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Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict by ecological experimentation

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Abstract.—We conducted a large-scale field experiment to test whether clam and oyster harvesting applied alone and in combination on intertidal oyster reefs have impacts on resident shellfish populations. This experiment was conducted to resolve a long-standing conflict between oyster (*Crassostrea virginica* (Gmelin, 1791)) and clam (*Mercenaria mercenaria* (Linneaus, 1758)) fishermen who contend that the other fishery causes high rates of mortality to their respective species. Intertidal oyster reefs located in two estuarine creeks near Wilmington, North Carolina, were harvested for clams only, oysters only, both clams and oysters, or were left undisturbed as controls. Experimental harvesting was conducted over a one-year period by a professional shellfisherman who used realistic fishing techniques (clam rakes and oyster tongs), intensity, and frequency. Harvesting impact on hard clam and oyster populations was assessed by sampling naturally occurring oysters before and after harvesting, and sampling both naturally occurring clams (all size classes) and transplanted, hatchery-raised clams (20–37 mm in length) after harvesting. Clam and oyster harvesting had obvious negative effects on populations of oysters. There was a substantial decrease in the number of live oysters on clam-harvested and oyster-harvested reefs compared with unharvested, control reefs. Clam and oyster harvesting, applied together, reduced oyster densities and killed unharvested oysters at a level similar to that caused by each type of harvesting applied separately. The effects of the shellfish harvesting on populations of hard clams varied between the two sites (i.e. creeks). In both creeks, clam harvesting, alone and combined with oyster harvesting, significantly decreased the number of live, naturally occurring clams. Oyster harvesting alone decreased the number of live, naturally occurring clams only at one site. Clam harvesting also decreased the number of live, transplanted clams on reefs, but there was no effect of oyster harvesting, because the transplanted clams were juveniles too small to be harvested with oyster tongs. Overall, the combined effect of both types of harvesting applied together did not have a negative synergistic effect on clam and oyster populations. Consequently, both clamming and oyster harvesting should be permitted on some reefs, but maintaining large populations of oysters and clams on intertidal oyster reefs will require protection of some reefs from both types of harvesting.

Marine fisheries are an important source of employment and protein for humans but can negatively affect marine organisms and ecosystems (Dayton et al., 1995; Engel and Kvitek, 1995; Botsford et al., 1997). The most obvious negative ecological effects of fishing result from over-harvesting of target species, incidental mortality of nontarget species ("bycatch"), and fishery-related disturbances to marine habitat (FAO, 1993; Dayton et al., 1995). Of course, fisheries over-exploitation and habitat destruction also threaten the sustainability of the fishing industry. At present, 44% of the worlds fish stocks are fully to heavily exploited, and 22% are overexploited or depleted, indicating most fisheries are not managed for long-term sustainability (Botsford et al., 1997). The degradation and destruction of marine biogenic habitat (e.g. coral reefs, seagrass beds, mangrove forests, and oyster reefs) by dredging, trawling, use of explosives, and poisoning reduces fishery production by removing habitat essential for the recruitment, growth, and survival of fishery and prey organisms (Winslow 1881, a and b; Peterson et al., 1987; Norse, 1993; Rothschild et al., 1994; NRC, 1995; Lenihan and Peterson,

1998). The sustainability of a fishery is often threatened when competing fisheries exploit a common resource or negatively impact a commonly used habitat. For example, when the bycatch of one fishery is within a food web supporting another fishery (West and Gordon, 1994), or when a fishery destroys habitat important to the life history of other fishery species (Russ and Alcala, 1996), heated political battles arise and the livelihood of many people may be lost. Resolving such fishery conflicts has important ecological and economic consequences and is of major concern to fisheries managers and ecologists worldwide (McAllister and Peterman, 1992). This paper presents the results of an experimental analysis of whether two economically valuable fisheries conflict and provides management recommendations to resolve the conflict.

High productivity of fishery stocks in estuaries and shallow water coastal habitats often induces intense exploitation of a common species or habitat by multiple, potentially conflicting fisheries (Peterson et al., 1987). In many estuaries along the Atlantic coast of the USA, intertidal oyster reefs are harvested for hard clams (*Mercenaria mercenaria*) year round,

of different choices among fishery management options. For example, it is appropriate to allow fishing mortality to exceed the biological reference point if the goal is to reduce an overly abundant fish stock. Likewise, they can be useful in projecting the likely growth of a population under more restrictive fishery management measures. In the end, however, they may be most useful as a reminder and a warning that there are limits to the productive capacity of fish population and that if we consistently exceed their limits, population declines are almost certain to occur (Francis, 1997; Myers, 1997).

Acknowledgments

Literature cited

Aitchison, J., and J. A. C. Brown.
1976. The lognormal distribution with special reference to its uses in economics. Cambridge Univ. Press, Cambridge, England, 176 p.

Beverton, R. J. H., and S. J. Holt.
1957. On the dynamics of exploited fish populations. U.K. Ministry of Agriculture, Fisheries and Food Fishery Investigations (series 2) 19, 533 p.

Caswell, H.
1989. Matrix population models. Sinauer Associates, Sunderland, MA, 328 p.

Clark, S. H., W. J. Overholtz, and R. C. Hennemuth.
1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northwest Atl. Fish. Sci. 3:1–27.

Clark, W. G.
1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734–750.

Cochran, W. G.
1977. Sampling techniques. Wiley and Sons, New York, NY, 428 p.

Cohen, J. E., S. W. Christensen, and C. P. Goodyear.
1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. Can. J. Fish. Aquat. Sci. 40:2170–2183.

Collie, J. S., and P. D. Spencer.
1993. Management strategies for fish populations subject to long-term environmental variability and depensatory predation. *In* G. Kruse, D. M. Eggers, R. J. Marasco, C. Pautzke, and T. J. Quinn, II (eds.), Proceedings of the international symposium on management strategies for exploited fish pop-

ulations, p. 629–650. Alaska Sea Grant College Program Report 93-02, Univ. Alaska, Fairbanks, AK.

DeAngelis, D. L., S. W. Christensen, and A. G. Clark.
1977. Responses of a fish population to young-of-the-year mortality. J. Fish. Res. Board Can. 34:2124–2132.

Francis, R. I. C. C.
1997. Comment: How should fisheries scientists and managers react to uncertainty about stock-recruit relationships? Can. J. Fish. Aquat. Sci. 54:982–983.

Gabriel, W. L., M. P. Sissenwine, and W. J. Overholtz.
1989. Analysis of spawning stock biomass per recruit: an example for George Bank haddock. N. Am. J. Fish. Manage. 9:383–391.

Getz, W. M., and R. C. Haight.
1989. Population harvesting: demographic models of fish, forest and animal resources. Princeton Univ. Press, Princeton, NJ, 391 p.

Goodyear, C. P., and S. W. Christensen.
1984. Bias-elimination in fish population models with stochastic variation in survival of the young. Trans. Am. Fish. Soc. 115:627–632.

Gulland, J. A., and L. K. Boerema.
1973. Scientific advice on catch levels. Fish. Bull. 71:325–335.

Johnson, L. W., and R. D. Riess.
1981. Introduction to linear algebra. Addison-Wesley, Reading, MA, 358 p.

Keyfitz, N.
1977. Introduction to the mathematics of populations with revisions. Addison-Wesley, Reading, MA, 490 p.

Mace, P. M.
1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. 51:110–122.

Myers, R. A.
1997. Comment and reanalysis: paradigms for recruitment studies. Can. J. Fish. Aquat. Sci. 54:978–981.

Myers, R. A., and P. Pepin.
1994. Recruitment variability and oceanography stability. Fish. Oceanogr. 3:246–255.

Overholtz, W. J., M. P. Sissenwine, and S. H. Clark.
1986. Recruitment variability and its implication for managing and rebuilding the Georges Bank haddock (*Melanogrammus aeglefinus*) stock. Can. J. Fish. Aquat. Sci. 43:748–753.

Pielou, E. C.
1974. Population and community ecology. Gordon and Breach Science Publishers, New York, NY, 424 p.

Quinn, T. J., II, and N. J. Szarzi.
1993. Determination of sustained yield in Alaska's recreational fisheries. *In* G. Kruse, D. M. Eggers, R. J. Marasco, C. Pautzke, and T. J. Quinn, II (eds.), Proceedings of the international symposium on management strategies for exploited fish populations, p. 61–84. Alaska Sea Grant College Program Report 93-02. Univ. Alaska, Fairbanks, AK.

Rothschild, B. J., and M. J. Fogarty.
1989. Spawning-stock biomass: a source of error in recruitment/stock relationships and management advice. J. Cons. Int. Explor. Mer 45:131–135.

Sissenwine, M. P., and J. G. Shepherd.
1987. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci. 44:913–918.

Tuljapurkar, S.
1989. An uncertain life: demography in random environments. Theor. Pop. Biol. 35:227–294.

and for oysters (*Crassostrea virginica*) in the fall and winter (i.e. October–March). In recent years, clam and oyster (i.e. "shellfish") harvesting on oyster reefs has led to conflict between the two fisheries, and between fishermen and habitat managers over the issue of habitat degradation, especially in the southeastern United States (e.g. Frankenberg[1]; Noble[2]). Oyster fishermen claim that the harvesting of clams from intertidal oyster reefs decreases resident oyster populations, and vice-versa, because each type of fishing kills or removes the other species. Rakes and hand tongs used for the two types of shellfishing appear to increase the mortality of the sessile reef animals by burying them beneath sediments, fracturing their shells, or causing other physical damage (Noble[2]). In addition, bodies of dead and wounded animals left behind may attract scavengers and predators, thereby increasing predation intensity on healthy live animals (Dayton et al., 1995). Habitat and fishery managers are concerned that the physical destruction of oyster reefs caused by shellfishing will negatively affect many other fishery organisms that recruit to and utilize oyster reef habitat, including many species of fishes (Breitburg et al. 1995, Lenihan et al., 1998, Luckenbach et al., 1998) and the blue crab (*Callinectes sapidus* (Rathbun)) (Bahr and Lanier, 1981; Zimmerman et al., 1989; Lenihan et al., 1998; Micheli and Peterson, 1999). Shellfishing also reduces the overall size of reefs because shell material is broken or removed along with the target species (Lenihan and Peterson, 1998; Coen[3]). Reducing the size of reefs is thought to decrease the abundance of clams because less habitat is available for adults and recruits (Arnold, 1984; Sponaugle and Lawton, 1990; Peterson et al., 1995). Decreasing the size (i.e. height) of oyster reefs also reduces oyster production because flow speed over reefs diminishes, causing sediment to accumulate and oyster growth and survival to decrease (Lenihan, 1999; Lenihan et al., 1999). In contrast to the negative effects of shellfish harvesting, many fishermen claim that "turning over" the shell matrix of oyster reefs during harvesting improves clam and oyster production because it removes accumulated sediment. In North Carolina and many other Atlantic coast states, both types of shellfishing are allowed on reefs and conflicts between the fisheries continue (e.g. Frankenberg[1]; Marshall[4]).

Whether oyster harvesting, clam harvesting, or both types of fishing activities together have negative impacts on shellfish populations of intertidal oyster reefs is a matter of opinion and has not been tested experimentally.

A comparison of the biological impact of various fishing practices by using large-scale field experiments is an efficient method of resolving many fishery-related conflicts (McAllister and Peterman, 1992) and is an important component of adaptive management strategies (Walters, 1986). Such experiments are usually designed so that replicate areas (i.e. treatments) are fished, by using each technique separately and by using a combination of techniques, while other areas (i.e. controls) are closed to fishing. For these experiments to be meaningful, they must be conducted on realistic temporal and spatial scales, and the fishing treatments must be applied through the actual fishery (McAllister and Peterman, 1992). The success of such experiments also depends heavily on close working relationships among fishermen, fishery ecologists, and fishery managers (Grumbine, 1997). For adaptive management, the results of initial (i.e. "prototype") experiments are used to design new management strategies that are subsequently tested on even larger temporal and spatial scales. Such adaptive management strategies and the use of experimental approaches are often discussed in fisheries management, but in reality are rarely attempted (e.g. Walters, 1986; Botsford et al., 1997).

We conducted a large-scale field experiment to test the effects of hard clam and oyster harvesting, separately and in combination, on oyster and hard clam populations living on intertidal oyster reefs in North Carolina. Specifically, we tested whether 1) the density of live and dead oysters varied among oyster reefs that were harvested for clams, harvested for oysters, harvested for clams and oysters, or were unharvested; 2) the density of live and dead clams varied among oyster reefs subjected to the same four harvesting treatments; and 3) the joint application of both shellfish harvesting practices has a synergistic (i.e. a multiplicative) effect on each species. If applying both types of harvesting to the same reefs enhances potential negative effects of each harvesting type, a possible management option would be to allow clam and oyster harvesting only on separate reefs. This experiment was designed and conducted with the combined effort of a clam and oyster fisherman,[5] ecologists,[6] and habitat

[1] Frankenberg, D. 1995. Report of North Carolina Blue Ribbon Advisory Council on oysters. North Carolina Department of Environmental Health, and Natural Resources, Raleigh, NC, 101 p.

[2] Noble, E. B. 1995. Destruction of oyster rocks by individuals taking clams by legal hand harvest methods. Report of the North Carolina Division of Marine Fisheries, Morehead City, NC, 11 p.

[3] Coen, L. D. 1995. A review of the potential impacts of mechanical harvesting on subtidal and intertidal shellfish resources. A report prepared by the South Carolina Department of Natural Resources, Marine Resources Research Institute, SC, 111 p.

[4] Marshall, M. 1996. North Carolina Division of Marine Fisheries, 3431 Arendell St., Morehead City, NC, 28557. Personal commun.

[5] Cummings, R. A. 1996. For address contact H. S. Lenihan, Institute of Marine Sciences, 3431 Arendell, Morehead City, NC 28557. Personal commun.

[6] Peterson, C. H., and H. C. Summerson. 1997. Institute of Marine Sciences, 3431 Morehead City, NC 28557.

managers,[7] and is a prototype experiment for adaptive management of shellfisheries in southeastern North America.

Methods

Study sites

The intertidal oyster reefs used in this study were located in two large tidal creeks, Pages and Whiskey Creeks, situated on the Intercoastal Waterway near Masonborough Inlet, Wilmington, North Carolina. The two creeks consisted of well-flushed sandy to muddy bottom tidal channels 0–2 m in water depth. Channels in each creek were separated by small to large patches of marsh (*Spartina alterniflora*) habitat surrounded by oyster reefs created by *Crassostrea virginica*. The two creeks were chosen because they have been permanently closed to fishing for about the last ten years owing to high coliform bacteria counts caused by the seepage of septic tanks from surrounding homes. Both creeks are highly productive, supporting large populations of fishes, birds, crabs, clams, and oysters. Tides in each creek are predominantly M-2 lunar tides, and the tidal range is 1–2 m in both creeks. Four large oyster reefs (9–13 m wide × 45–55 m long), each containing relatively high densities of oysters and hard clams, were chosen in each creek. The reefs were situated 150–200 m from the mouth of each creek. The salinity near the experimental reefs was 22–34 psu throughout the course of the experiment and water temperature was 3–30°C.

Three to five permanent 6-m long × 1-m wide transects were established haphazardly on each oyster reef by using PVC poles with rebar anchors between 1–14 June 1996. A total of sixteen transects were established in each creek at approximately 0.5 m above the mean low tide level. The sixteen transects provided a total of four replicates of each of the following four harvest treatments: clam harvesting only, oyster harvesting only, clam harvesting and oyster harvesting combined, and no harvesting. Reefs and transects were located in areas where disturbances caused by shellfishing, boat traffic, or other human activities did not normally occur. We found no evidence suggesting that experimental reefs were physically or chemically disturbed throughout the course of the experiment.

Sampling of clams and oysters

The density of live and dead oysters on each experimental oyster reef was measured between 5 and 10

[7] Carpenter, R., and M. Marshall. 1996. North Carolina Division of Marine Fisheries, 3431 Arendell St., Morehead City, NC 28557.

July 1996 before harvest treatments were applied. Oyster density was measured by counting (but not removing) oysters in three 0.25-m² permanent plots established in each of the sixteen transects in each creek. Plots were established by stretching a measuring tape between the two PVC poles marking each transect and by placing a PVC quadrat at 0.5-, 2.5-, and 3.5-m distance. All live and dead oysters were counted in each quadrat. The density of naturally colonized clams was not determined prior to the application of harvest treatments to avoid disturbing the reefs and potentially influencing the condition of the remaining clams and oysters. Instead, between 5 and 10 July, 16 hatchery-raised clams provided by ARC, Inc. of Atlantic, North Carolina, were placed in each of three 1-m² quadrats established within each 6-m transect. This introduction of transplanted clams was done to assure that enough clams were present for the experiment. The 1-m² quadrats were also placed at 0.5, 2.5, and 3.5 m distance along the transects. Before being transplanted, hatchery clams were dyed in Alizarin red dye in order to distinguish them from natural clam populations (Peterson et al., 1995). Of the 16 clams in each plot, eight were 20–25 mm in length, and eight were 27–32 mm in length.

Between October 1996 and March 1997, oysters were harvested with hand tongs during low tides within the 1) oyster harvesting and 2) clam and oyster harvesting treatments. Oysters were harvested for the same total period of time (3.75–4.0 h/transect) along the entire length of each transect. From August 1996 to May 1997, clams were harvested during low tides with clam rakes and clam tongs from the 1) clam harvesting and 2) clam and oyster harvesting treatments, and for approximately the same total period of time (i.e. 3.75–4.0 h/transect). The total number of naturally occurring and transplanted clams and oysters removed during the harvest was recorded. All harvesting was conducted by R. A. Cummings, a professional shellfisherman.

The density of live and dead clams and oysters remaining on experimental reefs was sampled 10–23 July 1997, after termination of the harvesting treatments. Clams and oysters were sampled several months after the last clam harvesting in May so that any potential long-term effects of harvesting were realized. For example, unharvested clams and oysters remaining on reefs may have been injured during harvesting and died after several weeks. Oysters were sampled by placing a measuring tape along the transects and counting all oysters within the three 0.25-m² quadrats at 0.5-, 2.5-, and 3.5-m distance along each transect. Clams were sampled by digging up the top 25 cm of sediment from each 1-m² sampling plot. The sediment was then passed through a 1-mm sieve to remove all clams.

Table 1

Mean square errors (MS), F ratios, and corresponding significance levels (P) of two-way fixed factor ANOVAs comparing densities of live and dead oysters, and proportions of dead oysters (per 0.25 m^2) among intertidal oyster reefs before application of experimental harvest treatments (sampled 5–10 July 1996). The main factors in ANOVAs were creeks (Pages and Whiskey Creeks) and harvest treatment (clamming, oystering, both, and neither).

Source	df	Live			Dead			Proportion dead		
		MS	F	P	MS	F	P	MS	F	P
Creek (C)	1	277.50	6.17	0.02	378.10	34.58	0.0001	0.03	30.11	0.0001
Harvest treatment (H)	3	31.03	0.69	0.57	0.41	0.04	0.99	0.001	0.48	0.70
C × H	3	31.74	0.71	0.56	12.27	1.12	0.36	0.001	1.19	0.33
Residual	24	45.01			10.93			0.001		

Statistical analyses

The density of live and dead oysters, and the proportion of the total number of oysters that were found dead before harvesting, were compared among treatments by using two-way, fixed factor analysis of variance (ANOVA) tests. The two main factors in the ANOVAs were creeks (Pages and Whiskey Creeks) and harvest treatments (clam harvesting, oyster harvesting, both, or neither). The same ANOVA model was used to test for differences in 1) the density of live and dead oysters, and the proportion of dead oysters (i.e. number of dead oysters/live + dead oysters) after harvesting, 2) the density of live and dead, and proportion of dead, naturally occurring clams after harvesting, and 3) the density of live and dead, and number of missing transplanted, hatchery-raised juvenile clams after harvesting. Before all ANOVAs, homogeneity of variances was tested by using Cochran's test (at α=0.05). When variances were heterogeneous, data were log transformed and homogeneity was retested. After ANOVAs, *post hoc* tests for differences among treatment means were conducted with Student-Newman-Keuls method (SNK) tests (at α=0.05).

Results

In July 1996, prior to the application of experimental harvests, the number of live and dead oysters (those observed with naked eye; >1 mm in length) and the proportion of dead oysters in experimental plots did not vary with the interaction of creeks and harvest treatment (ANOVA, *creek × harvest treatment interaction*, P=0.33–0.56; Table 1), nor among harvest treatments (P=0.57–0.99), but differed significantly between creeks (P=0.02–0.0001). Whiskey Creek had greater numbers of live and dead oysters and proportion of dead oysters than Pages Creek (Figs. 1 and 2).
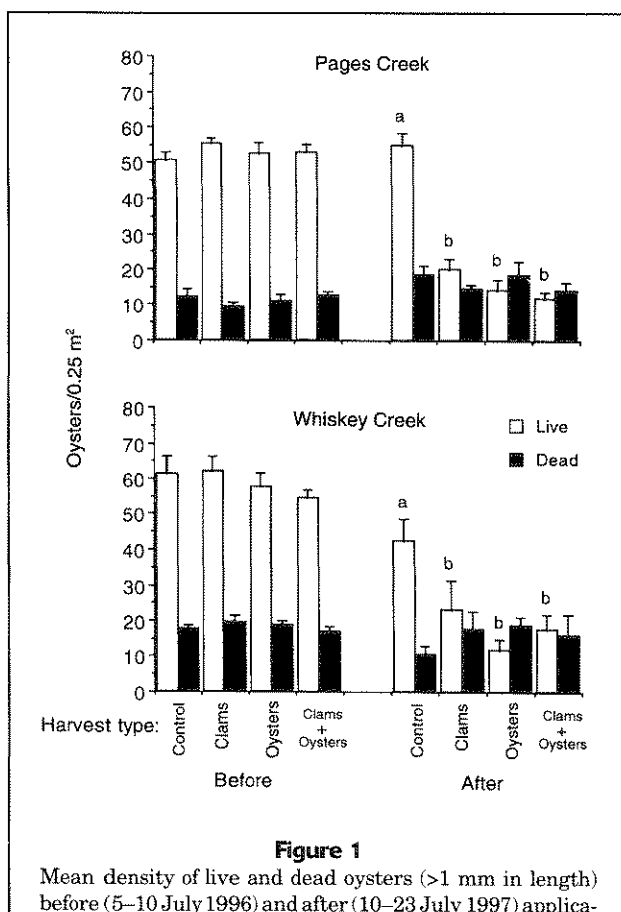

Figure 1

Mean density of live and dead oysters (>1 mm in length) before (5–10 July 1996) and after (10–23 July 1997) application of experimental harvest treatments in Pages and Whiskey Creeks, NC. Data are means and one standard error (n=4) of counts taken within 0.25-m^2 quadrats. Results of SNK *post hoc* comparisons are illustrated with letters above bars (a>b at P<0.05). Separate ANOVAs and SNK tests were used to compare numbers of live and dead oysters both before and after harvesting.

Experimental clam harvesting conducted from August 1996 to May 1997 removed only hard clams from experimental plots (Table 2). In contrast, a few clams

were caught in oyster tongs during oyster harvesting, which was conducted from October 1996 to March
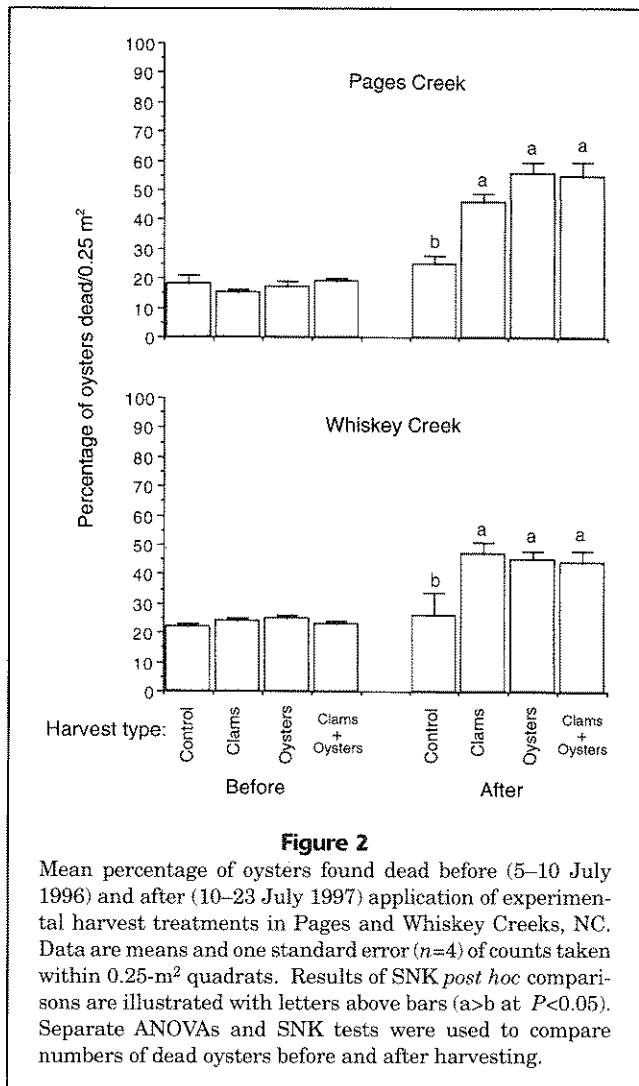

Figure 2

Mean percentage of oysters found dead before (5–10 July 1996) and after (10–23 July 1997) application of experimental harvest treatments in Pages and Whiskey Creeks, NC. Data are means and one standard error (*n*=4) of counts taken within 0.25-m² quadrats. Results of SNK *post hoc* comparisons are illustrated with letters above bars (a>b at *P*<0.05). Separate ANOVAs and SNK tests were used to compare numbers of dead oysters before and after harvesting.

1997. In both creeks, two to three times the number of clams were harvested during clam harvesting treatments than during oyster harvesting. Similar numbers of clams were removed from reefs in the clam harvesting and the combined clam and oyster harvesting treatments. Similar numbers of oysters were removed from plots harvested for oysters only and from those harvested for both oysters and clams (Table 2). According to visual observations, both types of harvesting inflicted obvious wounds (holes and cracks) to the shells of oysters (range: 5–13 individuals within each plot) that were not removed by harvesting.

In July 1997, after experimental clam and oyster harvesting, the density of live and dead oysters, and the proportion of dead oysters did not vary with the interaction of creeks and harvest treatment (ANOVA; *creek × harvest treatment interaction*, *P*=0.23-0.44; Table 3). There was also no significant difference in the density of live and dead oysters and the proportion of dead oysters between the two creeks (*P*=0.16–0.65; Table 3). In contrast, there was a highly significant effect of harvest treatment on the density of live oysters and the proportion of oysters found dead (*P*=0.0001; Table 3). At both sites, plots harvested for clams, oysters, or both had 2–4.5 times lower densities of live oysters and 2–2.5 times higher proportions of dead oysters than did unharvested control plots (SNK, *P*<0.05 for both contrasts; Figs. 1 and 2). There were no differences in the number of dead oysters among harvest treatments.

In July 1997, after experimental harvesting, the density of live, naturally occurring hard clams varied with the interaction of creeks and harvest treatments (ANOVA, *creek × harvest treatment interaction*, *P*=0.015; Table 4). At Pages Creek, there were greater numbers of live, naturally occurring clams in control reefs than in plots harvested for clams, oysters, or both (SNK; *P*<0.05; Fig. 3). At Whiskey Creek, there were more live, naturally occurring clams in both control and oyster-harvested plots than in plots harvested for clams and for both species (SNK, *P*<0.05 for both contrasts; Fig. 3). The number and proportion of dead, naturally occurring clams found in July 1997 did not vary with the interaction of creeks and harvest treatment (ANOVA, *creek × harvest treatment interaction*, *P*=0.09–0.87; Table 4), or between creeks (*P*=0.16–0.10; Table 4). There was also no significant effect of harvest treatment on the density of dead, naturally occurring clams (*P*=0.17; Table 4). However, there was a significant effect of harvest treatment on the pro-

Table 2

Mean number of clams and oysters removed from intertidal oyster reefs during experimental harvesting. Reefs were harvested for clams (clamming), oysters (oystering), both (clamming and oystering), or neither (controls). Transplanted, hatchery-raised clams were not removed during harvesting.

Harvest treatments	Pages Creek		Whiskey Creek	
	Clams	Oysters	Clams	Oysters
Controls	0	0	0	0
Clamming	3.47 ±1.1	0	11.77 ±7.37	0
Oystering	1.15 ±0.22	69.20 ±9.20	5.05 ±2.89	43.27 ±14.10
Clamming and oystering	3.46 ±0.75	89.40 ±58.32	12.59 ±5.84	34.97 ±8.26

Table 3

Mean square errors (MS), F ratios, and corresponding significance levels of (P) two-way fixed factor ANOVAs comparing densities of live and dead oysters, and proportions of dead oysters (per 0.25 m²) among intertidal oyster reefs after application of experimental harvest treatments (10–23 July 1997). The main factors in ANOVAs were creeks (Pages and Whiskey Creeks) and harvest treatment (clamming, oystering, both, and neither).

Source	df	Live			Dead			Proportion dead		
		MS	F	P	MS	F	P	MS	F	P
Creek (C)	1	18.45	0.21	0.65	55.52	1.02	0.32	0.02	2.10	0.16
Harvest treatment (H)	3	2192.00	25.25	0.0001	4.45	0.08	0.97	0.12	13.86	0.0001
C × H	3	132.90	1.53	0.23	67.70	1.24	0.32	0.01	0.93	0.44
Residual	24	86.82			54.54			0.01		

Table 4

Mean square erros (MS), F ratios, and corresponding significance levels (P) of 2-way fixed factor ANOVAs comparing densities of live and dead hard clams, and proportions of dead clams (per 1.0 m²) among intertidal oyster reefs after application of harvest treatments (10–23 July 1997) The main factors in ANOVAs were creeks (Pages and Whiskey Creeks) and harvest treatment (clamming, oystering, both, and neither).

Source	df	Live			Dead			Proportion dead		
		MS	F	P	MS	F	P	MS	F	P
Creek (C)	1	277.5	6.17	0.02	378.1	34.58	0.0001	0.03	30.11	0.0001
Creek (C)	1	0.13	0.03	0.85	10.7	2.15	0.16	0.07	2.94	0.10
Harvest treatment (H)	3	36.55	10.01	0.0002	8.97	1.80	0.17	0.16	6.19	0.003
C × H	3	15.60	4.27	0.015	12.28	2.47	0.09	0.01	0.23	0.87
Residual	24	3.65			4.98			0.03		

portion of dead, naturally occurring clams (P=0.003; Table 4). The proportion of dead clams in both creeks was much higher on harvested than on unharvested (i.e. control) reefs (SNK, P<0.05 for both contrasts; Fig. 4) but was similar among the three harvest treatments (SNK, P>0.05 for both contrasts; Fig. 4).

After harvesting, the density of live and dead hatchery-raised clams transplanted to reefs at the beginning of the experiment tended to vary with the interaction of creeks and harvest treatment, although not significantly (ANOVA, creek × harvest treatment interaction, P=0.07-0.08; Table 5). However, the density of live transplanted clams varied between creeks (P=0.03; Table 5) and among harvest treatments (P=0.04; Table 5). More transplanted clams were recovered alive in Pages Creek (mean ± 1SD: 3.21 ±1.62/m²) than in Whiskey Creek (2.22 ±1.45/m²). Fewer live transplanted clams were recovered from clam-harvested plots than from control plots in both creeks (SNK, P the interaction of <0.05; Fig. 5). The number of dead transplanted clams found after harvesting also varied between creeks (Pages Creek>Whiskey Creek; P=0.0001; Table 5) but did not vary significantly with harvest treatment (P=0.10; Table 5). At Pages Creek, there was a slight trend for greater mortality of transplanted clams on clam-harvested and clam- and oyster-harvested plots than in oyster-harvested and control plots only (Fig. 5). Most transplanted clams placed on reefs at the beginning of the experiment were not found at the end of the experiment ("missing" clams; Fig. 5). The number of missing transplanted clams differed with the interaction of creeks and harvest treatment (ANOVA, *creek × harvest treatment interaction*, P=0.03; Table 5) because fewer clams were recovered in our census in the oyster-harvested plots than in clam-harvested plots at Whiskey Creek only (SNK; P<0.05; Fig. 5).

Discussion

Our results clearly demonstrate that both clam and oyster harvesting significantly reduce oyster popula-
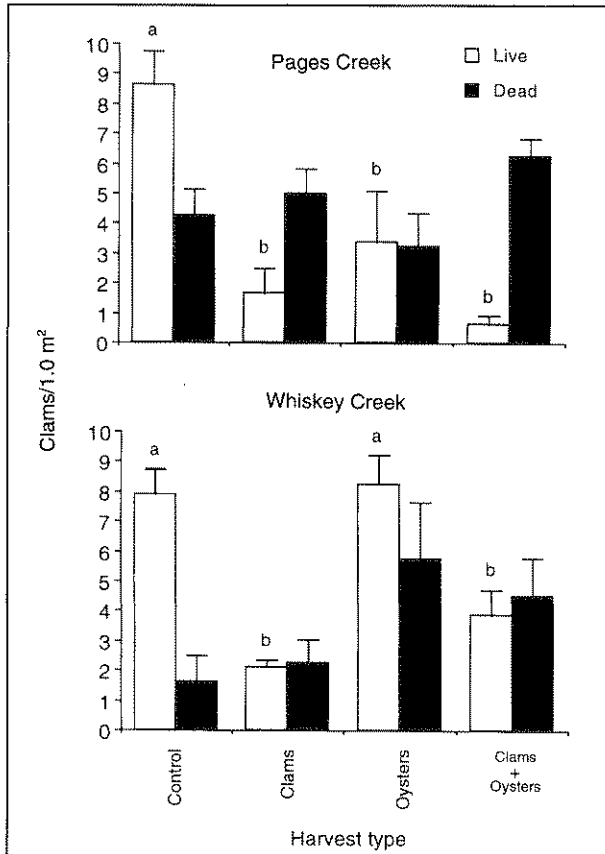
Figure 3

Mean density of live and dead naturally-occurring hard clams found after (10–23 July 1997) application of experimental harvest treatments in Pages and Whiskey Creeks, NC. Data are means and one standard error ($n=4$) of counts taken within 1.0-m^2 quadrats. Results of SNK *post hoc* comparisons are illustrated with letters above bars (a>b at $P<0.05$). Separate ANOVAs and SNK tests were used to compare numbers of live and dead clams.
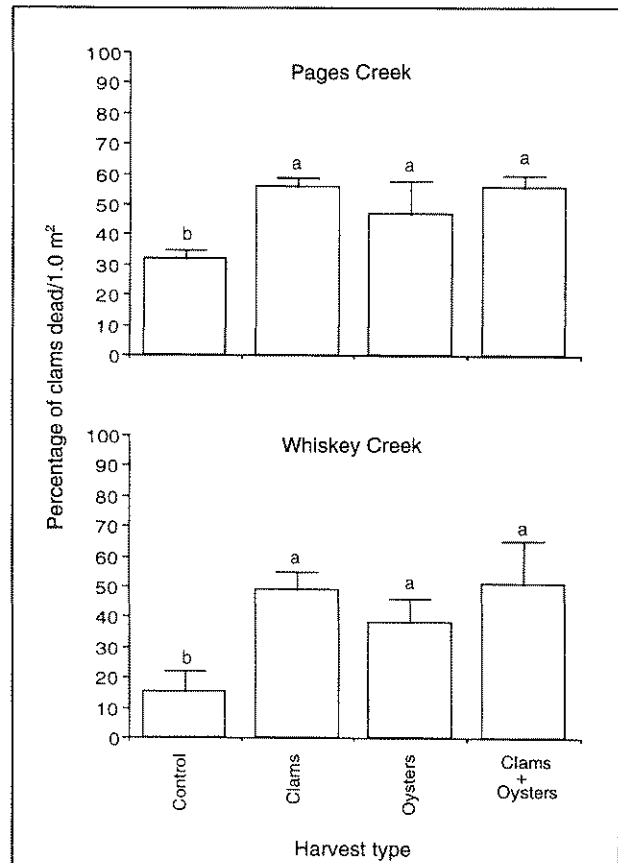

Figure 4

Mean percentage of naturally-occurring hard clams found dead after (10–23 July 1997) application of experimental harvest treatments in Pages and Whiskey Creeks, NC. Data are means and one standard error ($n=4$) of counts taken within 1.0-m^2 quadrats. Results of SNK *post hoc* comparisons are illustrated with letters above bars (a>b at $P<0.05$).

Table 5

Mean square errors (MS), F ratios, and corresponding significance levels (P) of 2-way fixed factor ANOVAs comparing numbers of live, dead, and missing hatchery-raised hard clams (per 1.0 m^2) among intertidal oyster reefs after application of harvest treatments (sampled 10–23 July 1997). Before application of harvest treatments, hatchery-raised juvenile clams were placed at equal densities (16 clams/m^2) on each reef. The main factors in ANOVAs were creeks (Pages and Whiskey Creeks) and harvest treatment (clamming, oystering, both, and neither).

Source	df	Live			Dead			Proportion dead		
		MS	F	P	MS	F	P	MS	F	P
Creek (C)	1	0.14	5.48	0.03	14.45	26.54	0.0001	41.63	19.33	0.0002
Harvest treatment (H)	3	0.08	3.24	0.04	1.28	2.35	0.10	2.03	0.94	0.44
C × H	3	0.07	2.67	0.07	1.40	2.58	0.08	7.65	3.55	0.03
Residual	24	0.03			0.54			2.15		

tions on intertidal oyster reefs. Both types of shellfish harvesting, applied separately or together, reduced the densities of live oysters by 50–80% compared with densities at unharvested reefs. Surprisingly, there was no difference among the effects of clam harvesting only, oyster harvesting only, and clam and oyster harvesting combined on the density of live oysters. We expected oyster harvesting to reduce oyster populations more than clam harvesting because oyster harvesting removes oysters whereas clam harvesting targets clams only (see Table 2). We do not know the effect of clam and oyster harvesting on oysters <1 mm in length; therefore further experiments should be conducted to determine their fate. Results of our experiment show conclusively that the density of live, adult oysters was significantly reduced on reefs that were harvested for clams only (Fig. 1). Therefore, clam harvesting has important negative effects on oysters, most likely through increased oyster mortality.

We did not investigate the specific mechanisms underlying the negative effect of clam harvesting on oyster populations, but observations made during experimental harvesting indicated that clamming with rakes killed oysters in two ways. First, during the process of clamming oyster shells were cracked or punctured (senior author, personal obs.) Severely wounded oysters probably died. Oysters were also indirectly killed during clamming when they were buried or smothered beneath sediments that were removed in the process of digging for buried clams (senior author, personal obs.). Another potential, but unobserved, mechanism potentially leading to enhanced oyster mortality during clamming was that predators (e.g. blue crab and the sheepshead fish, *Archosargus probatochephalus*) were attracted to the reefs by wounded oysters and by sediment disruption, thereby enhancing predation intensity on oysters (e.g. Dayton et al., 1995). It did not appear that oysters were spread around on the experimental reefs by clam harvesting, thus reducing their densities in sampling plots.

Effects of clam and oyster harvesting on naturally occurring populations of hard clams were less clear than effects of clam and oyster harvesting on oysters. Clam harvesting, both alone and in combination with oyster harvesting, decreased densities of live clams by 50–90% compared with unharvested reefs. This result was expected because clam harvesting removes large numbers of clams (see Table 2). Because clams are motile, it is possible that some clams emigrated from sampling plots following the harvest disturbance, thereby accounting for some reduction in clam density. However, this movement is unlikely to have accounted for a large proportion of the reduction in clam densities because the sampling plots covered much of the area on reefs inhabited by clams. Oyster harvesting
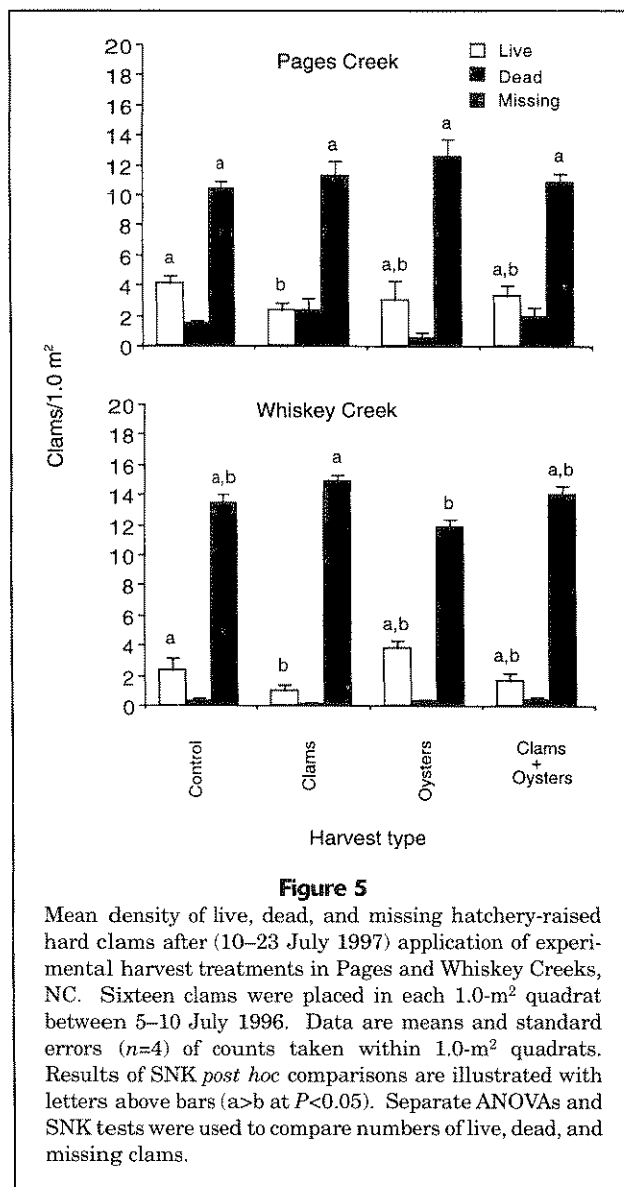

Figure 5
Mean density of live, dead, and missing hatchery-raised hard clams after (10–23 July 1997) application of experimental harvest treatments in Pages and Whiskey Creeks, NC. Sixteen clams were placed in each 1.0-m² quadrat between 5–10 July 1996. Data are means and standard errors ($n=4$) of counts taken within 1.0-m² quadrats. Results of SNK *post hoc* comparisons are illustrated with letters above bars (a>b at $P<0.05$). Separate ANOVAs and SNK tests were used to compare numbers of live, dead, and missing clams.

alone also reduced the density of live clams but only at one site, Pages Creek. At Whiskey Creek, the density of live clams after harvesting was similar between oyster-harvested and control plots, indicating that oyster harvesting had little effect on clam survival (Fig. 3). A negative effect of oyster harvesting on clams may be caused both by direct removal of clams as bycatch (Table 2) and enhanced clam mortality through mechanisms analogous to those hypothesized for oysters (see above). Some clams may also have emigrated from the oyster harvesting treatments following harvesting.

Patterns of survival and mortality of hatchery-raised clams transplanted to experimental reefs varied with site and harvest type (Table 5). Fewer live and dead transplanted clams were recovered from reefs at Whiskey Creek than at Pages Creek (Fig. 5). In con-

trast, there were greater numbers of missing transplanted clams at Pages Creek than at Whiskey Creek. Harvest type, specifically clam harvesting, influenced the number of live transplanted clams but had no significant effect on the number of dead or missing transplanted clams. Fewer live, transplanted clams were found in clam-harvested plots than were found in control plots at both sites (Fig. 5). Because few of the transplanted clams were removed from reefs by experimental harvesting, the negative effects of clam harvesting on densities of live, transplanted clams may be explained by increased clam mortality caused by clam harvesting. Overall, the effects of shellfish harvesting appear to be more variable and unpredictable for clams than for oysters. Our results indicate that both types of shellfish harvesting can have negative impacts on clam populations, but that this is a site-specific phenomenon.

Results of this study do not support the hypothesis that harvesting reefs for both clams and oysters has a negative synergistic impact on clam and oyster populations. Clam and oyster harvesting alone had similar negative effects on densities of live oysters, and the joint harvesting of both species on the same reefs did not decrease the density of live oysters any further. Similarly, the negative effects of clam harvesting on the density of live clams, and on survival of hatchery-raised clams were not enhanced when oyster harvesting was applied in combination with clam harvesting. Thus, the combined harvesting of both clams and oysters on intertidal reefs does not cause greater direct or indirect mortality of shellfish populations than that caused by clam or oyster harvesting conducted separately.

This experimental analysis has important implications for the management of intertidal oyster reefs and their associated molluscan fishery resources. First, maintaining high densities of oysters on some intertidal reefs, by preventing both clam and oyster harvesting, may help to preserve future oyster harvests and brood stock. Protecting some reefs from shellfishing will also help preserve the many ecological services that oysters and oyster reefs provide, such as improving water quality through the filtration of suspended particles (Officer et al., 1982; Dame et al., 1984; Newell, 1988) and creating essential recruitment, refuge, and foraging habitat for economically valuable fishes and crabs (Bahr and Lanier, 1981; Zimmerman et al., 1989; Lenihan et al., 1998). Preventing oyster and clam harvesting on some intertidal reefs will also potentially conserve clam populations from both the direct and indirect negative effects of shellfish harvesting, thereby protecting future clam harvests and brood stock. Overall, allowing the harvest of both clams and oysters on some natural and restored oyster reefs is a rational option because the

combined effect of both clam and oyster harvesting is no greater than the effect of each harvesting activity conducted alone. Thus, we recommend that both types of harvesting be allowed on some reefs but that other reefs be protected as refuges for shellfish populations and other reef-associated fauna.

In adaptive fishery and habitat management, the results of relatively small-scale, prototype experiments, like the one reported here, are used to design larger-scale comparisons of potential management options. Therefore, we recommend that the results of our experiment be used to design alternative shellfishery management options that can be implemented and monitored on relatively large spatial and temporal scales in North Carolina and other coastal states of North America. Our recommendation that some natural and restored oyster reefs be closed from shellfish harvesting and others opened or restored for the purpose of both clam and oyster harvesting can be used to identify potential management options. Further testing of the generality of our findings on larger spatial and temporal scales is necessary because our study was conducted at only two sites and over a one-year period. Therefore, our results may not apply to areas with different environmental conditions (e.g. different flow and sedimentary regimes, areas of low recruitment) and harvesting intensities (e.g. very low and high levels of harvesting). It is necessary to determine with experiments and simulation models how much oyster reef habitat should be preserved from harvesting to maintain sustainable oyster and clam brood stock populations and habaitat for the successful recruitment and survival of other fishery organisms.

The following steps should now be taken by fishery and habitat managers to improve management of the clam and oyster populations and intertidal oyster reef habitat: 1) identify overall management goals and possible options; 2) derive specific predictions based, at least in part, on the experiment results reported in this study; and 3) design monitoring programs to quantify the effect of each management option. Whenever possible, it is highly recommended that fishermen, fishery managers, and ecologists be included in designing and monitoring large-scale management experiments because collectively they will provide the highest level of rigor and reality.

Acknowledgments

Literature cited

Arnold, W. S.
　1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linne'). J. Exp. Mar. Biol. Ecol. 80:207–219.

Bahr, L. M. and W. P. Lanier.
　1981. The ecology of intertidal oyster reefs of the South Atlantic Coast: a community profile. U.S. Fish and Wildlife Service, Biological Services Program FWS/OBS/81/15, 63 p.

Botsford, L. W., J. C. Castilla, and C. H. Peterson.
　1997. The management of fisheries and marine ecosystems. Science (Wash. D.C.) 277:509–514.

Breitburg, D. L, M. A. Palmer, and T. Loher.
　1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: response to flow and structure. Mar. Ecol. Prog. Ser. 125:45–64.

Dame R. F., R. G. Zingmark, and E. Haskin.
　1984. Oyster reefs as processors of estuarine materials. J. Exp. Mar. Biol. Ecol. 83:239–247.

Dayton P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman.
　1995. Environmental effects of marine fishing. Aquat. Cons. 5:205–232.

Engel, J., and R. G. Kvitek.
　1995. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conserv. Biology 12:1204–1214.

FAO (Food and Agriculture Organization of the United Nations).
　1993. Annual report. Food and Agriculture Organization, Rome, Italy, 321 p.

Grumbine, R.E.
　1997. Reflections on "What is ecosystem management?" Conserv. Biol. 11:41–47.

Lenihan, H. S.
　1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual production. Ecol. Monogr. 69:251–276.

Lenihan, H. S., J. H. Grabowski, and G. W. Thayer.
　1998. Recruitment to and utilization of oyster reef habitat by fishes and blue crabs. National Research Council, National Marine Fisheries Service, Beaufort, NC. Tech. Rep., 130 p.

Lenihan, H. S., F. Micheli, S. W. Shelton, and C. H. Peterson.
　1999. The influence of multiple environmental stressors on susceptibility to parasites: an experimental determination with oysters. Limnol. Oceanogr. 910–924.

Lenihan, H. S., and C. H. Peterson.
　1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecol. Appl. 8:128–140.

Luckenbach, M. A., R. Mann, and J. E. Wesson (eds).
　1998. Oyster reef restoration: a symposium and synthesis of approaches. Virginia Institute of Marine Sciences Press, Gloucester Pt., VA, 266 p.

McAllister, M. K., and R. M. Peterman.
　1992. Experimental design in the management of fisheries: a review. N. Am. J. Fish. Manage. 12:1–18.

Michelli, F., and C. H. Peterson.
　1999. Estuarine vegetated habitats as corridors for predator movements. Conserv. Biol. 13:869–881.

NRC (National Research Council).
　1995. Understanding marine biodiversity: a research agenda for the nation. National Academy Press, Washington, D.C., 203 p.

Newell, R. I. E.
　1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? *In* Understanding the estuary: advances in Chesapeake Bay research: proceedings of a conference, p 536–546. Chesapeake Research Consortium Publication 129, CBP/TRS 24/88, Baltimore, MD.

Norse, E. A. (ed.).
　1993. Global marine biological diversity strategy. Center for Marine Conservation, Washington, D.C., 321 p.

Officer C. B., T. J. Smaya, and R. Mann.
　1982. Benthic filter feeding: a natural eutrophication control. Mar. Ecol. Prog. Ser. 9:203–210.

Peterson, C. H., H. C. Summerson, and S. R. Fegley.
　1987. Ecological consequences of mechanical harvesting of clams. Fish. Bull. 85:281–298.

Peterson, C. H., H. C. Summerson, and J. Huber.
　1995. Replenishment of hard clam stocks using hatchery seed: importance of bottom type, seed size, planting season, and density. J. Shell. Res. 14:293–300.

Rothschild B. J., J. S. Ault, P. Goulletquer, and M. Heral.
　1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar. Ecol. Prog. Ser. 111:29–39.

Russ, G., and Alcala, R.
　1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. Ecol. Appl. 6:947–961.

Sponaugle, S., and P. Lawton.
　1990. Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. Mar. Ecol. Prog. Ser. 67:43–53.

Underwood, A. J.
　1990. Experiments in ecology and management: their logic, functions and interpretation. Austr. J. Ecol. 15:365–389.

Walters, C. J.
　1986. Adaptive management of renewable resources. MacMillan Press, New York, NY, 415 p.

West, R. J., and G. N. G. Gordon.
　1994. Commercial and recreational harvest of fish from two Australian coastal rivers. Austr. J. Mar. Fish. Res. 45:1259–1279.

Winslow, F.
　1881a. Deterioration of American oyster beds. Pop. Sci. Mon. 20:29–43.
　1881b. Deterioration of American oyster beds. Pop. Sci. Mon. 20:45–156.

Zimmerman, R., T. J. Minello, T. Baumer, and M. Castiglione.
　1989. Oyster reef as habitat for estuarine macrofauna. NOAA Tech. Mem.NMFS-SEFC-249, 217 p.

Abstract.—In 1996 we surveyed the fishes living on and around seven offshore oil platforms in the Santa Barbara Channel area. We conducted belt transects at various depths in the midwater and around the bottoms of each platform using the research submersible *Delta*. The bottom depths of these platforms ranged from 49 to 224 m and the midwater beams ranged from 21 to 196 m. We found that there were several distinct differences in the fish assemblages living in the midwater and bottom habitats around all of the platforms. Both midwater and bottom assemblages were dominated by rockfishes. Platform midwaters were dominated by young-of-the-year (YOY) or juveniles up to two years old. Rockfishes larger than about 18 cm total length were rarely seen in the midwater. The fish assemblages around the bottoms of the platforms were dominated by larger individuals, primarily subadults or adults. Density of all fishes was similar between the bottoms and midwater of any given platform. However, the total biomass was much greater on the bottoms, owing to larger fish living there. There was a consistently greater number of species on the bottom than in the midwater of each platform, likely because of a larger variety of habitat types on the bottom. The fish assemblages also differed among platforms. We found significantly higher densities of young-of-the-year rockfishes around platforms north of Pt. Conception compared with those in the Santa Barbara Channel, probably because the more northerly platforms are located in the more productive waters of the California Current.

Fish assemblages around seven oil platforms in the Santa Barbara Channel area

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Petroleum production has been a part of the southern California economy since the nineteenth century. The earliest drilling took place on land, but by the early twentieth century a large number of piers lined the coast, tapping into offshore oil deposits. Hazel, the first offshore oil platform, was constructed off Summerland in 1958 (Carlisle et al., 1964). At the peak of oil drilling in the early 1980s, there were 30 platforms operating in southern and central California. Currently, there are 19 platforms in operation in the Santa Barbara Channel and off Point Conception (Fig. 1).

Oil platforms provide considerable habitat for marine organisms. The earliest structures were relatively small (23 m long at the surface), newer platforms, however, are over 100 m long (MBC[1]). Sessile invertebrates (primarily mussels, barnacles and anemones) encrust the pilings and well pipes and cover the bottom to form additional habitat.

Oil platforms have a finite economic lifespan and a number of them are becoming uneconomical to operate. In 1996, four platforms were removed from the Santa Barbara Channel, although not without controversy. There is considerable debate regarding the fate of these structures. Some interest groups would like to leave part or all of them in place, claiming protection of fish habitat; others favor complete removal. Understanding the biological communities on the platforms is crucial to making rational decisions regarding the fates of these structures. In addition, research on these platforms could also address questions regarding the role that artificial reefs might play in coastal fish communities. Ultimately, this research will allow us to contrast the fish assemblages on platforms with those of nearby reefs.

Currently, very little is known about the fish fauna around these platforms. One relatively comprehensive SCUBA survey examined fish populations around two shallow inshore platforms, Hazel and Hilda, during Hazel's first three years and Hilda's first year of operation (Carlisle et al., 1964). Additional cursory surveys were conducted around these two platforms in 1970 and 1975; Bascom et al., 1976; Allen and Moore[2]). With the exception of a short-term study of fishes around platform Hidalgo using a remotely operated vehicle (ROV) (Love et al., 1994) and a survey of recreational fishing around Santa Bar-

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[1] MBC (Marine Biology Consultants). 1987. Ecology of oil/gas platforms offshore California. Outer Continental Shelf (OCS) Study Minerals Management Service (MMS) 86-0094.

[2] Allen, M. J., and M. D. Moore. 1976. Fauna of offshore structures. South. Calif. Coast. Water. Res. Proj. Annu. Rep., Long Beach, CA, p. 179–186.