

Species densities of macrobenthos associated with seagrass: A field experimental study of predation

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ABSTRACT

Caging experiments in a wide variety of marine environments over a period of almost fifty years have produced dramatic density increases of macrobenthos in the absence of predators. This study utilized predator exclusion cages in seagrass areas of a subtropical estuary in east central Florida to determine if predicted increases in density would result.

Cages were erected at three sites in the Indian River estuary. At each of the three sites, four replicate box cores were taken, inside and outside the cages, at four sampling times over a period of five months. The 33 numerically most abundant taxa were selected for testing of differences in species densities by two-way multivariate analyses of variance with interaction.

The analyses showed that the effect of caging differed at the three sites. At two of the sites, species densities increased inside the cages, consistent with our expectations, while at the third site (St. Lucie) densities of species decreased. The presence of carnivorous decapod crustaceans inside cages in larger numbers at the St. Lucie site is advanced as an explanation for the un-predicted decrease in species densities at that location.

The use of caging in this experiment separated the predatory impact of fishes from that of the decapods, further clarifying the structure of the food web in this seagrass habitat.

1. Introduction

The pioneer benthic ecological work in Scandinavia during the early 1900's was prompted by the need to calculate the amount of food available for bottom fish (reviewed by Thorson, 1957). Quantitative methods of sampling developed by Petersen (1913) for the first time provided statistically well-founded density estimates of macrobenthos potentially available as fishfood. A static rather than a dynamic view of the role of the benthos as food for fishes prevailed until Blegvad (1928) experimentally protected the macrobenthos from fish predation with wire netting and demonstrated that up to 60 times as many individuals of certain bivalve molluscs and polychaetes were collected from caged versus uncaged areas of sea bottom after several months. More recently, caging techniques have been

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used as a simple and productive tool in viewing dynamic, functional predator-prey interactions and in gaining insight into effects of predation in structuring marine communities (reviewed by Dayton, 1971).

We have investigated effects of predation on the macrobenthos associated with the seagrass *Halodule* (= *Diplanthera*) *wrightii* Ascherson using predator exclusion cages at three sites in the Indian River estuary of east central Florida. Seagrasses have been extensively studied on a worldwide basis because of their high primary productivity and importance as feeding and nursery grounds for commercially and sportfishery valuable finfish and shellfish (McRoy, 1973). The role of macrobenthos in the seagrass-based food web, however, remains incompletely assessed (Thayer *et al.*, 1975).

Results from caging experiments in the rocky intertidal (Stephenson and Searles, 1960; Connell, 1961a, 1961b, 1970; Dayton, 1971), coral reefs (Bakus, 1964; Randall, 1965) and soft-bottom sediments (Blegvad, 1928; Naqvi, 1968; Woodin, 1974; Virnstein, 1976) led us to expect at the outset of this study that a decrease in predation pressure on seagrass-associated macrobenthos would result in: (1) a decrease in species diversity, and (2) an overall increase in species densities. In a previous paper (Young and Young, in press), species diversity was discussed. This paper reports on analyses of densities of numerically dominant macrobenthic species. Results of these analyses are interpreted in relation to the expected overall increase in density of macrobenthos as affected by caging.

2. Study areas

Three shallow-water, subtidal sites of similar water depth (tidal heights from 22-100 cm) were selected in well-sorted sediment (87.7-88.0% sand; 8.8-9.6% silt; 2.4-3.4% clay) with extensive cover of the seagrass *H. wrightii*. The northernmost site at Haulover Canal (28°44.1'N; 80°45.5'W) is located at the poorly flushed³, "blind" northern terminus of the Indian River estuary. The central site at Link Port (27°32.1'N; 80°20.9'W) is located between two of the three artificially maintained inlets which bisect the barrier island chain of the bar-built estuary. The Link Port site is moderately flushed³ on an aperiodic basis. The southernmost site at St. Lucie Inlet (27°10.9'N; 80°10.3'W) is extensively and periodically flushed³ by the inlet immediately to the south. The distance between the northern and southern sites is approximately 190 kilometers. Increasing ranges of water temperature (14-33°C vs 8-34°C) and salinity (32-34‰ vs 22-42‰) and decreasing predictability of tidal heights (astronomic vs wind-dominated effects) are evident in a south to north direction between St. Lucie and Haulover sites (Young and Young, in press).

3. The time required to renew one-half of the water at the Haulover Canal site is estimated to be on the order of 6 months or more, at the Link Port site from 1 week to 1 month and at the St. Lucie Inlet site from 1 day to 1 week depending on meteorological conditions.

3. Methods

A four-sided wire cage (12 mm mesh), 2 m on a side and 2 m high, was constructed at each site one month prior to the first sampling of each cage. Sides of each cage penetrated the sediment to 5 cm depth and extended above highest tidal stages. The outside of all cages was cleaned of detritus and algae as required. There were no observable changes of sediments inside cages throughout the experiment. The lack of significant differences (Student's *t*, 99% confidence) in seston flux measured inside and outside all cages suggested that there were no apparent disruptive influences of the cage structures on water current flow (Young and Young, in press). We assumed that the cages at all three sites were equally effective in excluding predators (operationally defined here as those animals that are too large to pass through 12 mm mesh).

Four replicate box cores of seagrass and sediment (15 cm × 15 cm × 20 cm deep = 4500 cm³) were taken from both inside and outside of the cage at each site on four sampling periods during October, November and December, 1974, and February, 1975. Four replicates, representing a total area of 900 cm², contained 90% or more of the expected species according to the test of Gauvin *et al.* (1956).

Core samples were washed through 1.0 mm mesh screen; specimens were sorted from debris, enumerated and identified after narcotization, fixation and preservation. The term "macrobenthos," as used here, is operationally defined as benthic invertebrates retained on a 1.0 mm mesh screen during the sampling and sorting processes.

Although 230 species of 24,288 individuals were recorded during the study, relatively few were abundant enough for analyses of species densities. For theoretical and empirical reasons, we chose as a threshold density a grand mean of about two (Jackson, 1972; Buzas *et al.*, in press). Thirty-three species met this criterion.

Field studies are often displayed and analyzed graphically. In the present instance, plots of species densities with time would require 198 graphs (33 species, three areas, inside and outside). Even if it were possible to publish so many figures, the data would be incomprehensible because individual plots do not all exhibit simple and consistent trends. A researcher trying simultaneously to digest so much information would be overwhelmed. Although univariate statistical techniques would reduce the number of contrasts required, a technique such as the analysis of variance would still require 99 separate analyses (33 species, 3 areas). The obvious solution is multivariate statistical analyses.

The experimental design of the study is ideally suited for two-way multivariate analysis of variance with interaction (see Appendix). The two-way MANOVA model allows us to test the significance of changes in species densities for the in-

dependent hypotheses: (1) overall inside vs outside (time is not considered), (2) overall time (inside vs outside is not considered), (3) interaction (changes with densities inside vs outside are not synchronous). The term interaction is used in the statistical sense throughout this paper and should not be confused with biological interaction. In the MANOVA, all the species of a particular group are analyzed simultaneously. Experience with the technique (Buzas, 1971; Buzas *et al.*, in press) has shown that the results of any particular analysis are not as greatly dominated by the most abundant species as they would be if the various species densities were added together to form a "standing crop".

At each site separate analyses were made for the groups: deposit feeders, suspension feeders, carnivores, herbivores-scavengers. Although grouping by mode of feeding incorporates an inherent bias toward those types assumed to have ecological importance, it is no more artificial, and perhaps less so for purposes of these analyses, than grouping according to major taxa.

4. Results

Table 1 compares the deposit feeders at the three sites. At Haulover, all three hypotheses of the analysis are significant, at Link Port, inside vs outside and time are significant and interaction is significant at the 90% level, while at St. Lucie, the hypotheses inside vs. outside and time are highly significant.

Suspension feeders are compared in Table 2, carnivores in Table 3 and herbivores-scavengers in Table 4. In all cases, the hypotheses for time and interaction are significant at Haulover. At Link Port none of the hypotheses is significant for suspension feeders, inside vs outside. Interactions are significant at the 95% level for carnivores, and inside vs outside and time are highly significant for herbivores-scavengers with interaction slightly less so. For the St. Lucie site, none of the hypotheses is significant at the 95% level for suspension feeders; for carnivores only time is significant, and both time (95% level) and inside vs outside (90% level) are significant for herbivores-scavengers.

In these latter groups, as in the case of the deposit feeders, maximum values inside and outside cages are observed to occur at different times for the same species. Numbers of species of suspension feeders and carnivores are higher at Haulover than at the other two sites, with the numbers of abundant species of those animals in the herbivores-scavengers groups comparable at all three sites.

The times of maximum abundance of any particular species inside as compared with outside the cage show a lack of synchronization at all three sites. Overall, at Haulover, most species had higher densities inside the cage; at Link Port, the densities were slightly higher inside than outside; and at St. Lucie there were slightly more individuals outside. Data on abundances of individual macrobenthic species from inside and outside cages at the three sites are available from the authors.

Table 1. Deposit feeders. Two-way MANOVA with interaction (P = polychaete; G = gastropod; A = amphipod; S = sipunculid). Plus (+) sign indicates inclusion in analyses. Zero (0) sign indicates deletion from analyses because of few or no individuals.

Species	Haulover	Link Port	St. Lucie			
1. <i>Cerithium muscarum</i> (G)	+	+	+			
2. <i>Diaostoma varium</i> (G)	+	+	+			
3. <i>Polydora ligni</i> (P)	+	+	+			
4. <i>Clymenella mucosa</i> (P)	+	+	+			
5. <i>Capitella capitata capitata</i> (P)	+	+	+			
6. <i>Tharyx annulosus</i> (P)	+	+	+			
7. <i>Prionospio heterobranchia</i> (P)	+	+	+			
8. <i>Streblospio benedicti</i> (P)	+	0	0			
9. <i>Terebella rubra</i> (P)	+	+	+			
10. <i>Aricidea</i> sp. A (P)	+	+	+			
11. <i>Melinna maculata</i> (P)	+	0	0			
12. <i>Branchioasychis americana</i> (P)	+	+	+			
13. <i>Haploscoloplos foliosus</i> (P)	+	+	+			
14. <i>Phascolion cryptus</i> (S)	+	+	+			
15. <i>Cymadusa compta</i> (A)	+	+	+			
16. <i>Grandidierella bonnieroides</i> (A)	+	+	+			
17. <i>Melita nitida</i> (A)	+	+	+			
Hypothesis	df	X^2	$P(X^2)$	df	X^2	$P(X^2)$
in vs out	17	39.22	.99	15	53.78	.99
time	51	127.92	.99	45	79.36	.99
interaction in-out vs time	51	73.63	.98	45	57.66	.90
				45	48.88	.68

Table 2. Suspension feeders. Two-way MANOVA with interaction (G = gastropod; Pel = pelecypod; P = polychaete; H = holothurian). Plus (+) sign indicates inclusion in analyses. Zero (0) sign indicates deletion from analyses because of few or no individuals.

Species	Haulover		Link Port		St. Lucie	
	df	X ² P(X ²)	df	X ² P(X ²)	df	X ² P(X ²)
18. <i>Crepidula fornicata</i> (G)						
19. <i>Brachidontes exustus</i> (Pel)			+		+	
20. <i>Amygdalum papyrium</i> (Pel)			+	0	0	
21. <i>Fabriciella</i> sp. A (P)			+	+	+	
22. <i>Fabriciella sabella</i> (P)			+	0	0	
23. <i>Potamilla</i> sp. A (P)			+	0	0	
24. <i>Synaptula hydriformis</i> (H)			+	0	0	
Hypothesis	df	X ² P(X ²)	df	X ² P(X ²)	df	X ² P(X ²)
in vs out	7	9.54 .78	2	1.28 .47	3	.28 .04
time	21	109.69 .99	6	4.82 .43	9	16.58 .94
interaction in-out vs time	21	39.60 .99	6	11.13 .92	9	14.28 .89

Table 3. Carnivores. Two-way MANOVA with interaction (G = gastropod; P = polychaete; T = tanaid). Plus (+) sign indicates inclusion in analyses. Zero (0) sign indicates deletion from analyses because of few or no individuals.

Species	Haulover	Link Port	St. Lucie			
25. <i>Marginella apicina</i> (G)	+	+	0			
26. <i>Exogone dispar</i> (P)	+	0	+			
27. <i>Dorvillea rudolphi</i> (P)	+	+	0			
28. <i>Podarke obscura</i> (P)	+	+	0			
29. Paratanaidae A (T)	+	+	+			
30. Nemertinea	+	+	+			
Hypothesis	df	X^2	$P(X^2)$	df	X^2	$P(X^2)$
in vs out	6	10.38	.89	5	12.62	.97
time	18	107.78	.99	15	12.52	.36
interaction in-out vs time	18	42.92	.99	15	26.28	.96

Table 4. Herbivores-scavengers. Two-way MANOVA with interaction (P = polychaete; I = isopod). Plus (+) sign indicates inclusion in analyses.

Species	Haulover	Link Port	St. Lucie			
31. <i>Laeonereis culveri</i> (P)	+	+	+			
32. <i>Erichsonella filiformis isabelensis</i> (I)	+	+	+			
33. <i>Cymodoce faxoni</i> (I)	+	+	+			
Hypothesis	df	X^2	$P(X^2)$	df	X^2	$P(X^2)$
in vs out	3	4.82	.81	3	21.03	.99
time	9	23.50	.99	9	34.42	.99
interaction in-out vs time	9	17.28	.96	9	16.15	.94

Table 5. Summary of significant hypotheses (X = significant at 95% level) for Haulover, Link Port and St. Lucie experiments (DF = deposit feeders; SF = suspension feeders; C = carnivores; H-S = herbivores-scavengers).

Hypothesis	Haulover				Link Port				St. Lucie			
	DF	SF	C	H-S	DF	SF	C	H-S	DF	SF	C	H-S
inside vs. outside	X				X		X	X	X			
interaction	X	X	X	X			X					
time	X	X	X	X	X			X	X		X	X

Table 5 summarizes results from Tables 1, 2, 3 and 4. The effects of the cages at the three stations may be compared by considering the numbers of significant hypotheses for inside vs outside and interaction at each location. At Haulover, all feeding groups show significant hypothesis for interaction, indicating that densities inside and outside the cages differ with time. The deposit feeders at Haulover differ in overall densities inside vs outside. This station is the only one at which all groups differ in their densities inside and outside the cages with time (i.e. interaction). Only carnivores at Link Port differ significantly in terms of the interaction hypothesis, while at St. Lucie, the deposit feeders appear to be the only feeding group affected by the presence of the cage.

The hypothesis for overall time differences is significant for more feeding types at more stations than is any other. These time differences are evident from an examination of chi-square values in Tables 1, 2, 3 and 4. Much of the variability between sites at the 4 sampling times can be accounted for by these overall time differences.

5. Discussion

A general pattern of inconsistency of cage effects upon densities of macrobenthic species is shown in this study. Although some species become abundant at different times in one cage or another, there does not appear to be any clear-cut way to predict which species will dominate in any particular cage. At the three sites the overall time hypothesis of the MANOVA model is significant, however, the same species do not have their maximum densities simultaneously. Consequently, the effect of a cage may well depend on the particular time an experiment is begun.

We expected initially that if the cages were effective as exclosures in preventing predators from feeding upon the macrobenthos at the experimental sites, certain species with r-selection characteristics would increase densities dramatically inside the cages over the several month period of our study. Densities of the polychaetes *Polydora ligni* and *Capitella capitata capitata*, defined by Grassle and Grassle (1974) as r-strategists or opportunists, predictably increased inside the cage at the Haulover site, but neither species increased consistently in density at St. Lucie or Link Port (Fig. 1). *Streblospio benedicti*, another opportunistic polychaete, un-

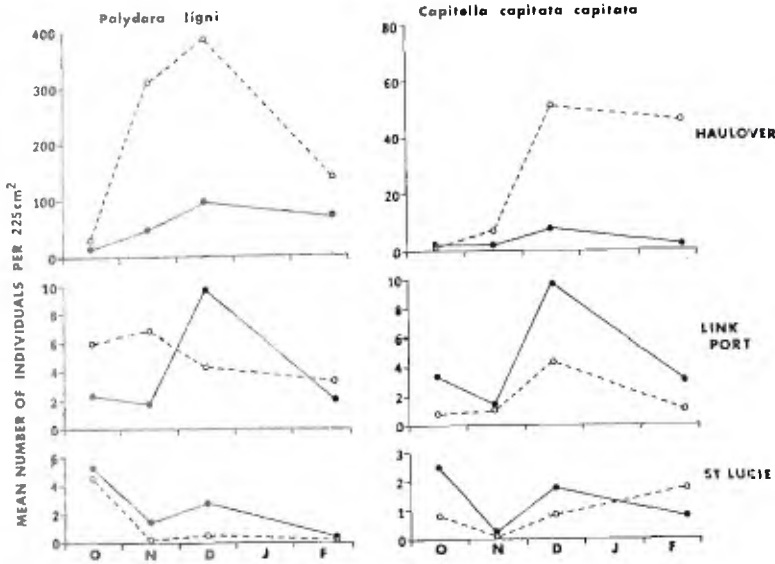


Figure 1. Mean number of individuals per 225 cm² of *Polydora ligni* and *Capitella capitata* from inside and outside cages at Haulover, Link Port and St. Lucie sites during October (O), November (N), December (D) of 1974 and February (F) of 1975. Dashed line and open circles indicate inside cage samples. Solid line and solid circles indicate outside cage samples.

predictably showed no consistent trend of increased densities inside or outside cages at any of the three sites.

Other macrobenthic species included in the MANOVA model, in addition to the classic opportunists discussed above, share certain characteristics toward the r-selection end point of the r-K continuum (Pianka, 1970). Those operationally defined characteristics for which we have preliminary evidence include: (1) rapid development, (2) small body size, (3) short life span, and (4) time-variable and nonequilibrium populations. Pianka (1970) states that populations of such species are usually well below the carrying capacity of the environment.

Only one of the 33 species included in the model, the sipunculid *Phascolion cryptus*, appears to be an exception to those criteria for r-selected species noted above. Specimens of this species may live for several years (M. Rice, personal communication) and preliminary evidence indicates that living space provided by empty gastropod shells may limit their densities.

Our expectation of an overall increase in density of macrofauna from caged versus uncaged samples was substantiated from the Haulover site (6899 vs 5125) and Link Port site (3112 vs 2392), but not supported from the St. Lucie Inlet site (1146 vs 1438), where caging resulted in an unexplained decrease in density

Table 6. Summary of data on decapod crustacean densities and species numbers inside and outside cages at Haulover, Link Port and St. Lucie sites.

	Haulover		Link Port		St. Lucie	
	In	Out	In	Out	In	Out
Xanthidae (mud crabs)	4	0	8	0	39	10
Alpheidae (pistol shrimps)	14	2	11	2	34	20
Portunidae (swimming crabs)	0	0	0	5	3	0
Total xanthids, alpheids and portunids	18	2	19	7	76	30
Total decapods	44	19	80	34	106	50
Percentage decapods of total macrofauna	0.6%	0.4%	2.6%	1.4%	9.2%	3.5%
Number species of decapods	9	6	12	12	24	19

(Young and Young, in press). An explanation for this contradiction is suggested by the MANOVA model.

Results of the MANOVA model (Table 5) indicate that caging effects were greatest at Haulover and least at St. Lucie, with Link Port being intermediate in response. There are more significant differences with treatment (inside vs. outside cages), time and interaction of treatment with time from Haulover (9) to Link Port (6) to St. Lucie (4). The model prompted us to look again at our data for potential predators that were sampled inside the cages.

Though numerically not abundant enough to be included in the MANOVA model, many of the decapod crustaceans sampled are known to have carnivorous habits. We realized that the relatively large sizes and the escape behavior of many of the decapods would lead to an underestimate of density with the sampling methods used in this study.

Despite these problems, greater total numbers of individuals and more species of decapods were sampled inside the cage at St. Lucie than at Haulover (Table 6). Within-cage samples from Link Port had an intermediate total number of species and specimens of decapods compared with St. Lucie and Haulover. Moreover, there were half as many specimens collected outside versus inside the cages at each site.

The percentage of decapods from the total assemblage of macrofauna at each site decreased markedly from the St. Lucie to Link Port to Haulover sites (Table 6). In addition, at St. Lucie a greater overall proportion of decapods were sampled for which carnivorous behavior has been documented, i.e. xanthid, alpheid, and portunid families (Landers, 1954; Darnell, 1958; Menzel and Hopkins, 1955; Ryan, 1956; McDermott, 1960; Hazlett, 1962; Ebling, *et al.* 1964; Muntz, *et al.* 1965).

We suggest that the cages were not effective as "exclosures" because they did not exclude important predators, the decapod crustacea. Although presumably important in regulating densities of certain prey species at all sites, decapods have a greater overall impact on the macrobenthos at St. Lucie than at Link Port and Haulover because of their higher density and diversity at that location. The south to north trend in the Indian River estuary of decreasing species richness and densities of decapods is demonstrated by other data (R. Gore, personal communication).

This interpretation provides an unexpected dividend in suggesting that decapod predation is largely responsible for "within-community regulation" (Young and Young, in press). Furthermore, the decrease in the caging effect, (i.e. the caging treatment viewed as an exclosure) from Haulover to Link Port to St. Lucie may be explained in terms of increased predation inside the cages by decapods.

These data, in addition, suggest that the cages provided a refuge for decapod crustaceans from predaceous fishes such as seatrout (*Cynoscion nebulosus*) and redfish (*Sciaenops ocellata*) commonly occurring in seagrass beds in the Indian River and known to eat preferentially decapods and other active live prey (Moody, 1950; Darnell, 1958; Tabb, 1961; Simmons and Breuer, 1962; Boothby and Avault, 1971). Kikuchi (1974) concluded that the majority of fishes in the seagrass (*Zostera marina*) habitat in Japanese waters feed primarily on motile animals, especially crustaceans. Carr and Adams (1973) came to essentially the same conclusion in a study of food habits of juvenile marine fishes in mixed seagrass (*Ruppia maritima* and *Halodule wrightii*) beds on the west coast of Florida.

The decapods as a group, therefore, appear to be important predators of other seagrass-associated macrofauna in the Indian River, and they, in turn, are fed upon by predaceous fishes. As defined by Dayton (1975), the functional importance of such a species group (i.e. "foundation species") does not necessarily have any relationship to its rank order of abundance or biomass. The cages served, in part, to separate experimentally the impact of decapod from fish predation upon the macrobenthos studied here (Fig. 2).

6. Speculations

Availability of prey, food preferences, and prey size are all significant factors in linking benthic predators to their prey (Levings, 1974). In modelling the food web of the North Sea, Steele (1974) assumed that the production of benthic infauna should be roughly doubled with the inclusion of invertebrate carnivores (e.g. the decapod *Crangon allmanni*). However, viewing predator-prey interactions primarily in terms of energy flow, as in the North Sea model, largely ignores the real differences between ecological efficiency (yield/food intake) and food-chain efficiency (yield/food abundance) (Dickie, 1970). The fish-decapod combination would be more efficient overall in utilizing the macrobenthos directly as food than fish

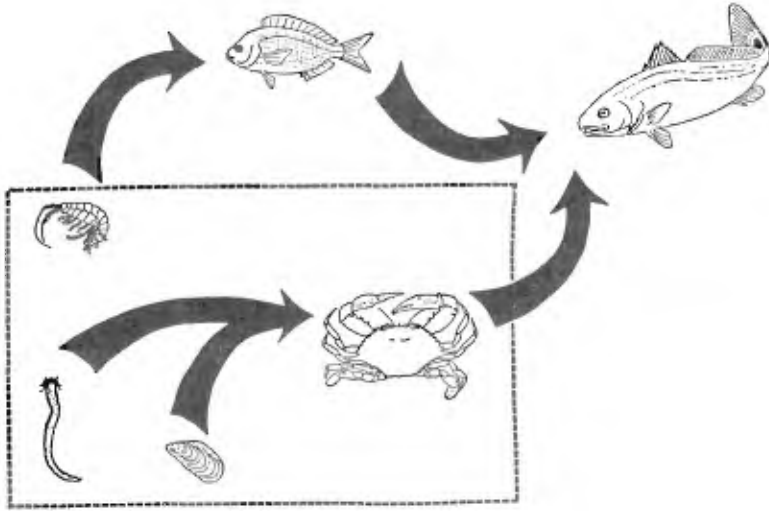


Figure 2. Simplified seagrass-associated feed web of the Indian River estuary, showing feeding relations between representative macrofauna, e.g. polychaete worms (*Laeonereis culveri*), molluscs (*Amygdalum papyrium*), decapod crustaceans (*Callinectes sapidus*), amphipod crustaceans (*Cymadusa compta*), pinfish (*Lagodon rhomboides*) and redfish (*Sciaenops ocellata*). Arrows indicate direction of energy flow and dashed line encompasses that part of the food web assumed to be directly affected by the cage.

predators alone would be. Perhaps the within-habitat increase in overall mean densities of macrofauna in "outside cage" samples from 3,994/m² at St. Lucie, to 6,644/m² at Link Port and 14,236/m² at Haulover is a reflection of the concurrent decrease in numbers of species and densities of decapod predators in the same south-north direction.

We suggest the macrobenthic species studied here are largely composed of r-strategists whose densities are strongly regulated by predation. Densities of macrofauna from the Indian River are not high in relation to densities reported from other areas (see Woodin, 1976). Although potential competitors for shared resources undoubtedly exist among the macrobenthos studied here, population sizes are largely controlled by predation, and competition for food and space is not important in regulating overall densities under natural circumstances.

Field experimentation by caging provides a dynamic view of overall predator-prey interactions. Because they are heavily preyed upon, certain species do not normally comprise a large part of the macrobenthos in terms of standing crop at any given time (e.g. density or biomass). These species, by definition, contribute a large component to the food web.

Understanding of the role of marine macrobenthos as food for higher consumers has not progressed far since the quantitative benthic ecological work of Petersen

and Blegvad over fifty years ago. Recently, Steele (1974) and Mills (1975) have stressed that knowledge of the intermediate levels of marine food webs is almost nonexistent. Such information is necessary for effective management and control of living resources from the sea. Ultimately, predator-prey relationships between individual species should be understood if marine food webs are to be comprehended with any clarity.

7. Summary

- 1) Thirty-three numerically dominant species of macrofauna were analyzed by two-way multivariate analyses of variance with interaction to compare species densities among samples taken from three different sampling sites, inside and outside cages. The MANOVA model demonstrated previously unrecognized differences in caging effects at the three sites.
- 2) At the three sites the overall time hypothesis of the MANOVA model was significant, however, the same species did not have their maximum densities simultaneously. The time when an experiment is begun may determine the effect of a particular cage.
- 3) In the case of two of the sampling sites, caging resulted in an increase in species densities inside the cages, while at the third site (St. Lucie), the densities of macrofaunal species decreased inside the cage.
- 4) Decapod crustacea sampled inside the cages were considered to be responsible for the decrease in densities of species in the St. Lucie cage. At the St. Lucie site, decapods were present in greater numbers both inside and outside the cage, compared with the other two sites.
- 5) Protecting decapod crustaceans from fish resulted in a greater impact by carnivorous decapod species upon the other macrofauna than in the uncaged situation. In the seagrass habitat, the cages served, in part, to separate the predatory role of fish from that of carnivorous decapods.
- 6) Thirty-two of the numerically dominant species selected for analysis share characteristics which group them as r-strategists. Their densities were strongly regulated by predation as well as by undetermined chance events.
- 7) Predation by decapods probably increased utilization of the seagrass-associated macrobenthos as food for fishes.

Acknowledgments. We are particularly indebted to D. Piacesi (Office of Computer Services, Smithsonian Institution) and G. Kerr (Information Systems and Data Management, Harbor Branch Science Consortium) for their help in programming and data processing. We thank B. Brown, S. Dudley, K. Krapf, M. Middleton and J. Miller for assistance in the field, processing, sorting and preliminary identifications of the macrofauna included in this study. Help in specimen identifications was provided by M. Pettibone, J. Simon and D. Dauer (polychaetes), D. Pawson (holothurians), R. Zimmerman and J. Barnard (amphipods), E. Estevez (isopods), R. Gore (decapods) and M. Rice (sipunculids). This work benefited from critical review of the

manuscript and helpful suggestions by D. Boesch, R. Gore, R. Jones and R. Virnstein. We thank H. Davis for typing the final manuscript.

This study was funded by the Harbor Branch Foundation, Inc. and by a grant from the Atlantic Foundation to the Smithsonian Institution. Contribution 61, Harbor Branch Foundation, Inc.

APPENDIX. The MANOVA Model.

Multivariate analysis of variance is the extension of the analysis of variance to a multivariate or more general case. By suitably constructing vectors for the independent variables, one-way, two-way or higher order MANOVAs can be obtained.

In matrix notation the model is written

$$\Omega : \underset{(N \times p)}{\tilde{X}} = \underset{(N \times q)}{\tilde{Z}'} \underset{(q \times p)}{\tilde{B}} + \underset{(N \times p)}{\tilde{E}}$$

where \tilde{X} is a matrix of observations on p species, \tilde{Z}' a matrix of q instrumental or "dummy" variates, \tilde{B} a matrix of "regression coefficients", and \tilde{E} a matrix of residuals. In the present analyses, \tilde{Z}' contained a vector of units, a vector to account for inside vs outside differences, 3 vectors for time differences, and 3 interaction vectors. The construction of such a two-way MANOVA with interaction model is discussed by Seal (1964), Buzas (1971) and Finn (1974).

Through matrix transposition, multiplication, inversion and subtraction, the sum of squares of the residual or the variance-covariance matrix $(N-q) \sum \tilde{\Omega}$, was estimated. To test the significance of the three hypotheses, three ω models were constructed by equating the appropriate $(q-s)$ row(s) of \tilde{B} to zero, where s is the number of rows in the ω model.

Comparison of the Ω model with each of the three ω models was made by calculating the ratio of the determinants of their respective variance-covariance matrices. This U variate is written

$$U_{p, q-s, N-q} = \frac{|(N-q) \sum \tilde{\Omega}|}{|(N-s) \sum \omega|}$$

Bartlett's approximate test (see Seal, 1964; Finn, 1974) for the significance of U ,

$$X^2_{p(q-s)} \approx [(N-q) - \frac{1}{2}(p-q+s+1)] \ln U,$$

was used to test the significance of the three hypotheses. A program written for the general case (general linear model) was used for computations and is available upon request.

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Received: 25 March, 1976; revised: 26 August, 1976.