0.0008$ for multiple contrasts to retain experiment-wise α) for three-way interaction of date × water depth × reef height. Means from the dates occurring before (30 May and 18 June), during (9 July, 18 July, and 19 July), and after (5 August) hypoxia/anoxia were pooled into time periods (before, during, and after) for the SNK contrasts.

experimental reefs in the Neuse River estuary during May–September ate crustaceans, according to their stomach contents (stomachs of gag grouper were not sampled and sheepshead ate molluscs). From May to July, stomach remains of these twelve species contained mainly crustaceans, but occasionally a few parts (cirri and jaws) of polychaete worms and unrecognizable, filmy material. During hypoxia/anoxia, 88% of fishes caught in traps on shallow-water reefs and tall reefs in deep water had prey in their stomachs. One hundred percent (by wet mass) of the stomach samples analyzed during hypoxia/anoxia contained mixtures of amphipods, grass shrimp, mud crab parts, and/or unidentified filmy material, except for southern flounder, which also ate small fishes (gobies and an unidentified species; Fig. 9).

Our assessment of abundances of both fishes and their crustacean prey on reefs differentially exposed to hypoxia/anoxia and covering periods of time before, during, and after hypoxia/anoxia suggests important relationships. At times and places of low DO (Fig. 5), both fish and crustacean abundances declined to zero (Figs. 6–8). Excluding data from short, deep reefs during and after hypoxia/anoxia, crustacean prey abundance was negatively related to abundance of crustacean-eating fishes (Fig. 10).

DISCUSSION

The combined effect of reef-height reduction through fishery disturbance and hypoxia/anoxia in deep waters can best explain the observed mortality of small epibenthic crustaceans on short (1-m) oyster reefs located in deep (6-m) portions of the Neuse River estuary during hypoxia/anoxia (Fig. 8). This same interaction of disturbances explained the mass mortality of oysters and loss of blue crabs from their burrows on short, deep oyster reefs in the Neuse River estuary during a previous year's hypoxic/anoxic event (Lenihan and Peterson 1998). This combination of disturbances apparently also induced the observed mass migration of large, mobile fishes from fishery-degraded reefs in hypoxic deep water to refuge reefs in oxygenated shallow water (Figs. 6 and 7). Here, those abnormally concentrated predatory fishes greatly reduced the abundance of their crustacean prey (Fig. 8), thereby exporting the impacts of habitat degradation through migration of consumers. These results constitute a spatially displaced trophic modification that was caused by the two disturbances. The combined effects of oyster dredging and oxygen depletion degraded habitat in one area (deep water), which indirectly caused the increased exploitation of prey in a remote refuge (reefs in shallow water).

That extended hypoxia/anoxia in estuaries kills sessile species (Tenore 1972, Seliger et al. 1985, Diaz and Rosenberg 1995), influences the movement and recruitment of fishes and swimming crabs (Breitburg 1992, Lenihan and Peterson 1998), and alters trophic

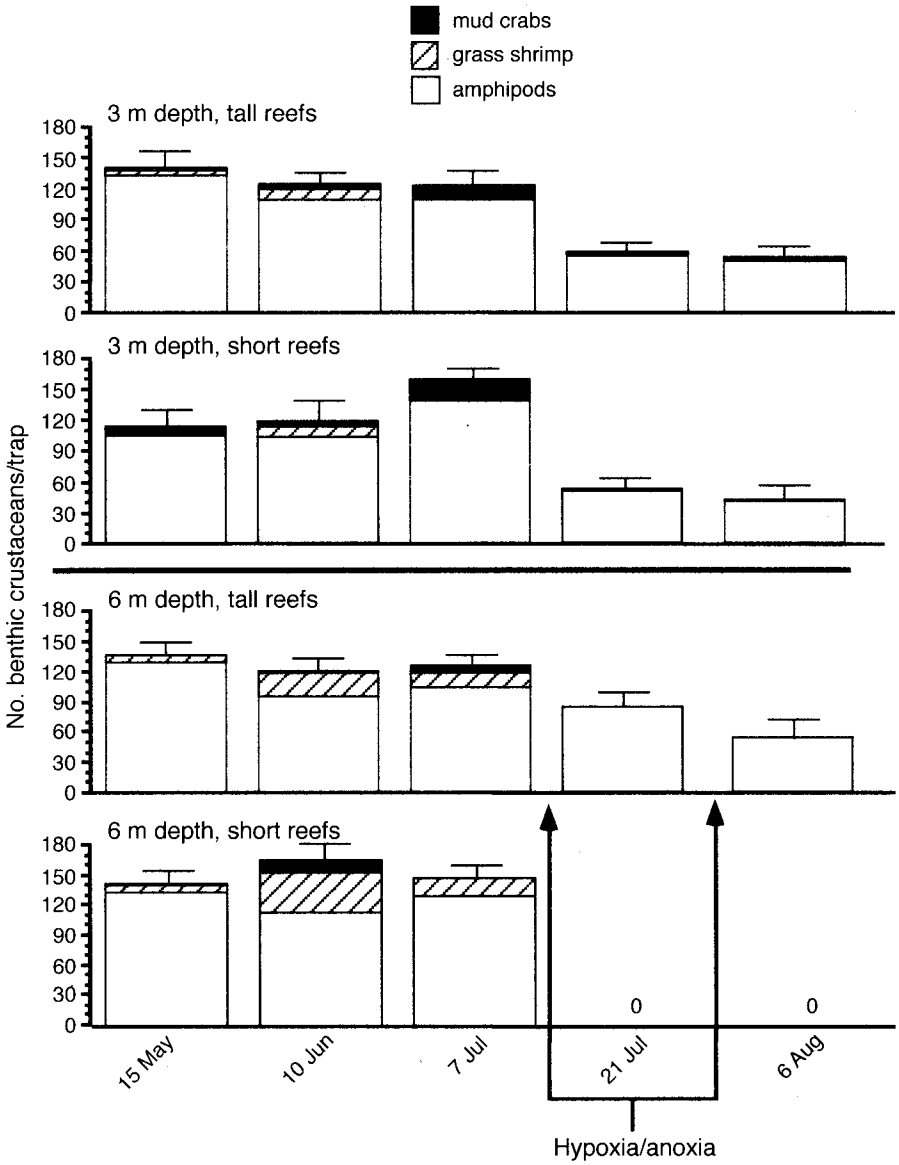

FIG. 8. Total numbers throughout spring–summer 1997 of live, reef-dwelling amphipods (*Dulichiella appendiculata, Elasmopus levis, Melita* sp., and *Microprodopus radii*), grass shrimp (*Palaemonetes vulgaris*), and mud crabs (*Panopeus herbstii*) sampled in habitat traps ($N = 5$ reefs per reef type) placed on the tops of replicate reefs of four types. Error bars represent 1 SE above the mean total abundance of all crustaceans combined for each treatment. One habitat trap was deployed on each replicate reef during each sampling date.

interactions among estuarine species (Pihl et al. 1992, Pihl 1994, Breitburg et al. 1997) is well established. Here we provide experimental evidence showing that the joint effect of two disturbances (hypoxia/anoxia and reef-habitat degradation) occurring in one area can cause a depression in food resources in another, undisturbed area (undegraded refuge reefs in shallow water) through the movement of consumers. Mass emigration of fishes and blue crabs away from estuarine areas that experience hypoxia/anoxia has been termed a jubilee and is described by Loesch (1960). Our study demonstrates the trophic impacts of concentrating those migrants in refuge habitats. Evidence of the trophic consequences of displacing and concentrating predatory fishes comes from both gut contents and regression analyses on the refuge reefs. Gut contents of the fishes captured in refuges revealed that they were feeding on crustaceans (Fig. 9). The relationship between the enhanced fish abundance and the reduction in crustacean prey (Fig. 10) implies a top-down trophic impact in a refuge habitat that is induced by remote disturbances.

TABLE 7. Results of a three-way crossed ANOVA testing whether the number of crustacean prey caught in habitat traps on experimental oyster reefs varied with date (15 May, 10 June, 7 July, 21 July, and 6 August), water depth (3 m vs. 6 m), reef height (short vs. tall), and their interactions.

Source of variation	df	SS	MS	F	P
Date	4	18.33	4.58	910.21	0.0001
Water depth	1	2.10	2.10	417.31	0.0001
Reef height	1	2.93	2.93	582.75	0.0001
Date × water depth	4	3.55	0.89	176.49	0.0001
Date × reef height	4	5.31	1.33	263.65	0.0001
Water depth × reef height	1	2.97	2.97	598.03	0.0001
Date × water depth × reef height	4	5.18	1.30	257.33	0.0001
Residual	80	0.40	0.005		

Three-way interaction: date × water depth × reef height

	Shallow		Deep	
	Tall reefs	Short reefs	Tall reefs	Short reefs
Before	A	A	A	A
During	C	C	B	D
After	C	C	C	D
	A = B A > C A > D	B > C B > D	C > D	

Notes: One trap was deployed on the top of each of five replicate reefs of each treatment for 7 d before being sampled. Provided also are results of SNK post-hoc comparisons (using Bonferroni's adjustment to $P = 0.0008$ for multiple contrasts to retain experiment-wise α) for the three-way interaction of date × water depth × reef height. Means from the dates occurring before (15 May, 10 June, and 7 July), during (21 July), and after (6 August) hypoxia/anoxia were pooled into time periods (before, during, and after) hypoxia/anoxia for the SNK contrasts.

Our experimental results have direct implications for conservation and management in estuarine ecosystems. First, the description of the higher trophic-level structure of an oyster-reef food web (Fig. 4), while restricted to our study area and period, is valuable to habitat and fisheries managers who wish to develop an ecosystem basis for management (Christensen et al. 1996, Crowder et al. 1996). Second, we identified and quantified

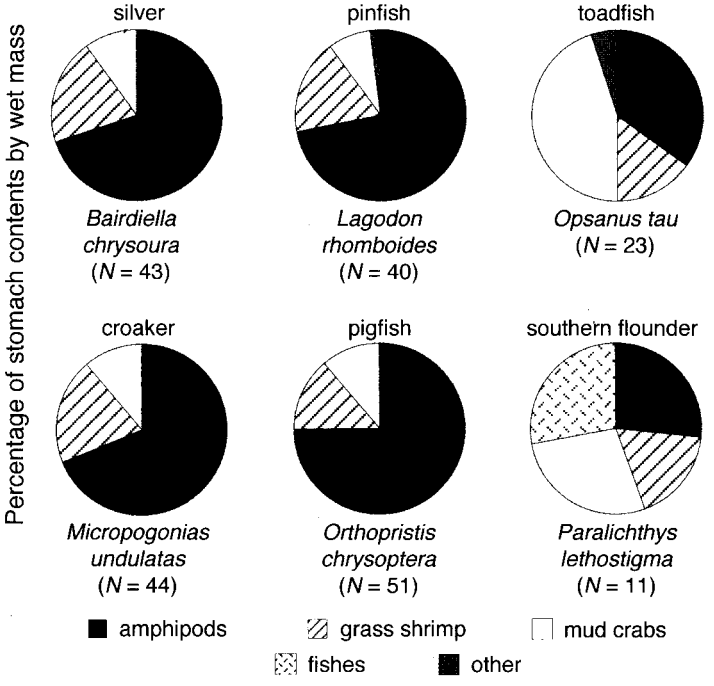

FIG. 9. Percentages by wet biomass of the various prey items collected in the stomachs of the different fish species caught on experimental reefs during hypoxia/anoxia in July 1997. Data are percentages of the total biomass of gut contents pooled from all the fishes of each species. Fishes were caught in traps only on reefs in oxygenated shallow water or on the tops of tall reefs in deep water.

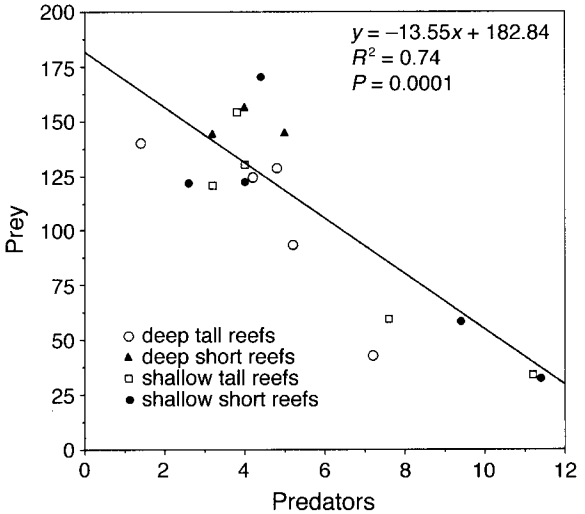

FIG. 10. Results of a linear least-squares regression of total numbers of crustacean prey on total numbers of mobile fishes through time (May–September 1997) on all four experimental reef types. Prey abundance was negatively related (R^2 = 0.74, P = 0.0001, N = 18 samples) to predatory fish abundance. Data points combine mean numbers of fishes caught in fish traps (Fig. 6) with mean catches of crustaceans in habitat traps (Fig. 8) for each date.

the fishes associated with oyster reef habitat. Previous studies had catalogued the fishes on oyster reef habitat (Arve 1960, Harding and Mann 1999) and the associated benthic invertebrates (Wells 1961, Bahr and Lanier 1981, Zimmerman et al. 1989). We found that both natural and restored oyster reefs are utilized by more fish, and a greater number of fish species, than unstructured sand-bottom habitat (Fig. 3). At least 18 of those fishes have value in commercial or recreational fisheries (Table 1), as do oysters and blue crabs. Twelve species of fishes were found on reefs as small juveniles (Table 1), implying that oyster reefs provide recruitment habitat. Our data on fish utilization provide a step in the direction of quantifying some of the ecosystem services (Peterson and Lubchenco 1997) provided by oyster reefs. Third, we found that the abundance and species richness of fishes utilizing restored reefs and natural reefs do not differ (Fig. 3), suggesting that the restoration of oyster reefs can regenerate their services as fish habitat. If the value of oysters in water filtration, which grazes down algal blooms, reduces turbidity, transfers energy to demersal food chains, and induces denitrification (Newell 1988), could also be estimated, then managers could assess whether the sum total of ecosystem services provided by oyster reefs can justify the costs of restoring and protecting oyster reef sanctuaries.

The success of restored oyster reefs, readily built with large mounds of oyster shell, in providing habitat for large predatory fishes is evident in our measurements of fish utilization of natural and restored reefs (Fig. 3). The need for restoration of oyster reefs is great because oysters and oyster reefs have declined in abundance and areal cover in the Chesapeake Bay and in other estuaries along the midAtlantic coast of North America by almost two orders of magnitude since about 1900 (Rothschild et al. 1994, Lenihan and Peterson 1998). Restoration efforts have been limited, perhaps because the goal of restoration has been enhancement of the oyster fishery, yet oyster diseases (Ford and Tripp 1996) have typically intervened to prevent sustainable oyster production even on restored reefs. This narrow focus on a single fishery fails to recognize that restored oyster reefs have value as habitat for a large suite of estuarine fishes even if no augmentation in commercial oyster harvest should result. Our data on fish utilization of restored oyster reefs, along with information on the habitat value of oyster reefs in many previous studies (Arve 1960, Benaka 1999, Harding and Mann 1999), imply that oyster reefs should be restored to enhance many ecological goods and services rather than simply to subsidize the oyster fishery.

That indirect trophic interactions occur in undisturbed refuge habitat as a consequence of migrations by higher trophic-level consumers from disturbed and degraded habitat nearby has important application to the design of oyster reef sanctuaries and, more generally, Marine Protected Areas (MPAs). MPAs are most often established either to preserve biodiversity within the reserve or to sustain production of exploited fishes, usually by serving as a source of propagules to subsidize populations outside the reserve (Allison et al. 1998). Our results imply that if MPAs were established near areas that experience perturbations that trigger the exodus of mobile consumers, the utility of the reserve as a biodiversity repository may be compromised as refugees modify the community through trophic and other interactions. To establish a truly natural marine reserve may be impossible (Jackson 1997), but the value of an MPA as a biodiversity repository may be maximized by locating it at an appropriate spatial distance from disturbed areas to reduce invasions by displaced organisms. Alternatively, the purpose of some MPAs may be to provide refuges from disturbance for mobile refugees, especially economically valuable predatory fishes or endangered species. This represents an important alternative motivation for establishment and siting of reserves. To protect the increasingly threatened apex predators in our now human-dominated ecosystems (Pauly et al. 1998), MPAs may often be needed. Our results imply that habitat restoration and management schemes for whole ecosystems should incorporate a broad spatial perspective that accounts for heterogeneity in habitat quality and the dispersal capabilities of species (Christensen et al. 1996).

Consideration of disturbances and the direct trophic and indirect consequences of migration of mobile higher trophic-level consumers should be incorporated into the spatially explicit metapopulation models now being applied in species conservation (e.g., Hanski 1999, Mc-

Carthy and Lindenmayer 1999, Hanski et al. 2000). This additional migratory process can play an important role not only in marine but also in freshwater aquatic (Power 1990) and terrestrial (Senft et al. 1997, Tilman and Kareiva 1997) systems. Such refinements in the modeling would require realistic spatial and temporal scales, consistent with the migratory potentials of the species involved. Multifactorial experiments conducted at realistic spatial scales, in concert with monitoring and dynamical modeling (Tuck and Possingham 2000), provide effective but underutilized methods for examining ecological complexities within heterogeneous, patchy environments (Walters 1986).

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