ECOLOGICAL CONSEQUENCES OF MECHANICAL HARVESTING OF CLAMS

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ABSTRACT

A field experiment was performed in 1,225 m^2 plots in each of two shallow estuarine habitats, a seagrass bed and a sand flat, in Back Sound, North Carolina (USA), to test the impact of clam raking and two different intensities of mechanical harvesting of clams ("clam kicking") for up to 4 years on 1) hard clam, *Mercenaria mercenaria*, recruitment, 2) seagrass biomass, 3) the density of benthic macroinvertebrates, and 4) the density of bay scallops, *Argopecten irradians*. The removal of adult hard clams with the contingent sediment disturbance had ambiguous effects on the recruitment of hard clams: in the sand flat recruitment tended to be lower (but not significantly) in intense-clam-kicking matrices than in controls, whereas in seagrass recruitment of hard clams did not not show a clear response to treatment. In the raking and light-clam-kicking matrices, seagrass biomass fell immediately by ≅25% below controls but full recovery occurred within a year. In the intense-clam-kicking matrices, seagrass biomass fell by ≅65% below levels expected from controls; recovery did not begin until more than 2 years passed, and seagrass biomass was still ≅35% lower than predicted from controls 4 years later. Clam harvest did not affect either the density or species composition of small benthic macroinvertebrates from sediment cores, probably because of their rapid capacity for recolonization and generally short life spans. In all treatments, densities of benthic macroinvertebrates (mostly polychaetes) were substantially higher in the seagrass than in the sand flat during October samplings but equal during March samplings. Bay scallop density declined with declining seagrass biomass across harvest treatments, but the intense-clam-kicking matrices contained even fewer bay scallops than their seagrass biomass would predict, perhaps because of enhanced patchiness of the remaining seagrass.

The relative inertia of the change in seagrass biomass following extensive destruction in the intensely kicked matrices suggests that seagrass replanting may be an extremely important means of returning disturbed, unvegetated areas to seagrass systems. Emergence during summer of a between-habitat gradient in infaunal densities (higher in seagrass than in sand) supports the hypothesis that seagrass provides a partial prey refuge for infaunal invertebrates. The failure of the benthic macroinvertebrate density to respond to clam harvest treatments in both sand flats and seagrass beds implies that the polychaetes which dominate recover rapidly from disturbance and are probably not adversely affected by clam harvest. The negative and long-lasting impact of intense hard clam harvest on seagrass biomass with its effects on other fisheries, including bay scallops, implies that hard clam fisheries should be managed to minimize the intensity of harvest within seagrass beds.

Technological innovation is frequently accompanied by an increased risk of harm to various aspects of the natural environment (e.g., Dickie 1974). While such innovation can be considered economically desirable and even inevitable, environmental managers still require ecological inputs to enable them to reach properly informed compromises between uncontrolled application of new technology and unnecessarily cautious protection of natural ecosystems. Because of its inherent lack of general principles and paradigms, ecology is rarely able to provide immediate answers to practical questions of the probable impact of new technology. Consequently, careful studies of the ecological impact of the application of each specific new technology are often necessary. Such studies can not only provide necessary applied information but also contribute to a better basic understanding of the specific system that is being explored.

Although fisheries biologists are renowned for managing harvests in a way that will sustain a maximum yield or maximize yield per recruit (Ricker 1975), studies are only occasionally undertaken to compare the environmental damage caused by alternative fishing gears and technologies (e.g., Caddy 1973; Peterson et al. 1983a). Such studies are most common in estuarine and other shallow-water fisheries, where high coastal productivity of diverse stocks induces intensive exploitation of a common area by multiple, potentially interfering fisheries. As technological advances in fishing gear have been made, this potential for interfishery competition has grown, as has the need for understanding the envi-

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Manuscript accepted January 1987.
FISHERY BULLETIN: VOL. 85, NO. 2, 1987.

ronmental consequences of the utilization of new, alternative technologies.

Fisheries for the hard clam, *Mercenaria mercenaria* (L.), and other sedentary benthic invertebrates require the use of either hand implements (rakes, hoes, etc.) or boat-drawn gear (dredges, trawls, etc.). Managers of benthic invertebrate fisheries may turn to the subdiscipline of benthic ecology to seek predictions of the relative environmental and ecological consequences of utilizing various alternative fishing gears or of permitting technologically new substitutions for traditional fishing methodologies. Unfortunately, benthic ecologists are frequently unable to provide confident answers to many questions, often either because the fisheries applications involve a far larger scale than can be or has been practically accommodated in basic experimental research designs or because the questions fall into an area of current debate and ongoing study in the basic science of the field.

One might take, as an example of the poor predictive capacity of benthic ecology, the question of whether widespread adoption of mechanical harvesters by commercial *M. mercenaria* fishermen will affect the future recruitment success of *M. mercenaria* in the local area of harvest. Most fisheries biologists agree that the mechanical harvesters are more efficient in gathering hard clams from a given area and cause more physical disruption of the bottom than the alternative hand methods of raking and tonging. Even given these assumed differences, benthic ecology provides mixed and conflicting predictions of the impact of switching to mechanical harvesters. Basic studies of adult-larval interactions, including some among suspension-feeding bivalves (Woodin 1976; Williams 1980; Peterson 1982b), might suggest that removal of large, adult suspension feeders would enhance the survivorship of settling larvae and thereby increase the recruitment success of *M. mercenaria* in the efficiently harvested areas. Yet, the experimental results on which such a prediction is based were achieved on a much smaller spatial scale and probably depend upon absolute density (or feeding rate) of all suspension feeders in an unspecified way. It is conceivable that the virtual removal of *M. mercenaria* over a substantial area might remove an important settlement cue (produced by adults) needed for larval habitat selection (e.g., Meadows and Campbell 1972; Gray 1974). If this were true, recruitment success of *M. mercenaria* would decline with the intensity of harvest. Similarly, benthic ecology provides conflicting predictions about the effects of the increased physical disburbance of mechanical harvesting on recruitment success of *M. mercenaria*. On the one hand, *M. mercenaria* recruits might be expected to suffer increased mortality from burial during massive sediment disturbance (Rhoads 1974; Myers 1977; Thistle 1981; Wilson 1981). Yet, larvae of many species settle more densely into disturbed bottoms (Gray 1974; McCall 1977; Hulberg and Oliver 1980). Again, these signals are conflicting but, even more importantly, experimental benthic ecology is unable to predict adequately whether the scale and intensity of disturbance during commercial clam harvesting are appropriate to invoke either of these processes.

Because of the restricted scale of past field experiments and the consequent limitations of benthic ecology in the applied arena, we designed controlled field experiments to test the impact of mechanical clam harvesting on a large scale, sufficient to provide environmental data to resource managers and to extend simultaneously the scope of basic experimental, benthic ecology. Specifically, we tested on a 1,225 m^2 scale whether the harvest of *M. mercenaria*, with its attendant physical disruption of the bottom, affected the 1) recruitment success of *M. mercenaria*, 2) biomass of seagrasses, 3) density of bay scallops, and 4) density of all other benthic macroinvertebrates. We tested these harvest effects in each of two common estuarine habitats, a sand flat and a seagrass bed, and followed not only the immediate response to harvesting but also the changes in most variables over a subsequent 3.5-yr period. Thus, the need for ecological data to use in fisheries management provided an opportunity to expand the temporal and spatial scale of experiments in marine benthic ecology and thereby evaluate our ability to extrapolate from previous theory based on smaller scales.

METHODS

To test whether the type and/or intensity of hard clam, *Mercenaria mercenaria* (L.), harvest has any detectable effect on 1) its own recruitment, 2) seagrass biomass, 3) bay scallop, *Argopecten irradians*, density, or 4) density of small benthic macroinvertebrates, we performed a large-scale field experiment at sites along the southern (barrier island) margin of Back Sound near Beaufort, NC (Fig. 1). This experiment was conducted in a seagrass meadow and in an unvegetated sand flat approximately 500 m to the west to permit a test of whether effects of harvest vary with habitat. This general area and its physical characteristics are described in several previous publications (Sutherland and Karlson 1977; Nelson 1979; Peterson et al. 1983b, 1984). Back

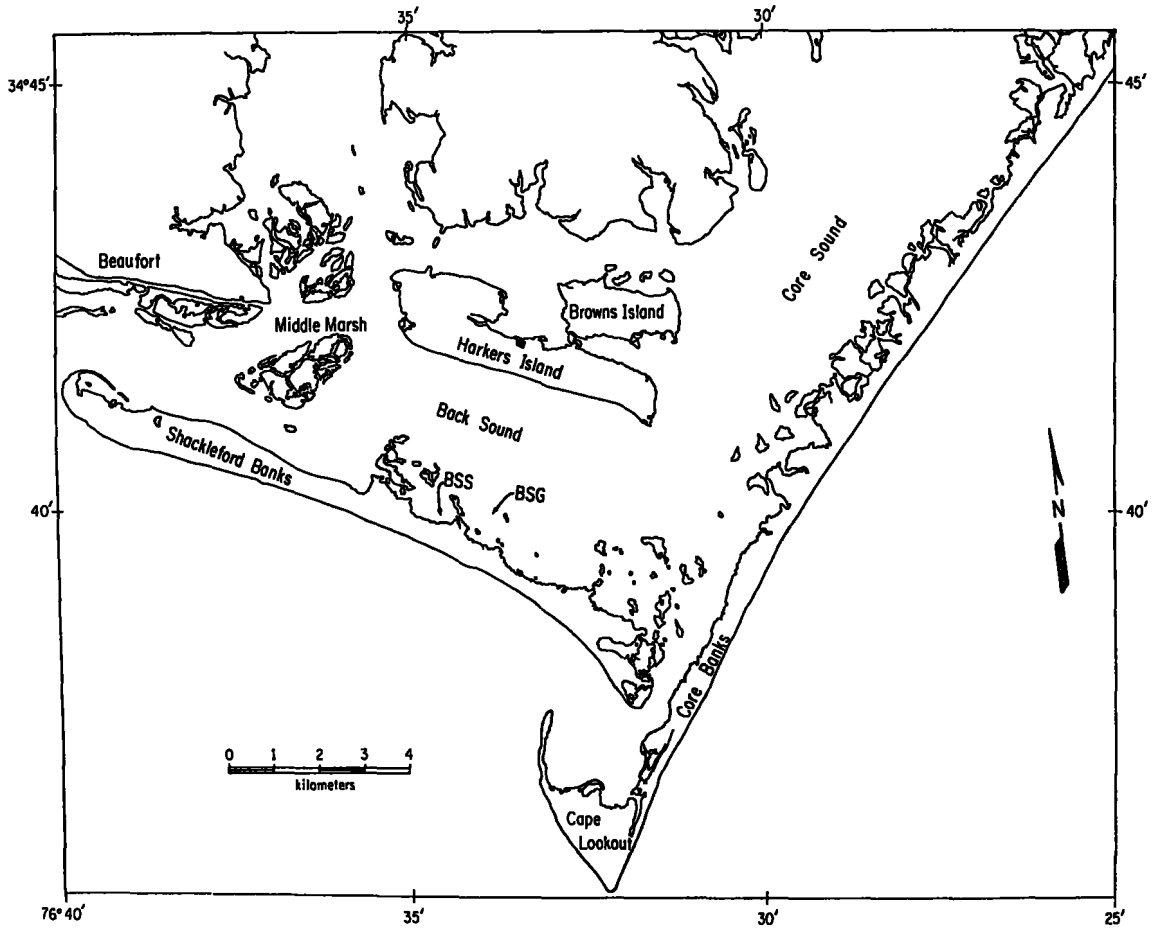

FIGURE 1.—The locations of the study sites in eastern North Carolina, near Cape Lookout. BSS indicates the sand-flat and BSG the seagrass-bed locations. Tick marks on the margins of the figure denote minutes of N. latitude and W. longitude.

Sound is a shallow marine lagoon with a lunar tide of about 0.6 m range, little salinity variation (28-34‰), and a wide seasonal temperature range from a winter monthly minimum of 2°-4°C to a summer monthly maximum of 29°-30°C. In January 1980, we selected in each habitat 6 square plots (matrices) of 1,225 m^2 area, each of which had a virtually constant water depth of about 0.1-0.3 m at low tide and homogeneous surface appearance. Specifically, all seagrass matrices held a spatially uniform cover of a seasonally varying mixture of two seagrasses, eelgrass *Zostera marina* and shoalgrass *Halodule wrightii*, whereas no sand-flat matrix contained seagrasses. These seagrass matrices had been continuously vegetated from at least 1974 until 1980 and the seagrass cover had not extended over the sand flat during that same period (Peterson et al. 1984).

Before harvest treatment, we subsampled all 6 matrices in each habitat to test whether there were any initial differences among matrices in response variables. This sampling occurred between 22 February and 31 March 1980 in the sand flat and from 1 April to 6 May 1980 in the seagrass bed. A fixed number (9 or 36) of uniformly distributed 0.25 m^2 subsamples was taken from each matrix to estimate abundance of hard clams, bay scallops, and seagrass (Table 1). A uniform sampling array was chosen to reduce the field effort and to avoid risk of sampling at or even near (<1 m) the same locations during subsequent sampling. A grid of marked ropes attached to equally spaced stakes was placed around the circumference of each matrix and moved to a new, randomly chosen set of positions for each new sampling date, thus producing a "frame shift" of the sampling template.

TABLE 1.—Temporal design of data collections and of experimental treatments for both habitats, 1980-84. Entries are numbers of samples[1] taken per matrix.

Parameter estimated	Spring 1980 22 Feb.- 6 May	Harvest treatment 12-30 May	Fall 1980 20 Oct.- 10 Nov.	Harvest treatment 19 Dec.- 22 Feb.	Spring 1981 2-13 Mar.	Fall 1981 4 Oct.- 3 Nov.	Fall 1982[2] 20-29 Oct.	Fall 1983[2] 28-31 Oct.	Fall 1984[2] 22-29 Oct.
Total hard clam density	36		36		9	36	9	9	0
Density of hard clam recruits	36		36		9	36	9	9	0
Seagrass dry mass	36		36		9	36	9	9	9
Bay scallop density	0		36		9	36	9	9	0
Density of benthic macro-invertebrates	6		6		6	6	0	0	0
Sediment size distribution parameters	3		0		0	0	0	0	0

[1]In all cases where 36 or 9 samples were taken per matrix, these were ¼ m^2 samples distributed uniformly across the matrix such that no sample fell within 1 m of any previous sample location. Where 6 or 3 samples were taken, these were chosen at random from a group of 9 uniformly distributed samples positioned in a similar way to avoid any overlaps. All sediment samples were cores of 5 cm diameter × 20 cm deep. Macroinvertebrate samples were cores of 10 cm diameter × 25 cm deep.

[2]Data taken from only the seagrass habitat on these dates.

To collect a repeatable sample, we first inserted a 0.25 m^2 circular metal sampling frame penetrating to a depth of 15 cm and used an hydraulic suction dredge to excavate the complete contents to that same depth. The material was collected in a 3 mm nylon mesh bag (for description and sampling efficiency, see Peterson et al. 1983b). All living *M. mercenaria* and *A. irradians* were removed from the mesh bag and placed in separate, labeled plastic bags for return to the laboratory. For all *M. mercenaria* we measured length in the longest anteroposterior dimension, and for all *A. irradians* we measured the distance from the flat top of the hinge to the ventral margin using vernier calipers. Seagrass material from the mesh bag was packaged in marked plastic bags in the field and returned to the laboratory, where it was gently rinsed in freshwater to remove attached salt and sediments, and dried to constant weight (2-4 days) at 105°C.

To estimate densities of small benthic macroinvertebrates, we took 9 uniformly distributed samples from each matrix in each habitat on 4 sampling dates (Table 1). We processed and analyzed a randomly chosen subset of 6 of these 9 samples for each matrix. The strategy of taking more samples than one expects to analyze is optimal when marginal costs of additional sampling are low, because extra replicates are then available for later analysis if among-sample variation proves so unexpectedly high as to reduce statistical power to an unacceptable level. Benthic invertebrates were collected using 10 cm diameter cores taken to a depth of 25 cm. Complete contents of each core were placed in separate plastic bags and gently sieved, in the laboratory, through 1 mm mesh. Sieve contents were held in bottles containing rose bengal in 10% buffered formalin until animal tissues were adequately stained and hardened. We later picked and identified to class (and to species in a subset of the samples) all animals in each sample.

In spring 1980, we also took 3 randomly located sediment cores (5 cm in diameter to a depth of 20 cm) from each matrix to characterize initial sediment conditions. Cores were transferred into individual plastic bags and frozen at −10°C until analysis of sediment size distribution by weight. We split each sample by coning and quartering (Ingram 1971) and then used standard Rotap dry sieving and pipetting procedures (Folk 1974) to estimate dry weights of sediments in each of several size classes. In addition, percent organic content was measured by weight loss on ignition at 550°C for 4 h (Gross 1981). Because our (customary) use of small-diameter cores to sample sediments failed to include large shell fragments and because such biogenic calcium carbonate appeared to be extremely common in 1 seagrass matrix, we designed a sampling procedure to estimate the relative degree of coarse shell. In October 1985, we used the suction dredge to excavate 3 haphazardly located 0.25 m^2 quadrats to a depth of 12 cm in each of the 6 matrices in each habitat. All shell fragments collected on a 3 mm

mesh were then cleaned with freshwater, dried at 60°C, and weighed to provide a quantitative indication of the relative degree of coarse shelliness in each matrix.

After our initial sampling in spring 1980, we applied harvest treatments on 2 occasions, 12-30 May 1980 and 19 December 1980-22 February 1981 with a single sampling of response variables in between (Table 1). We then sampled on 5 subsequent occasions to test for the existence and persistence of any treatment effects without applying any additional harvest treatments (Table 1). Of the 6 matrices in each habitat, 2 were left untouched as controls, 2 were given intense applications of "clam kicking", and the remaining 2 were subjected to lower but equal harvest intensities (judged by estimated percentage of spring 1980 *M. mercenaria* removed) of different types ("clam kicking" in one and hand raking in the other). Clam kicking is a mechanical form of clam harvest (described in detail in Guthrie and Lewis 1982) practiced in North Carolina which involves the modification of boat engines in such a way as to direct the propeller wash downwards instead of backwards. The propeller wash is sufficiently powerful in shallow water to suspend bottom sediments and clams into a plume in the water column, which allows *M. mercenaria* to be collected in a trawl net towed behind the boat (see Figure 2). To reproduce this process, we employed a commercial clam kicker and his boat. We measured in a crude way the relative intensity of the harvest treatment by counting all legally marketable (>2.54 cm in thickness in North Carolina) *M. mercenaria* removed and then estimating the percent removed of those available using the initial spring 1980 sampling (Table 2). We also recorded the number of

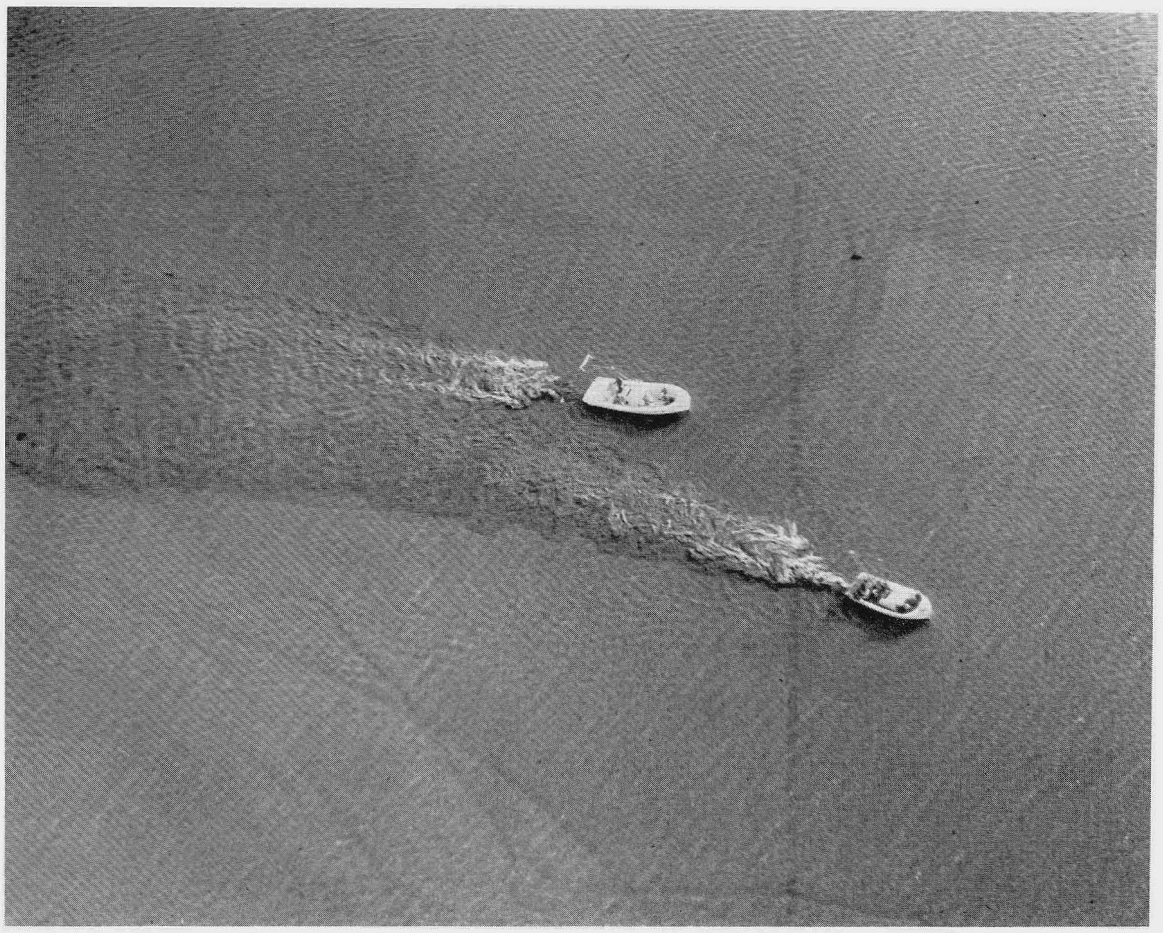

FIGURE 2.—Aerial photograph of a clam kicking boat in operation, showing the sediment plume in the wake and the tracks of previous kicking passes in the surrounding bottom.

TABLE 2.—The intensity of clam harvest treatments. All numbers and percents refer to legally harvested *Mercenaria mercenaria* >2.54 cm in thickness.

	Treatment date and parameter estimated								
	May 1980			Winter 1980-81			Both applications pooled		
Habitat and harvest treatment	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest
Sand flat									
Control I	0	0	0	0	0	0	0	0	0
Control II	0	0	0	0	0	0	0	0	0
Raking	191	16	170 min	140	11	210 min	331	27	380 min
Light-Kicking	140	17	2 passes 9 min	177	22	4 passes 30 min	317	39	6 passes 39 min
Intense-Kicking I	176	65	4 passes 20 min	165	61	3 passes 30 min	341	125	7 passes 50 min
Intense-Kicking II	384	47	8 passes 43 min	394	48	9 passes 87 min	778	95	17 passes 130 min
Seagrass bed									
Control I	0	0	0	0	0	0	0	0	0
Control II	0	0	0	0	0	0	0	0	0
Raking	134	1.9	275 min	925	13	2,125 min	1,059	15	2,400 min
Light-Kicking	91	1.4	2 passes 9 min	963	15	18 passes 121 min	1,054	16	20 passes 130 min
Intense-Kicking I	136	2.6	4 passes 22 min	2,608	49	32 passes 179 min	2,744	52	36 passes 201 min
Intense-Kicking II	1,033	12	12 passes 73 min	3,168	36	23 passes 156 min	4,201	48	35 passes 230 min

passes of the kicking boat and the minutes of clam kicking applied (Table 2). All *M. mercenaria* collected were returned to the laboratory for size-frequency estimates. The cumulative removals from the 2 clam harvesting applications produced relative treatment intensities acceptably close to our initial intentions (Table 2). For the hand raking treatment, we used short-handled rakes with 6-10 prongs of ≅14 cm in length separated by 3.5 cm gaps (see description and photograph of "pea digger" in Peterson et al. 1983a). We attempted to equalize the intensities of the raking and light-kicking treatments by removing equal percentages of the legally harvestable *M. mercenaria* from each of these two treatment matrices (Table 2). We also recorded the length of time actually spent raking as another indication of treatment intensity (Table 2).

RESULTS

Initial Sampling and Estimation of Shelliness

Within each habitat (sand flat and seagrass bed), one-way ANOVA was used on log $(x + 1)$-transformed data (which eliminated heteroscedacity in Cochran's tests) to assess whether any response variables differed significantly among the 6 matrices in spring 1980 prior to application of harvest treatments. There was no significant ($\alpha = 0.05$) initial variation among sand-flat matrices in any parameter: average total density of hard clams, average density of hard clam recruits (length <2.5 cm), average dry mass of seagrass, average density of all benthic macroinvertebrates, and sediment size (ϕ) (Table 3). Furthermore, the average percent organic content of sediments did not vary significantly among sand-flat matrices ($P > 0.05$ in ANOVA on angular-transformed proportions). Bay scallops were so rare in this initial sampling that we do not even record their densities in Table 3: bay scallops showed no significant difference among matrices in either habitat. The seagrass matrices exhibited significant initial variation in all parameters except average total density of hard clams and bay scallop density (Table 3). Variation in the other 4 parameters was not consistent across all seagrass matrices. A posteriori Duncan's tests, used to identify how specific seagrass matrices differed, show that the control II and raking matrices had significantly higher densities of hard clam recruits than all other seagrass matrices in spring 1980. Average seagrass biomass was significantly greater in intense-kicking I and significantly lower in control I than in all other seagrass matrices in the initial sampling. Control I also initially possessed a significantly higher average density of benthic macroinvertebrates, about 3 times the levels in the other seagrass matrices (Table 3). Duncan's test on mean ϕs revealed that in seagrass the raking and light-kicking matrices possessed

significantly higher initial ϕ values (finer sediments), although the differences among matrices were small. Percent organic content did not differ significantly ($P > 0.05$) among seagrass matrices in a one-way ANOVA on angular-transformed proportions.

The results of this initial sampling in spring 1980 prior to any application of clam harvest treatments imply that the sand-flat matrices were initially quite homogeneous. Consequently, any treatment effects can be expected to appear as significant differences that emerge among matrices in some or all samplings after application of the treatments. However, the initial differences among seagrass matrices imply that treatment effects may not be so readily identified. For those variables that exhibited initial differences among matrices, we performed two different tests of the effects of treatment. We performed simple ANOVA's to test for differences following treatment and we also, by subtraction of matrix means for spring 1980, adjusted the data from each matrix for initial differences and tested by ANOVA for significant changes in the differences among matrices. The first approach is appropriate if one believes that initial differences among matrices do not reflect intrinsic between-matrix differences that require adjustment, whereas the second approach assumes that initial differences among matrices would be expected to persist or recur in the absence of any treatment. An examination of how replicate matrices vary over time helps resolve which test procedure is more appropriate, but we performed both tests to provide a more robust set of conclusions.

Although all matrices in each habitat were chosen to be homogeneous in surface appearance, our October 1985 estimates of coarse shelliness of the surface (0-12 cm) sediments demonstrated that seagrass control I had almost 10 times the amount of coarse shell than any of the other seagrass matrices. The average ($\pm$SE) mass of shell fragments >3 mm in the top 12 cm of the 0.25 m^2 area in seagrass control I was 5,257 g ($\pm$701) compared with a range of 375 ($\pm$70) to 777 ($\pm$135) g across the other 5 seagrass matrices. This substantially larger amount of shell ($P < 0.001$ in a one-way ANOVA) seemed to be present during the entire experiment. Because surface shell fragments could greatly influence seagrass growth and especially *M. mercenaria* recruitment and survival (see Castagna and Kraeuter 1977), this physical anomaly of seagrass control I renders it a questionable control for the various treatment matrices. Similar data on surface shelliness taken from the sand matrices in October 1985 revealed no significant differences ($P > 0.05$) among matrices in a one-way ANOVA, with mean ($\pm$SE)

TABLE 3.—Contrasts among replicate matrices within each habitat before application of harvest treatments. Data are sample means ($\pm$SE) from spring 1980 (22 Feb.-6 May). Sample sizes appear in Table 1. Superscripts A and B indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly. Where ANOVA was nonsignificant, no means differ significantly.

	Habitat and sample average for each paramenter									
	Sand flat					Seagrass bed				
Future matrix designation	Total hard clam density per ¼ m^2	Density of hard clam recruits[1] per ¼ m^2	Seagrass dry mass (g per ¼ m^2)	Density of benthic inverte-brates per 0.008 m^2	Graphic mean sediment size (ϕ)	Total hard clam density per ¼ m^2	Density of hard clam recruits[1] per ¼ m^2	Seagrass dry mass (g per ¼ m^2)	Density of benthic inverte-brates per 0.008 m^2	Graphic mean sediment size (ϕ)
Control I	0.50 (0.14)	0.22 (0.10)	0.00	6.00 (1.34)	2.14 (0.00)	2.42 (0.44)	0.17^{B} (0.06)	10.36^{C} (2.38)	16.50^{A} (4.32)	2.75^{B} (0.21)
Control II	0.33 (0.10)	0.17 (0.07)	0.00	4.67 (0.76)	2.16 (0.03)	2.28 (1.72)	0.81^{A} (0.16)	14.37^{B} (2.23)	4.33^{B} (0.88)	2.94^{B} (0.12)
Raking	0.47 (0.13)	0.17 (0.06)	0.00	4.67 (0.84)	2.17 (0.04)	2.19 (0.38)	$0.53^{A,B}$ (0.14)	16.01^{B} (3.49)	4.83^{B} (1.11)	3.38^{A} (0.07)
Light-Kicking	0.25 (0.09)	0.06 (0.04)	0.00	6.00 (1.26)	2.16 (0.02)	2.28 (0.33)	0.39^{B} (0.11)	19.56^{B} (2.62)	5.67^{B} (2.08)	3.46^{A} (0.07)
Intense-Kicking I	0.36 (0.14)	0.17 (0.07)	0.00	3.17 (0.83)	2.10 (0.02)	1.83 (0.28)	0.39^{B} (0.10)	41.22^{A} (4.03)	6.50^{B} (1.52)	2.84^{B} (0.15)
Intense-Kicking II	0.47 (0.14)	0.17 (0.07)	0.00	5.67 (1.38)	2.18 (0.01)	2.56 (0.36)	0.27^{B} (0.09)	28.44^{B} (4.17)	5.67^{B} (2.33)	2.69^{B} (0.05)
Statistical significance[2]	NS	NS	NS	NS	NS	NS	***	***	*	**

[1]Recruits defined as <2.5 cm in length (see Peterson et al. 1983b for size data on 0 year class as support).
[2]* - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA comparing matrices before experimental initiation.

mass of shell fragments >3 mm ranging from 28 (±7) to 157 (±121) across the 6 sand-flat matrices.

Our field plots were closed to all commercial and recreational shellfishing during the 4 years of the experiment by proclamation of the North Carolina Division of Marine Fisheries to avoid disruption of the experiments. However, on 7 occasions out of 50 days of observation, we observed clammers within the boundaries of our plots: 5 times in seagrass control matrix I and once in both the seagrass raking matrix and the intense-kicking II matrix. This represents significantly more illegal clamming in control I than would be expected by chance alone ($P < 0.01$ in a binomial test). Thus, the seagrass control I matrix may not represent a true control for our experiment.

Posttreatment Sampling

Mercenaria mercenaria Recruitment

In the sand-flat habitat there were only two Octobers during which *M. mercenaria* recruits were sampled: October 1980 after the initial application of the clam harvest treatments and October 1981 after both treatment applications. In neither sampling did a one-way ANOVA on log (x + 1)-transformed counts (which removed heteroscedacity in Cochran's tests) reveal significant ($\alpha = 0.05$) variation in average density of recruits among sand-flat matrices (Table 4). Furthermore, a two-way ANOVA on log (x + 1)-transformed counts from both time periods, done to increase the power of the test of matrix differences, also failed to reveal any significant variation in average recruitment among sand-flat matrices. Despite the failure to demonstrate statistical significance in *M. mercenaria* recruitment among sand-flat matrices, the average density of recruits in the control matrices during these two Octobers was more than double (on untransformed scale) the average density in the 2 high-intensity clam kicking matrices (Fig. 3). Some of this difference may have been present even before treatments were applied (Fig. 3), but it is also possible that the high local variability in recruitment lowers the power of this test of harvest treatment to a degree that even a twofold difference is undetectable.

During 4 Octobers, *M. mercenaria* recruitment was estimated in the seagrass habitat (Table 4). One of these, October 1980, fell after the first harvest treatment (which Table 2 shows to have been very light in the seagrass plots) but before the second, more intense treatment. The other 3 samplings came in successive years, increasingly far from the actual time of application of the harvest treatments. Because of the preexisting significant differences

TABLE 4.—The impact of clam harvesting on recruitment of *Mercenaria mercenaria*. Entries are mean numbers (± SE) of recruits per ¼ m^2. Recruits are defined as all individuals <2.5 cm in length in October of each year. For 1980 and 1981, n = 36 samples from each treatment matrix in each habitat, whereas for 1982 and 1983, n = 9 for seagrass and 0 for sand flat.

	Habitat and date							
	Sand flat			Seagrass bed				
Treatment matrix	1980	1981	Unweighted average	1980	1981	1982	1983	Unweighted average
Control I	0.33 (0.11)	0.17 (0.06)	0.25	0.94 (0.21)	0.61^{A} (0.13)	$0.67^{A,B}$ (0.24)	0.67 (0.24)	0.72
Control II	0.36 (0.11)	0.06 (0.04)	0.21	0.72 (0.15)	0.28^{B} (0.09)	$1.33^{A,B}$ (0.47)	1.56 (0.77)	0.97
Raking	0.44 (0.13)	0.14 (0.08)	0.29	0.81 (0.14)	0.22^{B} (0.07)	$0.78^{A,B}$ (0.32)	1.67 (0.55)	0.87
Light-Kicking	0.19 (0.08)	0.08 (0.05)	0.14	0.61 (0.13)	0.11^{B} (0.05)	2.11^{A} (0.68)	0.33 (0.17)	0.79
Intense-Kicking I	0.11 (0.05)	0.03 (0.03)	0.07	0.42 (0.11)	$0.39^{A,B}$ (0.10)	0.22^{B} (0.15)	0.67 (0.17)	0.43
Intense-Kicking II	0.22 (0.07)	0.08 (0.05)	0.15	0.56 (0.14)	$0.33^{A,B}$ (0.10)	0.56^{B} (0.24)	0.33 (0.24)	0.45
Statistical significance[1]	NS	NS	NS	NS	**	*	NS	*

[1] * - $P < 0.05$, ** - $P < 0.01$ in one-way ANOVA's on each date and two-way ANOVA's over all dates, reported in the unweighted average column. These analyses were performed on log-transformed data, which eliminated or reduced heteroscedacity in Cochran's tests. Superscripts A and B indicate significant differences in Duncan's test at $\alpha = 0.05$. No Duncan's test results are given for the unweighted averages in the seagrass bed because the two-way ANOVA exhibited highly significant ($P < 0.001$) interaction between date and treatment.

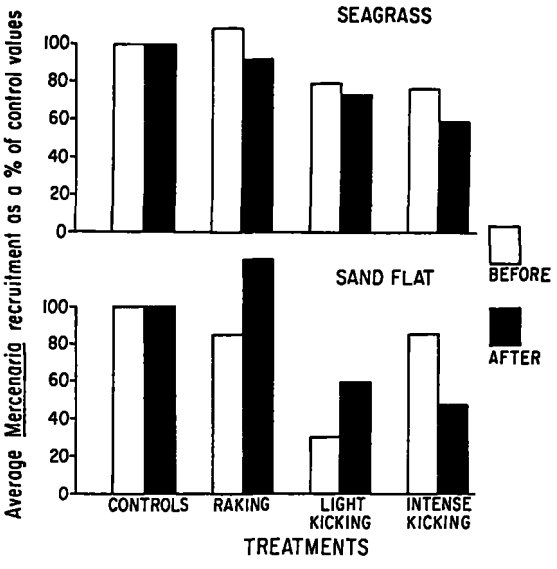

FIGURE 3.—Average density of *Mercenaria* recruits (<2.5 cm in length) before harvest treatments in spring 1980 and after in October 1980 and 1981 (averaged together). ANOVA's showed no significant effect in the sand flat but several significant changes after treatment in the seagrass bed (see Table 4). Seagrass matrices are grouped together for illustration of effects on the basis of results of Duncan's tests performed on 1980 and 1981 data adjusted for spring 1980 differences in recruit densities. Consequently, these groupings separate those seagrass matrices that changed in recruitment pattern after treatment.

among seagrass matrices in *M. mercenaria* recruitment, we analyzed the posttreatment data by both simple ANOVA to test for differences in each postharvest sampling and by ANOVA on adjusted data to test for significant changes away from the initial differences. The results of these two different sorts of analysis were inconsistent. ANOVA's on simple recruit densities [log $(x + 1)$-transformed, which homogenized variances in Cochran's tests] demonstrated significant differences among matrices in October 1981 and 1982, but not in 1980 or 1983. Duncan's tests on the 1981 and 1982 results showed few significant differences and no consistent difference in these 2 years (Table 4). The unweighted means suggest that *M. mercenaria* recruitment may have been less in the 2 intensely kicked matrices, but the two-way ANOVA had a significant date by treatment interaction preventing application of Duncan's test.

Despite an indication of lower *M. mercenaria* recruitment in the 2 intensely kicked matrices (Table 4), ANOVA's performed on recruit data adjusted for initial differences among matrices to test whether those differences changed after treatment revealed a different pattern. Only the 1980 and 1981 results were significant (both at $P < 0.001$). The patterns of change in recruitment among matrices were the same in Duncan's tests on both 1980 and 1981 data (Fig. 3). The shelly control I exhibited over 4 times as much recruitment in October 1980 and 1981 as in spring 1980, while control II exhibited about a 40% decrease after harvest (Fig. 3). Raking and light-kicking matrices behaved similarly, showing about the same value after harvest as before. The 2 intense-kicking matrices showed about a 30% increase in *M. mercenaria* recruitment after harvest (Fig. 3). Thus, the ANOVA's on adjusted data produce results dependent upon whether control I is discarded or averaged together with control II.

This demonstrates that conclusions about how clam harvest affects *M. mercenaria* recruitment are not robust to the decision of how to treat the shelly control or to the relaxation of the assumption that matrices are expected to repeat any initial differences in recruitment in the absence of treatment as an intrinsic characteristic. The choice of analysis might be made by examining whether matrices that are treated identically show similar or dissimilar patterns of recruitment in different years. A comparison of all posttreatment recruit data in the 2 intensely kicked matrices (Table 4) reveals that they never differed from one another significantly, although the mean difference and even ranking between them varied. The 2 control matrices diverged radically from one another (Table 4), but unpredictable illegal clamming in matrix I may be at least partly responsible. Because of the ambiguities in these data, it is impossible to draw any firm conclusion on how treatments affected *M. mercenaria* recruitment in the seagrass.

Seagrass Biomass

Because of substantial and significant differences among seagrass matrices in seagrass biomass in spring 1980 before application of any treatment, we analyzed the posttreatment data by both simple ANOVA to identify significant differences among matrices after treatment and also by ANOVA on adjusted observations to test for significant change in the initial pattern of biomass differences among matrices. The results of these 2 types of analysis are qualitatively identical, so we present only the results on adjusted data. We prefer this analysis because the *Zostera marina* and *Halodule wrightii* in North Carolina are perenials that do not readily and quickly spread into new areas (Thayer et al. 1985), so that initial patterns of difference in seagrass biomass

might be expected to persist in the absence of treatment effects. All ANOVA's were performed on untransformed data (seagrass biomass or differences in seagrass biomass) because Cochran's test for heteroscedacity was nonsignificant on 2 of the 6 data sets and log and square root transformations failed to reduce the significance level ($P < 0.05$ on 2 and $P < 0.01$ on the other 2).

There was a clear and large effect of intense kicking. The ANOVA's on adjusted data were highly significant for every posttreatment sampling date, indicating that the initial differences among seagrass matrices in average seagrass biomass shifted significantly after application of harvest treatment and never returned to initial levels even by fall 1984. The 2 intense-kicking treatments had consistently low seagrass even after the first light treatment but especially after both treatment applications. Light kicking and raking never differed significantly from one another in seagrass biomass. The shelly control I matrix diverged from the other control (II) in having low values in all posttreatment samplings, often grouping with the 2 intense-kicking matrices in the Duncan's test (Table 5).

Average biomass of seagrass in each treatment matrix is compared in Figure 4 to the changes that would be predicted from the average biomass in the 2 untreated control matrices. This approach smoothes out the seasonality and other temporal variability by normalizing all the treatment means to the control values. It assumes that the differences among matrices observed in spring 1980 in average biomass would be expected to persist indefinitely and then calculates what percent of the expected seagrass biomass each treatment matrix actually exhibited on each sampling date. This assumption is clearly violated by the divergent behavior of the 2 control matrices, but it provides a conservative estimate of the effects of harvest because the average of the 2 controls includes control matrix I, which exhibited low seagrass biomass, perhaps because of enhanced illegal clamming. Clam harvest treatments immediately reduced seagrass biomass below the expected amounts, with greater effects of the second, more intense (see Table 2), harvest treatments. The 2 intense clam-kicking treatments exhibited a decline of about 65% in expected biomass from spring 1980 until spring 1981, while biomass declined by about 25% below expected in the raking and light-kicking matrices. Seagrass biomass recovered to equal and even exceed expected values by the very next sampling period in fall 1981 in the raking and light-kicking matrices, and remained high for the next 3 years. However, recovery in seagrass biomass in the 2 intense-kicking matrices did not begin to occur until sometime in fall 1982-fall 1983 (Fig. 4) and was not yet complete by fall 1984. In fall 1984, almost 4 years after the second harvest treatment, average biomass of seagrass in the 2 intense-kicking plots was only 65% of the expected levels. These estimates are conservative if the shelly control (I) matrix is actually a poor control for this experiment because we used the mean of both controls as an expected value for Figure 4. Scheffé a priori contrasts of matrix means (in Table 5) show that, despite the divergence of the 2 controls, the mean seagrass biomass was significantly ($P > 0.05$) less in the 2 intense-kicking matrices than expected from the 2 controls in all sampling periods after application of both harvest treatments. This test provides the statistical justification for our presentation of differences in Figure 4.

TABLE 5.—The impact of clam harvesting on the average seagrass dry mass (± SE) per ¼ m^2 within the seagrass habitat. Data presented for each date and matrix are the mean (± SE) dry mass of seagrass per sample minus the mean dry mass in spring 1980 for that particular matrix (from Table 3). Sample sizes appear in Table 1. Clam harvesting treatments occurred between spring 1980 and fall 1980 and again between fall 1980 and spring 1981. Superscripts A-D indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

Treatment matrices	Fall 1980	Spring 1981	Fall 1981	Fall 1982	Fall 1983	Fall 1984
Control I	2.2(2.9)^{C,D}	19.5(11.2)^{A}	7.4(3.3)^{B}	11.9(6.1)^{A}	1.2(4.4)^{B}	8.0(7.2)^{B}
Control II	19.7(2.7)^{A}	25.8(4.0)^{A}	20.0(2.0)^{A}	22.8(5.2)^{A}	40.1(5.9)^{A}	40.8(3.8)^{A}
Raking	7.7(1.8)^{B,C}	10.5(3.2)^{A}	15.2(2.0)^{A,B}	13.6(5.1)^{A}	38.2(7.0)^{A}	41.1(5.4)^{A}
Light-Kicking	13.8(2.9)^{A,B}	14.4(6.0)^{A}	15.3(3.0)^{A,B}	13.6(3.5)^{A}	31.9(4.7)^{A}	35.7(5.1)^{A}
Intense-Kicking I	−1.5(2.7)^{D}	−21.2(6.9)^{B}	−18.8(4.3)^{C}	−29.0(6.1)^{C}	−18.8(6.0)^{C}	5.6(9.1)^{B}
Intense-Kicking II	7.1(3.7)^{B,C}	−9.1(5.4)^{B}	−12.2(3.1)^{C}	−11.3(7.2)^{B}	9.2(10.8)^{B}	1.5(4.4)^{B}
Statistical significance[1]	***	***	***	***	***	***

[1] *** - $P < 0.001$ in one-way ANOVA's on untransformed dry masses, comparing the matrix means on each separate date. ANOVA's were performed on the differences from spring 1980 matrix means because of pre-existing significant differences among matrices in spring 1980 before application of harvest treatments.

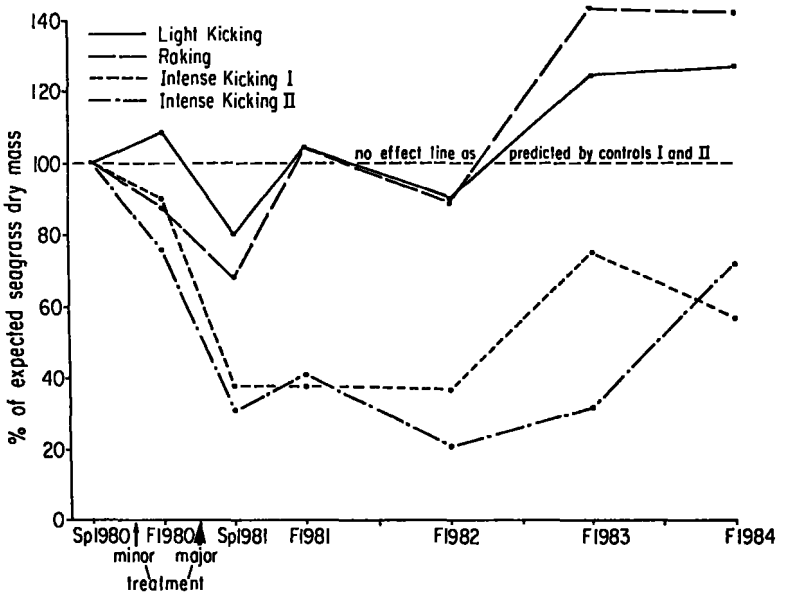

FIGURE 4.—Percent difference between observed average biomass of seagrass in each treatment matrix and expected biomass based on the assumption that initial differences between the two control matrices and each treatment matrix would be expected to remain constant across time. The expected biomass is then plotted as 100% (the no effect line). Times of the two clam harvest treatments are indicated with arrows on the x-axis.

Benthic Macroinvertebrates

In the sand-flat habitat, the average density of benthic macroinvertebrates never varied significantly among matrices (Table 6) in any of the 3 posttreatment sampling dates [one-way ANOVA's were run on log $(x + 1)$-transformed counts, using a separate analysis for each date]. The sums over all 3 posttreatment dates of the average macroinvertebrate densities per core are nearly identical for each sand-flat matrix and a two-way ANOVA on log $(x + 1)$-transformed densities from all 3 time periods revealed no significant difference among matrices.

In the seagrass habitat, analogous one-way ANOVA's done separately for each date, demonstrated that the average density of benthic macroinvertebrates did not differ significantly among seagrass matrices in fall 1980 or spring 1981 (Table 6). A significant difference among matrices did appear in fall 1981, and in a two-way ANOVA on all 3 posttreatment dates together. Despite the statistical significance of 2 of 4 ANOVA's, actual differences in mean densities among seagrass matrices were proportionately small. Furthermore, Duncan's tests revealed a pattern of differences among matrices (Table 6) that was identical to the initial pattern of significant differences in the spring 1980 sampling before treatment (see Table 3).

Although the sums of the sample means from each of the 3 posttreatment sampling dates (Table 6) imply that benthic macroinvertebrate densities in the seagrass habitat were about double those in the sand flat, this pattern was not consistent across seasons. Nested ANOVA's, done on log $(x + 1)$-transformed counts and performed separately for each sampling date, showed that there was no significant difference between habitats during either spring sampling period (spring 1980 or 1981), whereas average densities of benthic macroinvertebrates were significantly greater ($P < 0.001$ in fall 1980 and $P < 0.005$ in fall 1981) in the seagrass habitat in both of the Octobers.

Although the clam harvesting treatments did not affect total density of benthic macroinvertebrates in either habitat, species composition might still have been altered. We identified all individuals in 16 cores in each habitat from the spring 1980 pretreatment sampling (4 cores randomly chosen from each control matrix and from each intense-kicking matrix) and in 16 cores in each habitat from the spring 1981 posttreatment sampling (drawn equally from each of the same matrices). This comparison holds season constant and permits us to test for any gross shifts

TABLE 6.—The impact of clam harvesting on average density (± SE) of benthic macroinvertebrates per 0.008 m^2. n = 6 samples for each treatment matrix at each sampling date. Samples were taken to 25 cm and passed through 1 mm mesh. Superscripts A-C indicate significant differences among matrices in Duncan's test at α = 0.05, with those means sharing capital letter superscripts not differing significantly.

	Habitat and date							
	Sand flat				Seagrass bed			
Treatment matrix	Fall 1980	Spring 1981	Fall 1981	Sum	Fall 1980	Spring 1981	Fall 1981	Sum
Control I	8.0 (2.7)	5.7 (1.2)	8.0 (1.4)	21.7	34.3 (7.8)	9.3 (1.8)	16.2^{A} (2.9)	59.8^{A}
Control II	11.7 (1.5)	7.7 (1.4)	4.2 (0.8)	23.6	19.0 (2.0)	10.5 (1.6)	$11.0^{A,B}$ (1.6)	40.5^{B}
Raking	6.5 (0.5)	8.2 (1.0)	4.8 (0.8)	19.5	39.8 (5.1)	6.8 (1.1)	$12.0^{A,B}$ (2.4)	58.6^{B}
Light-Kicking	12.3 (2.6)	11.5 (3.0)	4.5 (0.9)	28.3	29.5 (8.6)	5.8 (1.3)	$7.8^{B,C}$ (1.3)	44.1^{B}
Intense-Kicking I	7.8 (0.7)	8.7 (1.7)	6.3 (1.4)	22.8	23.5 (4.8)	8.7 (2.9)	6.5^{C} (1.2)	38.7^{B}
Intense-Kicking II	9.7 (2.2)	6.0 (1.3)	5.0 (0.8)	20.7	34.5 (10.7)	6.3 (1.1)	6.0^{C} (0.9)	46.8^{B}
Statistical significance[1]	NS	NS	NS	NS	NS	NS	**	***

[1] ** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA's (for each separate date) and two-way ANOVA's (for sums) on average macroinvertebrate counts per core (transformed by log (x + 1)).

in species composition as a function of the intense-kicking treatment. Table 7 presents the results of these species identifications and shows that no major shift in species composition of the most abundant species occurred in either the sand-flat or seagrass habitat following the application of the intense-kicking treatment. Polychaetes dominated the fauna of both habitats and the same species of polychaetes tended to be represented at similar densities both before and after intense clam kicking.

Bay Scallop Densities

Bay scallops were never encountered in sampling the sand-flat matrices, so we have no test of whether clam harvest treatment affects bay scallops in areas lacking seagrass. One-way ANOVA's on log (x + 1)-transformed counts (which removed heteroscedacity in Cochran's tests) demonstrated significant (α = 0.05) differences among seagrass matrices in average bay scallop density on only 2 sampling dates, fall 1980 and fall 1983 (Table 8). Duncan's test on the fall 1980 data showed that bay scallop density in control I was significantly ($P < 0.05$) lower than in every other matrix except intense-kicking II, and that there were no other significant differences between pairs of matrices. Because the fall 1980 sampling occurred before the major application of clam harvest treatments (see Table 2), this sampling period may be considered a pretreatment sampling. Extremely low seagrass biomass in control I in fall 1980 (Table 5) may explain the significantly lower bay scallop densities in that matrix on that date.

The fall 1983 sampling occurred after a period of more successful bay scallop recruitment than occurred before any other sampling date (Table 8) and, thus, provided more "substrate" on which effects of clam harvest treatments may have operated. Duncan's test on mean bay scallop densities for fall 1983 demonstrated that the matrices split into two separate groups: a low-density group, made up of control I and the 2 intense-kicking matrices, and a high-density group, comprised of control II, the raking, and light-kicking matrices (Table 8). Within each group, no matrices differed significantly (α = 0.05) from any other, but all differences between groups were statistically significant. Because fall 1983 bay scallop densities were so much greater than at any other sampling date, the sums over all five sampling periods also exhibited significant differences among matrices in an analogous two-way ANOVA, and Duncan's tests separated the matrices into groupings virtually identical to those detected for the fall 1983 data set alone (Table 8).

A contrast of the bay scallop results of fall 1980 and fall 1983 demonstrates that after application of the second intense-kicking treatment in the seagrass habitat in winter of 1980-81, bay scallop densities declined to join the already low value of control I,

which together formed a group of low-density bay scallop matrices. About 84% of the variance in bay scallop densities in fall 1983 is explained by seagrass biomass in a simple linear regression. Figure 5 presents the relationship between average seagrass biomass and bay scallop densities on a 1,225 m^2 scale, which suggests that the 2 intense-kicking matrices contained even fewer bay scallops than predicted from their reduced seagrass biomass. This is similarly illustrated from calculations of the mean numbers of bay scallops per 100 g of seagrass in each matrix in fall 1983: control I (5.7), control II (5.1), raking (4.7), light kicking (4.3), intense-kicking I (2.0), and intense-kicking II (2.3).

TABLE 7.—For each habitat, total numbers of individuals found in four randomly chosen cores from each of the two controls and the two intense-kicking matrices on two dates, one before and one after clam-harvest treatment. All species with total counts greater than two are listed separately.

Species	Spring 1980 Before treatment		Spring 1981 After treatment	
	Controls	Intense-kicking	Controls	Intense-kicking
Sand-flat habitat				
Aricidia fragilis	7	1	6	5
Notomastus hemipodus	3	4	5	5
Platynereis dumerilii	1	0	5	7
Axiothella sp.	3	2	1	7
Drilonereis magna	5	5	0	1
Spiochaetopterus oculata	0	2	3	3
Arabella iricolor	3	1	1	2
Glycera sp.	5	1	0	0
Others[1]	5	2	2	1
Seagrass habitat				
Axiothella sp.	23	8	7	4
Platynereis dumerilii	12	8	14	1
Notomastus hemipodus	20	7	4	0
Tharynx marioni	3	4	3	2
Nereis falsa	0	1	5	5
Glycera sp.	3	4	2	1
Melinna maculata	1	0	6	3
Onuphis jenneri	0	1	3	3
Lumbrinereis sp.	0	0	4	3
Spiochaetopterus oculata	1	0	4	0
Spionidae	4	0	0	1
Sthenelais limicola	0	1	1	1
Arabella iricolor	0	2	1	0
Poecilochaetus sp.	3	0	0	0
Onuphidae	0	0	3	0
Others[1]	1	2	1	1

[1]These include molluscs, an amphipod, and additional polychaetes.

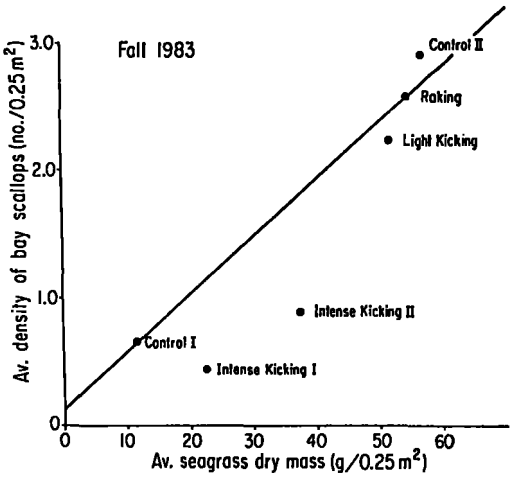

FIGURE 5.—Relationship between the average density of bay scallops, *Argopecten irradians*, and the average biomass of seagrass in fall 1983 samplings of each control and treatment matrix of the clam harvest experiment in the seagrass matrix. Clam harvest treatments had been applied in spring 1980 and again in winter 1980-81.

TABLE 8.—The effect of clam harvesting in the seagrass habitat on average bay scallop, *Argopecten irradians*, density per ¼ m^2 (± SE). Sample sizes per treatment matrix were 36 in fall 1980 and fall 1981 and 9 in spring 1981, fall 1982, and fall 1983. No data are presented for the sand flat because of the rarity of bay scallops in that habitat. Superscripts A-C indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

Treatment matrix	Sampling date					
	Fall 1980	Spring 1981	Fall 1981	Fall 1982	Fall 1983	Sum
Control I	$0.11(\pm 0.05)^{B}$	$0.44(\pm 0.24)$	$0.05(\pm 0.04)$	$0.11(\pm 0.16)$	$0.66(\pm 0.33)^{B}$	1.37^{C}
Control II	$0.63(\pm 0.11)^{A}$	$1.00(\pm 0.37)$	$0.14(\pm 0.07)$	$0.22(\pm 0.15)$	$2.89(\pm 0.51)^{A}$	4.88^{A}
Raking	$0.53(\pm 0.14)^{A}$	$0.78(\pm 0.28)$	$0.16(\pm 0.06)$	$0.44(\pm 0.24)$	$2.56(\pm 0.67)^{A}$	4.47^{A}
Light-Kicking	$0.75(\pm 0.18)^{A}$	$0.33(\pm 0.33)$	$0.14(\pm 0.07)$	$0.89(\pm 0.42)$	$2.22(\pm 0.46)^{A}$	4.33^{A}
Intense-Kicking I	$0.50(\pm 0.12)^{A}$	$0.22(\pm 0.15)$	$0.03(\pm 0.03)$	$0.00(\pm 0.00)$	$0.44(\pm 0.29)^{B}$	$1.19^{B,C}$
Intense-Kicking II	$0.39(\pm 0.11)^{A,B}$	$0.56(\pm 0.18)$	$0.14(\pm 0.07)$	$0.55(\pm 0.24)$	$0.88(\pm 0.35)^{B}$	2.52^{B}
Statistical significance[1]	**	NS	NS	NS	***	***

[1]** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA on log $(x + 1)$-transformed sample counts, comparing matrix means on each date and in a two-way ANOVA over all dates (in the sums column).

DISCUSSION

The one-way ANOVA's which we performed to test the significance of differences in parameter means among matrices at any given sampling date can demonstrate heterogeneity among matrices. If there is no significant heterogeneity, we probably can conclude safely that there was no effect of treatment on that parameter at that sampling date, assuming that equivalent levels of the parameter prevailed before application of the treatment (which was not always true). If, on the other hand, the one-way ANOVA demonstrates significant differences among matrices, this result does not necessarily imply that the treatment was the cause. Replication in these ANOVA's is generated from subsamples within each individual matrix. These subsamples taken from within a given matrix are not independent because of their spatial proximity. Consequently, matrices can diverge in various ways from one another over the course of an experiment, caused by extraneous events that act on the scale of the plot (matrix) to destroy independence among subsamples. This experimental design would be termed pseudoreplication (Hurlbert 1984), and permits a test of whether plots differ significantly and does not allow an unambiguous assignment of observed differences to the treatment applied (but see Stewart-Oaten et al. 1986). For that reason, we replicated both our control matrices and our intense-kicking matrices in each habitat. These permit us to use a priori contrasts, with replication of 2 separate, independent plots, to test unambiguously whether the most important treatment (intense clam kicking) was responsible for observed changes. Appreciation of the differences between these two sorts of analyses is necessary to interpret properly the results of this study.

Although we designate our heavier clam-kicking treatment "intense", it probably falls well short of the effort that commercial clammers would apply to a productive seagrass bottom; we took only an estimated 50% of the clams legally available for harvest (Table 2). Consequently, the intensity of harvest that we applied in the seagrass is not unreasonably high. In the sand-flat system, we took approximately 100% of the estimated numbers of legally available clams in our intense treatments. Although higher than the percent taken in the seagrass, this probably better approximates the fishing intensity that is applied to productive unvegetated areas by commercial clammers. Efficiency of returns remained high even in the high-intensity kicking matrices, as compared with hand raking. In the sand flat, light kicking produced an average of 8.1 clams per minute and intense kicking 6.2 clams per minute, compared with a return of only 0.9 clams per minute from hand raking (Table 2). In the seagrass bed, light kicking yielded an average of 8.1 clams per minute and intense kicking 16.1 clams per minute, in contrast to a return of only 0.4 clams per minute from hand raking (Table 2). Thus, efficiency of harvest, defined as clams caught per unit of time, was clearly greater by over an order of magnitude with the mechanical technique than with the traditional hand method. The improved efficiency during clam kicking in the seagrass as harvest intensity increased from taking about 15% to about 50% of available clams is probably caused by the gradual removal of seagrasses which, when present, reduce the efficiency of clamming.

To test whether hard clam harvest affects its own recruitment in the area of harvest, we counted new recruits (<2.5 cm in length, Peterson et al. 1983b). Recruitment, when estimated in this fashion, confounds both larval (and postlarval) settlement with subsequent early mortality from time of settlement until October. Consequently, we do not directly test the hypothesis that natural densities of adult hard clams inhibit larval settlement in their vicinity. Furthermore, our clam harvest treatment not only removes many larger hard clams, but it also disturbs the bottom sediments. Consequently, there are several plausible mechanisms by which our clam harvest treatments may affect October recruitment of hard clams: 1) reduction of adult hard clam density may affect hard clam settlement (positively, if negative adult-larval interactions predominate, as suggested by most past studies: Woodin 1976; Williams 1981; Peterson 1982b) or survivorship from settlement until October (no a priori prediction from the literature on what direction this effect may take), or 2) disturbance of the bottom may alter hard clam settlement (positively, if hard clam larvae select disturbed sediments, which seems unlikely, or negatively if hard clam larvae avoid disturbed sediments) or early survivorship (negatively, if the clam harvest buries small clams too deeply to reemerge or if disturbance has removed protective seagrass or shell materials and thereby made juvenile hard clams more vulnerable to predators (Peterson 1982a; Summerson and Peterson 1984)).

Our data on hard clam recruitment are sufficiently ambiguous to preclude any definitive answers to the question of how clam harvest affects subsequent recruitment. In the sand flat, there was no significant effect of harvest treatment, but the 2 intensely kicked matrices yielded only 50% of the recruits

produced by the 2 controls (Fig. 3). In the seagrass, *M. mercenaria* recruitment may also have been reduced by harvest treatments (Table 4), but the conclusion depends upon the assumption that the shelly control I was an adequate control for recruitment data. Given the enhanced survivorship of *M. mercenaria* recruits in shell (Castagna and Kraeuter 1977) and the significant illegal clamming in seagrass control I, this assumption is questionable.

It is possible that removal of adult hard clams enhances larval settlement over a larger spatial scale than the 1,225 m^2 experimental plots because depletion of larvae by feeding from the water column should extend over a larger spatial scale (Peterson 1982b). Although it is possible that our sampling was on too fine a scale to detect such an effect, our sampling occurred on a far larger spatial scale by 3 orders of magnitude than any previous experimental test of adult-larval interactions and, thus, should have provided for greater opportunity to detect any positive effect of adult hard clam removal. The failure to demonstrate a response in the sand flat may be a different consequence of scale. Newly recruited hard clams may settle more heavily where adult densities have been reduced but the effect may be diffused away by the physical dispersal of new recruits by tidal currents and waves. As a consequence of such multiple interpretations, we can best conclude that on the scale of our experiments no dramatic increase in hard clam recruitment occurs with intense mechanical harvest of adult hard clams in seagrass and harvest may even reduce recruitment in both unvegetated and vegetated areas.

The effect of various clam harvest treatments in the seagrass bed on seagrass biomass (Fig. 4) is the most obvious result of this study. Clam harvest of all types had an immediate impact in reducing the seagrass biomass. Reduction of seagrass increased with harvest intensity, as was demonstrated both by the enhanced effect of the second treatment application, which was much more intense than the first, and also by the larger effects of intense kicking as compared with the other treatments (Fig. 4). Although the seagrass biomass in the raking and light-kicking matrices recovered to levels predicted from the controls within a year's time, the seagrass biomass in the intense-kicking matrices did not even begin to recover for 2 years and had not fully returned to predicted, control levels after 4 years. These results imply that if sufficient seagrass is destroyed, recovery is slow. Because our intense-kicking treatment removed only an estimated 50% of available hard clams and because the efficiency of hard clam capture per unit time of harvest was greater in the intense treatment than in the light treatment in the seagrass habitat, we suspect that commercial clam kickers would apply even more harvest intensity than we did in the this intense-kicking treatment. Consequently, the effects of commercial clam kicking in seagrass beds are probably underestimated by our data (Fig. 4). Furthermore, by using both control matrices (including the shelly one) in estimating the effects of harvest on seagrass biomass, we intentionally provide an additional conservative bias. Clam kicking at a low level (≅15% of available hard clams harvested) does not appear to be any more destructive of seagrass than hand raking that same number of clams, but the lack of replication of these two types of treatment matrices renders this a tentative conclusion.

The extremely slow recovery of seagrass in the intensely kicked seagrass matrices raises the possibility that seagrass beds and unvegetated sand flats may exist as alternative stable states (Sutherland 1974; Connell and Sousa 1983; Peterson 1984) on many of the same shallow bottoms of sounds and coastal lagoons. That is, a given shallow bottom may exist as either a seagrass bed or an unvegetated sand flat, but whichever state it occupies it is likely to retain for a relatively long period of time. Transformation from one state to another may require some input of external energy. Because great changes in current regime and surface sediment character are associated with the presence and growth of seagrasses (Ginsburg and Lowenstam 1958; Orth 1977; Fonseca et al. 1983; Peterson et al. 1984; Eckman in press), it is reasonable to hypothesize that destruction of seagrass may result in sufficiently higher energy at that site that natural reestablishment could be difficult. Certainly, the slow return of seagrass following intense clam kicking in our experiments implies that seagrass recovery even in previously vegetated areas is tenuous. If seagrass beds and unvegetated bottoms do tend to represent alternative stable states for large areas of the estuarine and sound bottom, then denuding of vegetation would have long-lasting effects, even beyond what we have demonstrated. Furthermore, transplantation of relatively dense seagrass may be necessary to produce rapid reversion back into a vegetated system (for reviews of disturbance, recovery, and transplantation of seagrasses see Zieman 1982; Thayer et al. 1985). Because of the important roles that seagrasses play in promoting estuarine productivity and coastal fisheries (Thayer et al. 1975), intense clam kicking in vegetated areas could have long-lasting and

serious impacts on many commercially important fisheries. Our own data imply a potentially negative impact on hard clam recruitment (Table 4) and a clear reduction in bay scallop abundance (Table 8) in part because of reduction in seagrass biomass.

Clam harvesting had no detectable effect on the abundance of small benthic invertebrates. The density data did not even suggest an effect (Table 6) and the composition of the most abundant species did not change, even with intense clam kicking (Table 7). This lack of response is probably a consequence of the dominance of small polychaetes in these invertebrate data. Small polychaetes make up most of the total infaunal density and all of the most abundant species. Small polychaetes tend to exhibit rapid turnover, quick colonization and short life spans, relative to molluscs, echinoderms, and many other invertebrates; consequently, they may be expected to recover more rapidly after disturbance. The large seasonal variability in total macroinvertebrate density at our seagrass sites is a reflection of the short-term response times of this fauna, which is known to exhibit large seasonal fluctuations in density in North Carolina (Commito 1974).

Like several previous studies of the densities of benthic infauna (Kikuchi 1966; Warme 1971; Orth 1977; Reise 1977, 1978; Stoner 1980; Summerson and Peterson 1984), our data demonstrate higher densities inside the seagrass bed than on unvegetated bottoms in October. However, the difference in infaunal density between habitats appears to vary seasonally, as shown previously (Reise 1978; Stoner 1980). In spring, the two habitats had approximately equal densities of infauna. Because estuarine densities of epibenthic predators, both fishes (Adams 1976; Orth and Heck 1980) and crustaceans (Heck and Orth 1980), also vary seasonally such that our fall samplings occur after months of high density and our spring samplings after a low-density season for epibenthic consumers, these new observations provide further support for the hypothesis (see review of concepts in Kikuchi 1980; experimental evidence in Reise 1977; Orth 1977; Summerson and Peterson 1984) that seagrass provides a natural refuge from predation for infaunal invertebrates.

Intense clam kicking caused a substantial decline in the average density of bay scallops in the seagrass habitat (Table 8). Most of the variation among matrices in the total densities of bay scallops and in the fall 1983 densities, when numbers were high, could be readily explained by the variation among matrices in average seagrass biomass. Bay scallops recruit to seagrass blades where they remain attached by byssal threads for the first few months of life. In addition, adult bay scallops, which are mobile, tend to be found in seagrass beds, as our failure to encounter them in the sand-flat samples illustrates. Their feeding may be more efficient in the slower currents of the seagrass environment (Kirby-Smith 1972). Consequently, it is not surprising that reductions in bay scallop density accompanied the declines in average seagrass biomass in our experiments. However, the apparent effect (Fig. 5) of intense clam kicking that persists even after the seagrass biomass effect is removed was a surprise. Because the application of clam kicking is necessarily patchy (it forms a trail behind the path of the boat) and, thus, produces an increase in the patchiness of the vegetation (see standard errors in Table 5), we suspect that this residual effect of intense clam kicking is a reflection of that enhanced seagrass patchiness. We hypothesize that the average biomass of seagrass present in our plots is more attractive (in a broad sense) to bay scallops when it is more uniformly distributed over a given area than when it is clumped into more discrete patches at least on the 0.25 m^2 scale of our samples.

The implications of this study for the management of the hard clam fishery depend upon the specific values attributed to various factors. Our data show clearly the enhanced efficiency that the mechanical clam harvesting process known as clam kicking brings to the fisherman who adopts it instead of hand raking. Yet the enhanced efficiency may itself be a danger if the resource is thereby overfished beyond its capacity to sustain harvest. Our data on the negative impacts of clam harvest do not permit one method to be selected in preference to another except to the degree that hand raking might never reach the same harvest intensity and, therefore, might not cause the same magnitude of effects on seagrass beds and their fauna. Outside seagrass beds, clam kicking does not appear to have any serious negative impacts on other parameters of ecological value with the possible exception of hard clam recruitment. This effect is probably a necessary price to pay for the harvest of the adult, marketable clams. Inside seagrass beds, effects of clam kicking on seagrass biomass and bay scallop abundance are quite serious and long-lasting. Because seagrass contributes so substantially to the production of many coastal fisheries (Thayer et al. 1985), any regulation that might limit the intensity of clam fishing in that habitat would probably be beneficial. Restriction of the much more efficient mechanical clam harvesters to unvegetated bottoms may be a suitable mechanism for limiting the total harvest pressure in seagrass beds and, thereby, preserving other fish-

eries in the face of emerging new technology, which has the potential to enhance greatly the user conflicts for limited and interdependent coastal and estuarine resources.

ACKNOWLEDGMENTS

We thank D. Guthrie for his advice and help in applying the clam kicking treatments using his boat and gear. Field and laboratory assistance in this project was provided by W. G. Ambrose, Jr., B. F. Beal, K. L. Bowers, P. Boyd, M. E. Colby, P. B. Duncan, S. H. Larson, J. Purifoy, G. W. Safrit, Jr., P. S. Smith, and N. T. Sterman. Loans of equipment by H. J. Porter and D. Spitsbergen are gratefully acknowledged. W. Garner, Jr., M. Marshall, F. Munden, and D. Spitsbergen provided useful advice concerning the data needed for hard clam management. H. E. Page and V. Page provided graphics services. We thank D. Colby and S. Muga for improving our presentation and sharpening our inferences. R. B. Deriso and D. Colby provided statistical advice. The project was supported by the Institute of Marine Sciences of the University of North Carolina at Chapel Hill and by the Office of Sea Grant, NOAA, U.S. Department of Commerce under grant #NA81AA-D-00026 and the North Carolina Department of Administration.

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