The Journal of the Elisha Mitchell Scientific Society, 115(4), 1999, pp. 257–269

EXPERIMENTAL REMOVAL OF HIGH TROPHIC LEVEL PISCIVORES AND THE EFFECTS ON RESIDENT REEF FISH ASSEMBLAGES IN ONSLOW BAY, NORTH CAROLINA

R. O. PARKER JR.

NOAA, National Ocean Service
Center for Coastal Fisheries and Habitat Research
Beaufort, NC 28516

L. E. GREENE

United States Coast Guard
Marine Safety Office Hampton Roads
Norfolk Federal Building
Norfolk, VA 23510-1888

Abstract: High trophic level fishes (Serranidae, Carangidae, Haemulidae, Labridae) were removed from two of four reef areas in northern Onslow Bay, North Carolina to determine the short and long-term effects of predator removal on resident reef fishes. Reef fish assemblages from depths of 17 to 23 m were censused monthly during the summer for a period of four years. Total numbers of adult piscivores dropped at the experimental sites during the removal period but complete removal proved to be impossible. One year following the removal period, adult piscivores populations at the experimental sites exceeded their original densities. We observed 40% fewer reef fish species at these inshore sites compared to a more environmentally stable offshore site. There were more northern species inshore and more tropical species offshore.

Key Words: Reef fishes; predator removal; fishing mortality.

INTRODUCTION

Sport and commercial fishing on reefs generally results in the disproportionate removal of large piscivores (Huntsman, 1979). Effects of predator removal on the biological diversity and structure of reef fish assemblages is not known. Continuous harvesting of major predators may result in a decline or loss of economically valuable species, leaving those of less value (Connell, 1975; Emery, 1978). Loss of economically valuable species from the system may have serious repercussions on the local economies of coastal areas of North Carolina and other coastal states.

One of the central controversies in ecology concerns the relative importance of competition and predation in the control and functioning of communities (MacArthur, 1972; Sih et al., 1985). The competition hypothesis (Dobzhansky, 1950; Pianka, 1966) states that highly diverse communities arise in environments which are stable over long periods of time as a result of competition-maintained niche diversification. The predation hypothesis (Paine, 1966, 1971) argues that predation results in such low prey population sizes that severe resource limitation and competition are precluded. Removing upper trophic level predators from reef fish assemblages as occurs during heavy fishing may have a profound effect on other resident fishes, and may result in a decrease in biological diversity or the collapse of fisheries. Therefore, it is important to determine the effects of predator removal so that informed management practices can be implemented. Knowledge of community dynamics and species interactions following exploitation, and the time required for these events to take place are critical to successful management of fish stocks on reefs and the maintenance of high species diversity in the systems. The primary objective of this study was to determine the short and long-term effects of predator removal on resident reef fishes.

METHODS

Four sites similar in size and topography are located along a north-south meridian in northern Onslow Bay, Atlantic Ocean. The four, 6–18 ha, patch reefs are called the Northwest Places and are located approximately 20 km SSW of Cape Lookout, North Carolina (Fig. 1). Reefs, separated by 2–4 km, are in depths of 17–23 m and support reef fish assemblages which contain large resident piscivores. Two of the sites were designated as experimental (predator removal) sites and the other two sites were designated as controls. Although we did not attempt to remove predators at the control sites, all sites were fished by the public, including one headboat[1]. Limited manpower precluded measuring public fishing effort; however, private boat fishing effort appeared to be significant. Study sites were delineated using a GPS (Global Positioning System) receiver and a depth sounder to determine size of reef and distance between reefs. Permanent 250 m transect lines were installed at all sites to facilitate repeatability and because of limited bottom time and visibility, and fishes were counted 5 m on either side, covering a total survey area of 2,500 m^2, per site. Transects consisted of 5 mm diameter line anchored with 1 m single flanged hurricane anchors 50 m apart in sand adjacent to rock outcroppings. Surveys were completed in 20 minutes. A small float was attached 5 m from the beginning of each transect and counts were not made if visibility was <5 m.

Preliminary underwater visual assessment of the resident reef fish assemblages was conducted in July 1994 by four divers (in pairs, alternating dives) using a modification of the Discrete Group Censusing (DGC) method (Greene and Alevizon, 1989; Greene and Shenker, 1993) to determine species composition and abundance. Resident piscivores (black sea bass, *Centropristis striata,* bank sea bass, *C. ocyurus,* gag, *Mycteroperca microlepis,* scamp, *M. phenax* (Parrish, 1986; Matheson et al., 1986) were divided into those larger or smaller than 250 mm total length (TL) because we believed the larger sizes were the main predators of the large prey species, Separate counts were made of adults and juveniles of all other species.

Following preliminary fish counts, high trophic level resident piscivores 250 mm TL and larger from the two designated experimental sites were removed over a period of one year. All other species and smaller size classes were released. Predator removal was accomplished by fish traps, hook and line fishing, and later,

[1] A headboat is a recreational fishing vessel with a passenger capacity of more than six anglers, and passage is usually charged on a per person (i.e., per "head") basis.

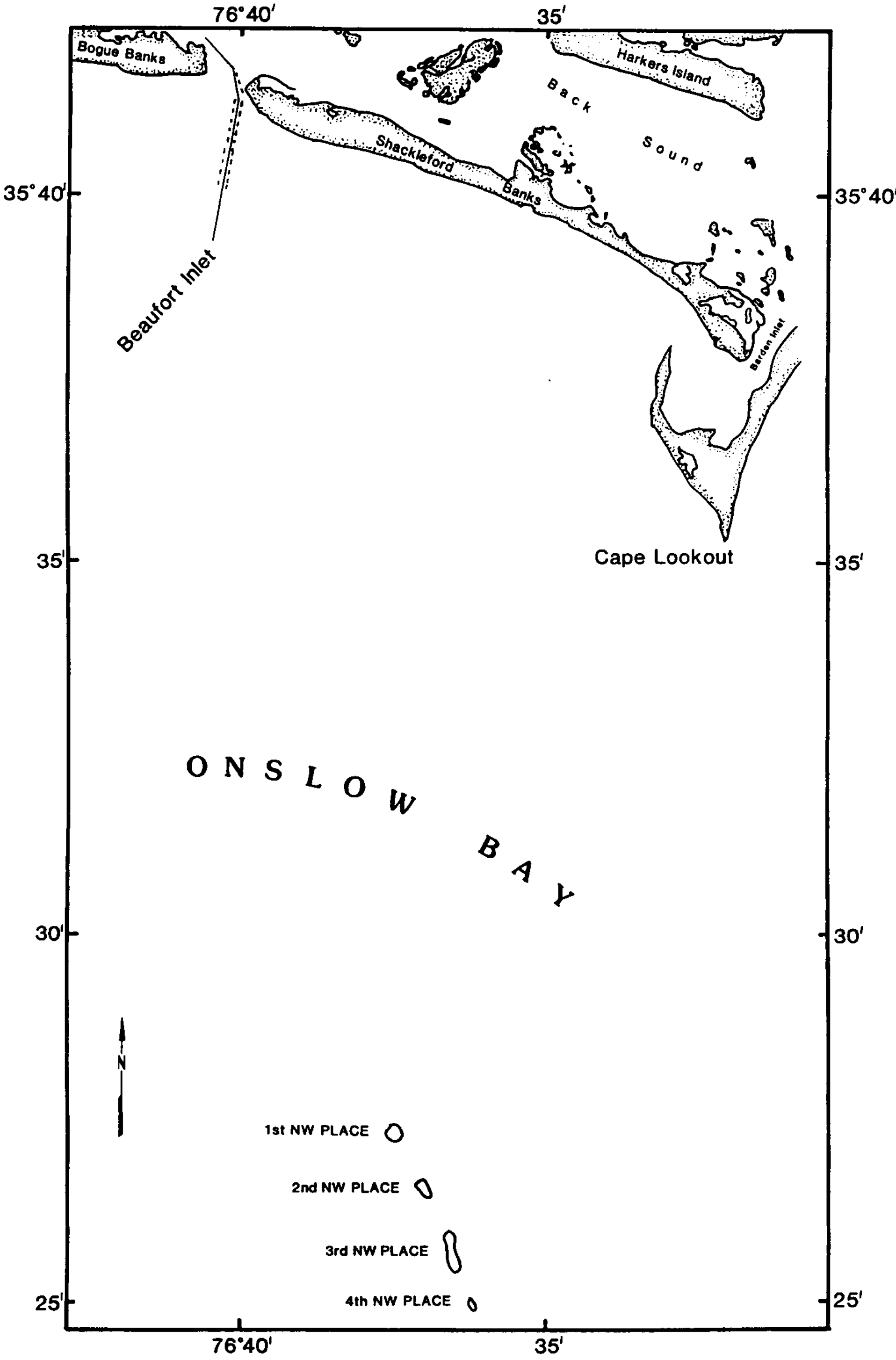

FIG. 1. Four study sites (collectively named the Northwest Places) in Onslow Bay, North Carolina, 20 km SSW of Cape Lookout, depths of 17–23 m.

spear fishing. Two Morton fish traps and one chevron trap, baited with "cigar minnows" (round scad, *Decapterus punctatus*), were set, retrieved, and located with a GPS receiver aboard the R/V *Onslow Bay*. For bottom fishing, we used four, 4/0 Penn reels on short boat rods with 3/0-6/0 hooks using 22.7 kg test monofilament line weighted with 454 g of lead. Baits were squid or "cigar minnows." Monthly visual assessments were made to determine if all large resident piscivores had been removed. Spear fishing was conducted using pole spears and spear guns during the final two months of the removal period.

After the removal phase, we continued to monthly monitor all four reefs using the DGC method until visibility (water clarity) prohibited visual counts in the late fall. We resumed counting in the spring when visibility permitted. Monitoring continued for 24 months after the predator removal was completed. Three null hypotheses tested in this study were:

(1) removal of top trophic level predators will not result in increased densities of prey species within the assemblage.
(2) removal of top trophic level predators will not result in decreased species diversity (richness and evenness) within the assemblage.
(3) removed top trophic level predators will not be replaced by immigration of other adults but will be replaced by newly settled juveniles.

The fish species composition of the Northwest Places were compared with that of an offshore site, the "210 Rock," because a recent study there implicated global warming (Parker and Dixon, 1998). This will provide information on the extent of expansion of the tropical community and baseline data for future studies.

RESULTS

Recently, the notion that predation often has a greater effect on community structure than previously believed has gained favor among investigators (Connell, 1978; Bohnsack, 1982; Doherty and Williams, 1988; Shpigel and Fishelson, 1991). Few studies have attempted to manipulate predator or prey species in reef fish assemblages (e.g., Connell, 1974, 1975; Thresher, 1983; Doherty and Sale, 1985; Shpigel and Fishelson, 1991; Caley, 1993; Beets, 1997).

Shpigel and Fishelson (1991) investigated the effects of grouper removal on resident reef fish assemblages in the Red Sea. They reduced grouper density to only 21.6% of the original population size, but found that other piscivorous species expanded into the vacated niche. Also, the typical prey species of the groupers showed no significant differences in abundance or species composition 36 months later. The high number of predatory species other than grouper in the Red Sea apparently precluded the attempt to eliminate all major predators and thus test the predation hypothesis in that system.

Rocky reefs of Onslow Bay, in the northern South Atlantic Bight, are much less faunistically complex than the reefs in the Red Sea and provide a simpler system with which to work. It was thought that the low species richness and low density of large predators on these reefs would permit removal of nearly all large piscivores and eliminate the possibility of niche expansion that was observed in the Red Sea.

Upper trophic level piscivores of the food chain play an important role in the reef ecosystems of tropical and subtropical seas (Randall and Brock, 1960; Munro, 1974). Large groupers are the major predators on reefs along the U.S. southeastern coast and are among the most prized commercial and recreational fishes of this area. Intensive fishing pressure that the near-shore reefs receive results in the removal of large numbers of predators from reef fish assemblages. Effects on lower trophic level fishes and the ability of the predator stocks to recover is unknown.

Fifty-seven species of fishes representing 29 families were observed during this study (Table 1). This compares to 96 species representing 38 families on a study site ("210 Rock") 24 km further offshore in depths of 27–33 m (Parker and Dixon, 1998, Table 1). Over twice as many northern[2] species were seen at the inshore sites than the offshore site, seven versus three. However, tropical[2] species were much more abundant offshore, 78 versus 40. Six tropical species were observed only on the inshore sites while 44 tropical species were seen only on the offshore site. Forty-four species were common to both locations.

During 1994–1995 we removed 78 and 53 adult (>250 mm) piscivores (Serranidae, Carangidae, Haemulidae, Labridae) from experimental sites 2 and 4, respectively (Table 2). After one year of intense fishing, we noted that we could not remove all of the adult piscivores but did reduce the number substantially. Counts of adult piscivores in July 1995 on the experimental sites were 75% and 58% less than counts in July 1994 (Table 3). Whereas, counts of adult piscivores on the control sites were 61% less (because of an exceptionally high count, 62 versus an average of 16 for the other three sites, in July 1994) and 87% more (within the range of counts during the year) than counts in July 1994. Each Northwest Place reef was surveyed four or five times during the next 24 months. High seas and poor visibility prevented us from making 47 of 88 planned monthly surveys.

During the predator removal period (July 1994–August 1995) abundance of adult piscivores was a fraction of juvenile abundance at the experimental sites (Table 3, Fig. 2). Conversely, adult piscivore abundance was at least half the juveniles abundance at the control sites. Once predator removal ceased, the adult predator populations at the removal sites exceeded their original densities in about 12 months while juvenile predator populations remained about the same (August 1996 Table 3; Fig. 2, sites 2 and 4). There were no apparent relationships over time in counts of abundance of species or species composition at the test or control sites, and there were large differences in the initial distribution of total numbers of adult piscivores (Tables 3, 4).

DISCUSSION

As with similar studies (Lassig, 1982; Stimson et al., 1982; Thresher, 1983; Doherty and Sale, 1985; Shpigel and Fishelson, 1991), our experimental design also proved to be fraught with difficulties. We were unable to remove all large (>250 mm) predatory fishes from the experimental sites, even though our Northwest Place reefs are much less faunistically complex than those of the Red Sea. Complete removal of all top-trophic level predators from a system by fishing is difficult, short of using methods resulting in total mortality of all fishes. Even in

---

[2] For rationale of classification of northern and tropical (southern) species see Parker and Dixon, 1998.

Table 1. Species and frequency of observation by divers during predator removal study at the Northwest Places (1994–1997) compared to an offshore dive site ("210 Rock", 1990–1993), 11 and 31 dives, respectively, off Beaufort, North Carolina.

Species	1994–1997 (Inshore)		1990–1993 (Offshore)	
Rhincodontidae				
Ginglymostoma cirratum, nurse shark[1]	1	9.1		
Carcharhinidae				
Carcharhinus obscurus, dusky shark			1	3.2
Dasyatidae				
Dasyatis sp., stingray	2	18.2	2	6.5
Muraenidae				
Gymnothorax moringa, spotted moray (S)	1	9.1	5	16.1
Ophichthidae				
Myrichthys breviceps, sharptail eel (S)			4	12.9
Congriidae				
Conger sp. or *Paraconger caudilimbatus*, conger (N)	1	9.1		
Synodontidae				
Synodus foetens, inshore lizardfish (S)	1	9.1	6	19.4
Gadidae				
Urophycis earlli, Carolina hake (S)	3	27.3	2	6.5
Batrachoididae				
Opsanus sp., toadfish[2] (S)	5	45.5	1	3.2
Holocentridae				
Holocentrus ascensionis, longjaw squirrelfish (S)			10	32.3
Aulostomidae				
Aulostomus maculatus, trumpetfish (S)			7	22.6
Fistulariidae				
Fistularia petimba, red cornetfish (S)			2	6.5
Serranidae				
**Centropristis striata*, black sea bass (N)	11	100.0	21	67.7
**C. ocyurus*, bank sea bass(S)	10	90.9	30	96.8
C. philadelphica, rock sea bass (S)	1	9.1		
Diplectrum formosum, sand perch (S)	2	18.2	6	19.4
**Epinephelus morio*, red grouper (S)			10	32.3
**E. adscensionis*, rock hind (S)			13	41.9
**E. guttatus*, red hind (S)			2	6.5
**E. cruentatus*, graysby (S)			5	16.1
**E. nigritus*, warsaw grouper (S)	2	18.2		
Hypoplectrus unicolor, butter hamlet (S)			20	64.5
Liopropoma eukrines, wrasse bass (S)			20	64.5
**Mycteroperca microlepis*, gag (S)	11	100.0	30	96.8
**M. phenax*, scamp (S)	11	100.0	30	96.8
**M. interstitialis*, yellowmouth grouper (S)			8	25.8
Rypticus maculatus, whitespotted soapfish (S)	6	54.5	21	67.7
Serranus subligarius, belted sandfish (S)	11	100.0	23	74.2
S. tigrinus, harlequin bass (S)			17	54.8
S. phoebe, tattler (S)			3	9.7

Table 1. Continued.

Species	1994–1997 (Inshore)		1990–1993 (Offshore)	
Priacanthidae				
Priacanthus arenatus, bigeye (S)			18	58.1
P. cruentatus, glasseye snapper (S)			3	9.7
Apogonidae				
Apogon pseudomaculatus, twospot cardinalfish (S)	3	27.3	15	48.4
Rachycentridae				
Rachycentron canadum, cobia	2	18.2	2	6.5
Echeneidae				
Remora remora, remora			1	3.2
Carangidae				
Caranx ruber, bar jack	2	18.2	11	35.5
C. bartholomaei, yellow jack	2	18.2	5	16.1
Decapterus punctatus, round scad	1	9.1	5	16.1
**Seriola dumerili,* greater amberjack	7	63.6	28	90.3
**S. rivoliana,* almaco jack			11	35.5
S. zonata, banded rudderfish			4	12.9
Coryphaenidae				
Coryphaena hippurus, dolphin			2	6.5
Lutjanidae				
**Lutjanus campechanus,* red snapper (S)			1	3.2
**L. apodus,* schoolmaster (S)			2	6.5
**Rhomboplites aurorubens,* vermilion snapper (S)	4	36.4		
Gerreidae (mojarra)			1	3.2
Haemulidae				
**Haemulon plumieri,* white grunt (S)	4	36.4	30	96.8
**H. aurolineatum,* tomtate (S)	11	100.0	26	83.9
Orthopristis chrysoptera, pigfish (N)	10	90.9		
Sparidae				
**Archosargus probatocephalus,* sheepshead (N)	10	90.9		
**Calamus leucosteus,* whitebone porgy (S)	11	100.0	18	58.1
**C. nodosus,* knobbed porgy (S)	9	81.8	30	96.8
**Diplodus holbrooki,* spottail pinfish (S)	11	100.0	14	45.2
**Pagrus pagrus,* red porgy (S)	1	9.1	14	45.2
Stenotomus chrysops, scup (N)	11	100.0		
Sciaenidae				
Equetus umbrosus, cubbyu (S)	11	100.0	27	87.1
E. lanceolatus, jacknife-fish (S)			11	35.5
Mullidae				
Mulloidichthys martinicus, yellow goatfish (S)	1	9.1	9	29.0
Pseudupeneus maculatus, spotted goatfish (S)	2	18.2	17	54.8
Upeneus parvus, dwarf goatfish (S)	9	81.8		
Ephippidae				
Chaetodipterus faber, Atlantic spadefish	9	81.8	9	29.0

Table 1. Continued.

Species	1994–1997 (Inshore)		1990–1993 (Offshore)	
Chaetodontidae				
Chaetodon ocellatus, spotfin butterflyfish (S)			22	71.0
C. sedentarius, reef butterflyfish (S)	2	18.2	13	41.9
C. striatus, banded butterflyfish (S)			6	19.4
Pomacanthidae				
Holacanthus bermudensis, blue angelfish (S)	6	54.5	30	96.8
H. ciliaris, queen angelfish (S)	5	45.5	21	67.7
H. tricolor, rock beauty (S)			2	6.5
Pomacanthus paru, French angelfish (S)			4	12.9
Pomacentridae				
Abudefduf tauras, night sergeant (S)			9	29.0
Chromis multilineata, brown chromis (S)			1	3.2
C. insolata, sunshinefish (S)			14	45.2
C. scotti, purple reeffish (S)			29	93.5
C. cyaneus, blue chromis (S)			7	22.6
C. enchrysurus, yellowtail reeffish (S)			25	80.6
Pomacentrus partitus, bicolor damselfish (S)	6	54.5	24	77.4
P. variabilis, cocoa damselfish (S)	4	36.4	27	87.1
P. fuscus, dusky damselfish (S)			11	35.5
Sphyraenidae				
Sphyraena barracuda, great barracuda	3	27.3	11	32.4
S. borealis, northern sennet (N)	5	45.5		
Labridae				
Bodianus pulchellus, spotfin hogfish (S)			29	93.5
B. rufus, Spanish hogfish (S)			26	83.9
Clepticus parrae, creole wrasse (S)			3	9.7
Halichoeres bivittatus, slippery dick (S)	11	100.0	27	87.1
H. garnoti, yellowhead wrasse (S)			13	41.9
**Lachnolaimus maximus,* hogfish (S)	2	18.2	24	77.4
**Tautoga onitis,* tautog (N)	10	90.9	13	41.9
Thalassoma bifasciatum, bluehead (S)			21	67.7
Scaridae				
Scarus sp. (S)			11	35.5
Sparisoma viride, stoplight parrotfish (S)			2	6.5
Sparisoma sp. (S)			11	35.5
Blenniidae				
Parablennius marmoreus, seaweed blenny (S)	9	81.8	7	32.4
Gobiidae				
Coryphopterus punctipectophorus, spotted goby (S)			5	16.1
Gobiosoma oceanops, neon goby (S)			2	6.5
G. sp. (S)			2	6.5
Ptereleotris calliura, blue goby (S)	7	63.6	11	35.5
Acanthuridae				
Acanthurus bahianus, ocean surgeon (S)			9	29.0
A. coeruleus, blue tang (S)	2	18.2	17	54.8
A. chirurgus, doctorfish (S)	2	18.2	21	67.7
Scombridae				
**Scomberomorus cavalla,* king mackerel			1	3.2

Table 1. Continued.

Species	1994–1997 (Inshore)		1990–1993 (Offshore)	
Balistidae				
Aluterus scriptus, scrawled filefish (S)			1	3.2
**Balistes capriscus*, gray triggerfish (S)	9	81.8	13	41.9
Monacanthus hispidus, planehead filefish (S)	10	90.9	29	93.5
Bothidae				
Paralichthys oblongus, fourspot flounder (N)	1	9.1		
Ostraciidae				
Lactophrys quadricornis, scrawled cowfish (S)	1	9.1		
L. sp., boxfish (S)			1	3.2
Tetraodontidae				
Canthigaster rostrata, sharpnose puffer (S)			3	9.7
Sphoeroides spengleri, bandtail puffer (S)	1	9.1	22	71.0
**S. maculatus*, northern puffer (N)			1	3.2
Chilomycterus schoepfi, striped burrfish (S)	1	9.1		
SPECIES	57		96	
FAMILIES	29		38	

[1] Nondesignated species were not the main concern of this study (e.g., sharks, jacks, and mackerels).
[2] Opsanus sp. is likely an undescribed offshore form.
* Target species (important in the recreational and commercial fisheries).
S Tropical species.
N Temperate species.

Ohio farm ponds, fishermen were unable to catch all large, largemouth bass, *Micropterus salmoides* (Parker, pers. diving obser., Ohio Div. Wild.). Other experimental artifacts, were encountered, such as poor visibility and high sea-state, hampering our sampling efforts. Also, immigration of new piscivores probably confounded our results. It is possible that these four Northwest Place reefs were too closely spaced and that instead of four independent habitats, the system would be better described as one larger habitat. None of the three null hypotheses of this study were accepted.

One cannot conclude from our results that heavy fishing pressure does not dramatically reduce reef fish populations on the small Northwest Place reefs in Onslow Bay, North Carolina. Although there were no apparent relationships established over time in counts of abundance or species composition at the test or control sites, there was a large drop in total numbers of adult predators at the

Table 2. Number of adult (>250 mm) piscivores (Serranidae, Carangidae, Haemulidae, Labridae) removed at the Northwest Places, 1994–1995.

Fishing Method	Experimental Sites 2	Experimental Sites 4
Hook and Line	45	33
Spear Fishing	10	14
Fish Traps	23	6
TOTAL	78	53

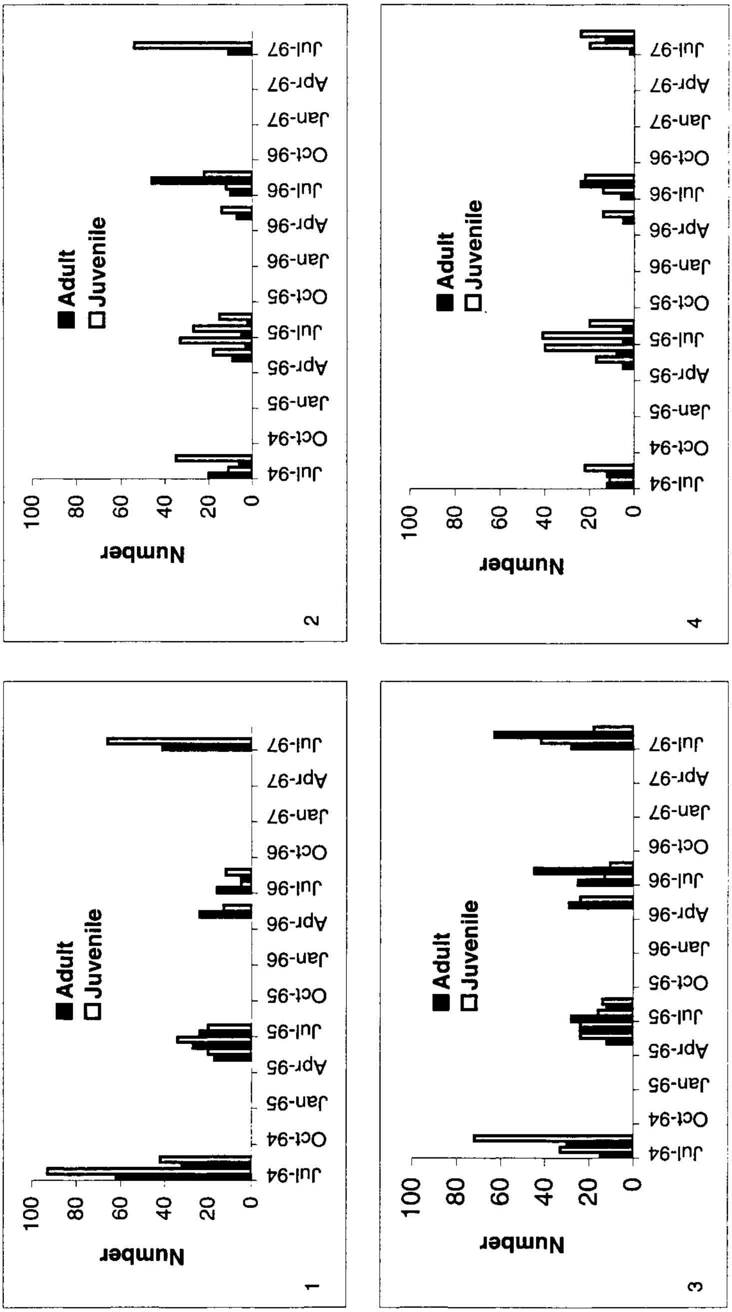

FIG. 2. Standardized piscivore counts by date at the Northwest Places, sites 1 and 3 were controls.

Table 3. Piscivore counts (fishes <250 mm in parentheses) by date and site at the Northwest Places, fishing versus recovery period, 1994–1997.

Date	Site 1	2[1]	3	4[1]
Fishing				
Jul 1994	62 (93)	20 (11)	15 (33)	12 (11)
Aug	32 (42)	6 (35)	30 (72)	12 (22)
May 1995	17 (20)	9 (18)	12 (24)	5 (17)
Jun	27 (34)	3 (33)	24 (24)	8 (40)
Jul	24 (20)	5 (27)	28 (16)	5 (41)
Aug	*	2 (15)	12 (14)	5 (20)
Recovery				
May 1996	24 (13)	7 (14)	29 (24)	5 (14)
Jul	16 (5)	10 (12)	25 (13)	6 (14)
Aug	5 (12)	46 (22)	45 (11)	24 (22)
Jul 1997	41 (66)	11 (54)	28 (42)	2[2] (20)
Aug			63 (18)	13 (24)

[1] Experimental site.
* Blanks indicate counts missed because of poor visibility or adverse sea conditions.
[2] >30 adult grouper, in a cluster were observed outside the transect.

removal sites. This effect, however, appeared to be short lived and did not seem to effect other populations of fishes on those sites. Based upon this study, and previous studies that attempted to test the predation hypothesis (Russ, 1985; Caley, 1993; Hixon and Beets, 1993; Carr and Hixon, 1995; Jennings et al., 1995; Beets, 1997; Jennings and Polunin, 1997), we agree with the assertion by Jennings and Polunin (1997) that, "... the structure of reef fish communities is rarely governed by a single dominant process, but by a range of processes such as

Table 4. Number of species present by date and site at the Northwest Places, fishing versus recovery period, 1994–1997.

Date	Site 1	2[1]	3	4[1]
Fishing				
Jul 1994	22	23	20	18
Aug	24	20	20	22
May 1995	16	16	14	17
Jun	24	16	20	19
Jul	22	18	19	19
Aug		16	22	17
Recovery				
May 1996	20	20	16	18
Jul		12	16	14
Aug	15	18	22	16
Jul 1997	25	19	11	14
Aug			25	17

[1] Experimental site.

recruitment variability, predation, competition, physical disturbance, and oceanographic conditions, which operate on different scales in different circumstances."

In addition to documenting the attempted complete piscivore removal, the value of this study is the 36 months of cataloging fish assemblages on four inshore natural reefs in northern Onslow Bay, North Carolina. They serve as a valuable baseline, especially when compared to data gathered on reefs further offshore, and which have shown recent changes that may be attributable to global warming (Parker and Dixon, 1998). This study showed that there are about 40% fewer species on the Northwest Place inshore sites compared to the "210 Rock" offshore site in Onslow Bay, and there are more northern species inshore, but more tropical species offshore. The Gulf Stream keeps the outer reefs of Onslow Bay bathed with warmer water throughout the year (Parker and Dixon, 1998). This is the first time reef fish assemblages of these inshore reefs have been studied, and these data may prove invaluable in future studies that may attempt to quantify the effects of global environmental changes on reef fish assemblages in North Carolina.

Acknowledgments: We thank the Captain of the R/V *Onslow Bay,* Doug Willis, for consistently putting us on station without the aid of surface buoys. Also, we thank our support divers: Mike Burton, Bob Dixon, Larry Krepp, Roger Mays, Julie Scope, and Paula Whitfield for making this effort possible.

REFERENCES CITED

BEETS, J. 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Mar. Ecol. Prog. Ser. 148:11–21.

BOHNSACK, J. A. 1982. Effects of piscivorous predator removal on coral reef fish community structure. Pp. 258–267 in G. M. Cailliet and C. A. Simenstat (eds.), Gutshop '81. Fish Food Habits Studies. Proceedings of the Third Pacific Workshop. Washington Sea Grant Publ. WSG-WO 82-2.

CALEY, M. J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. Mar. Biol. 117:33–43.

CARR, M. H., AND M. A. HIXON. 1995. Predation effect on the early post-settlement survivorship of coral-reef fishes. Mar. Ecol. Prog. Ser. 124:31–42.

CONNELL, J. H. 1974. Ecology, field experiments in marine ecology. Pp. 21–54 in R. N. Mariscal (ed.), Experimental Marine Biology. Academic Press, NY.

———. 1975. Some mechanisms producing structure in natural communities. Pp. 460–490 in M. L. Cody and J. M. Diamond (eds.), Ecology and Evolution of Communities. Belknap-Harvard University Press, Cambridge, MA.

———. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

DOBZHANSKY, T. 1950. Evolution in the tropics. Am. Sci. 38:208–221.

DOHERTY, P. J., AND P. F. SALE. 1985. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 4:225–234.

———, AND D. McB. WILLIAMS. 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. 26:487–551.

EMERY, A. R. 1978. The basis of fish community structure: marine and freshwater comparisons. Env. Biol. Fish. 3:33–47.

GREENE, L. E., AND W. S. ALEVIZON. 1989. Comparative accuracies of visual assessment methods for coral reef fishes. Bull. Mar. Sci. 44:899–912.

———, AND J. M. SHENKER. 1993. The effects of human activity on the temporal variability of coral reef fish assemblages in the Key Largo National Marine Sanctuary. Aquat. Cons. 3:189–205.

HIXON, M. A., AND J. P. BEETS. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63:77–101.

HUNTSMAN, G. R. 1979. Predators' role in structuring reef fish communities. Pp. 103–108 in H. Clepper. (ed.), Predator Prey Systems in Fisheries Management. Sport Fish. Inst. Washington, DC.

JENNINGS, S., E. G. GRANDCOURT, AND N. V. C. POLUNIN. 1995. Effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14:225–235.

———, AND N. V. C. POLUNIN. 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs 16:71–82.

LASSIG, B. R. 1982. The minor role of large transient fishes in structuring small-scale coral patch reef assemblages. Ph.D. thesis, Macquarie University, Sidney, Australia.

MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, NY. 269 p.

MATHESON, R. H., III, G. R. HUNTSMAN, AND C. S. MANOOCH III. 1986. Age, growth, mortality, food, and reproduction of the scamp. *Myteroperca phenax*, collected off North Carolina and South Carolina. Bull. Mar. Sci. 38:300–312.

MUNRO, J. L. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Part 5b. Serranidae (Hinds and Groupers). Res. Rep. Zool. Dept. Univ. West Indies, No. 3.

PAINE, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65–75.

———. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52:1096–1106.

PARKER, R. O., JR., AND R. L. DIXON. 1998. Changes in a North Carolina reef fish community after 15 years of intense fishing—with global warming implications. Trans. Am. Fish. Soc. 127:908–920.

PARRISH, J. D. 1986. The trophic biology of snappers and groupers. Pp. 405–464 in J. J. Polovina and S. Ralston (eds.), Tropical Snappers and Groupers: Biology and Fisheries Management. Westview Press, Inc., Boulder, CO.

PIANKA, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100: 33–46.

RANDALL, J. E., AND V. E. BROCK. 1960. Observations on the ecology of Epenepheline and Lutjanid fishes of the Society Islands, with emphasis on food habits. Trans. Am. Fish. Soc. 89:9–16.

RUSS, G. R. 1985. Effects of protective management on coral reef fishes in the Philippines. Proc. Sixth Internat. Coral Reef Symp. 6:219–224.

SIH, A., P. CROWLEY, M. MCPEEK, J. PETRANKA, AND K. STROHMEIER. 1985. Predation, competition, and prey communities: a review of field experiments. Ann. Rev. Ecol. Syst. 16:269–311.

SHPIGEL, M., AND L. FISHELSON. 1991. Experimental removal of piscivorous groupers of the genus *Cephalopholis* (Serranidae) from coral habitats in the Gulf of Aqaba (Red Sea). Env. Biol. Fish. 31:131–138.

STIMSON, J., S. BLUM, AND R. E. BROCK. 1982. An experimental study of the influence of muraenid eels on reef fish sizes and abundance. Hawaii Sea Grant Quar. 4:1–6.

THRESHER, R. E. 1983. Habitat effects on reproductive success in the coral reef fish, *Acanthochromis polyacanthus* (Pomacanthidae). Ecology 64:1184–1199.

Received 27 May 1999