PREDATOR CAGING EXPERIMENTS IN SOFT SEDIMENTS: CAUTION ADVISED

Robert W. Virnstein
Harbor Branch Foundation
R.R.1, Box 196
Fort Pierce, Florida

Abstract: Field experiments in which predators were excluded from soft-sediment communities have been done in the York River, Virginia, the Indian River, Florida, and the shallow continental shelf off southeast Florida. The York River experiments revealed that predators on infaunal macrobenthos are important in determining community structure and population densities. There appeared to be only two major predators in shallow water – the blue crab *Callinectes sapidus* (Crustacea: Portunidae) and the spot *Leiostomus xanthurus* (Pisces: Sciaenidae). The same experiments in the Indian River, a coastal lagoon, showed no differences in infaunal densities inside and outside exclosures. The differences between results in the two geographic areas are attributed to the greater abundance in the Indian River of small decapod predators which were not excluded by the cages. These decapod predators actually increased in abundance in exclosures. Preliminary results from experiments on the shallow sandy shelf indicate that decapods and fishes are probably important here also as predators on the macrofauna. One must not assume the only effect of caging to be predator exclusion or inclusion. Cages may alter the physical environment or attract large predators; caging studies must be carefully planned and cautiously interpreted. This paper reviews problems of caging experiments encountered in the design, field, and interpretation stages. Consideration of all these potential problems is a necessity for a successful caging experiment.

Introduction

Manipulative field experiments are valuable tools for the study of biological interactions. Past work on marine rocky intertidal areas (see reviews by Connell, 1972, 1975) has demonstrated the importance of biological interactions (i.e., competition and predation) in controlling community structure and species abundances. If predation is a controlling factor limiting prey density, then removal of predation should permit an increase in the prey density. Recently, there has been a large increase in predator caging experiments in soft sediments. (By "soft sediment" I mean as opposed to hard substrate; the term would include

ISBN 0-12-751850-9

sand as well as mud bottoms.) In this environment, however, manipulations, maintenance, observations, and sampling are much more difficult than for populations on hard substrates. Such field experiments must be interpreted cautiously, since cages frequently affect the sedimentary environment (Virnstein, 1977; McCall, 1977).

The objective of this paper is to present an overview of caging experiments in soft-sediment environments, based on my own experiences as well as others'. I suggest some possible reasons why the same or similar experiments in different habitats have yielded completely different results. Consideration of pitfalls discussed in this paper will lead perhaps to a more consistent and realistic approach to the design and interpretation of future experiments.

Methods

Predator exclusion experiments were conducted in the York River, Virginia (37° 15′N., 76° 30′W), in the Indian River, Florida (27° 32′N., 80° 21′W), and on the shallow shelf off southeast Florida (27° 33′N., 80° 03′W). The York River studies were reported in Virnstein (1977). The shallow shelf data are preliminary. In all three studies, 0.5 m by 0.5 m by 15 cm high predator exclosure cages covered with 12 mm mesh wire were set out in spring. The infauna was then sampled after 2 months or more. All samples were washed through a 0.5 mm mesh sieve, unless noted otherwise.

Sampling was either by 0.007 m^2 (York River grass bed data) (Orth, 1975; 1977), or 0.005 m^2 cores (Virnstein, 1977), or 0.0225 m^2 "post-hole" samplers (from large cages in the Indian River) (Young *et al.*, 1976; Young and Young, 1977), or with a 0.1 m^2 hand-held scoop (shallow shelf experiment). The 31.6 cm wide scoop sampler was pushed 5 cm into the sediment and pushed horizontally through the sediment 31.6 cm. The sampler was then tilted up, dumping the sample into an attached cloth bag closable by a drawstring. Table 1 summarizes the number of samples, sample sizes, and dates for each experiment.

Table 1. Sampling schedule, number, and size at each of three sampling areas.

	Date set out	*Date sampled*	*Number of replicate samples*	*Area of each sample*
York River, Va.	July 73	Sept 73	10	0.005 m^2
	May 74	July 74	10	0.005 m^2
	August 74	Oct. 74	10	0.007 m^2
	April 75	June 75	5	0.005 m^2
Indian River, Fla.	Sept. 76	Nov. 76	4	0.005 m^2
	Sept. 76	Nov. 76	4	0.0225 m^2
	April 77	June 77	4	0.005 m^2
Florida shelf	April 77	July 77	1	0.1 m^2

Results

York River, Virginia

The area studied was a su
water, in the lower York River,

Infaunal densities in exc
ure 1), especially in cages se
Densities in some cages were e
yearly mean density in 1974 of
inside cages, competitive inter

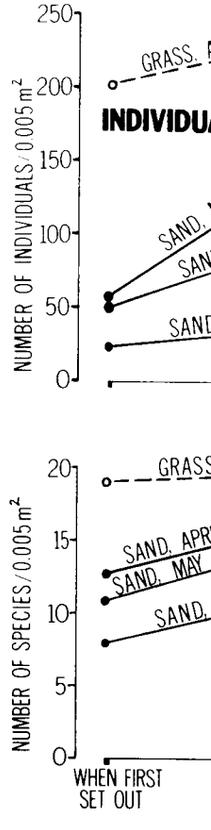


Figure 1. Mean numbers of in by 0.5 m cages in p sure cages are given Densities outside ca stant from start to ment.

nvironment, however, manipulations,
ng are much more difficult than for
ield experiments must be interpreted
ffect the sedimentary environment

sent an overview of caging experiments
my own experiences as well as others'.
ame or similar experiments in different
ent results. Consideration of pitfalls
ps to a more consistent and realistic
of future experiments.

ere conducted in the York River, Vir-
n River, Florida (27° 32'N., 80° 21'W),
orida (27° 33'N., 80° 03'W). The York
n (1977). The shallow shelf data are
n by 0.5 m by 15 cm high predator
esh wire were set out in spring. The
ns or more. All samples were washed
ted otherwise.
York River grass bed data) (Orth, 1975;
7), or 0.0225 m² "post-hole" samplers
Young *et al.*, 1976; Young and Young,
oop (shallow shelf experiment). The
d 5 cm into the sediment and pushed
cm. The sampler was then tilted up,
h bag closable by a drawstring. Table 1
le sizes, and dates for each experiment.

and size at each of three sampling areas.

te sampled	*Number of replicate samples*	*Area of each sample*
Sept 73	10	0.005 m²
July 74	10	0.005 m²
Oct. 74	10	0.007 m²
June 75	5	0.005 m²
Nov. 76	4	0.005 m²
Nov. 76	4	0.0225 m²
June 77	4	0.005 m²
July 77	1	0.1 m²

Results

York River, Virginia

The area studied was a subtidal fine sand bottom, 1.5 m deep at mean low water, in the lower York River, a sub-estuary of the temperate Chesapeake Bay.

Infaunal densities in exclosure cages increased within two months (Figure 1), especially in cages set out in spring (reported in Virnstein, 1977). Densities in some cages were extremely high (to 233,000/m²), as compared to a yearly mean density in 1974 of 11,000/m² outside cages. At these high densities inside cages, competitive interactions presumably became important, but since

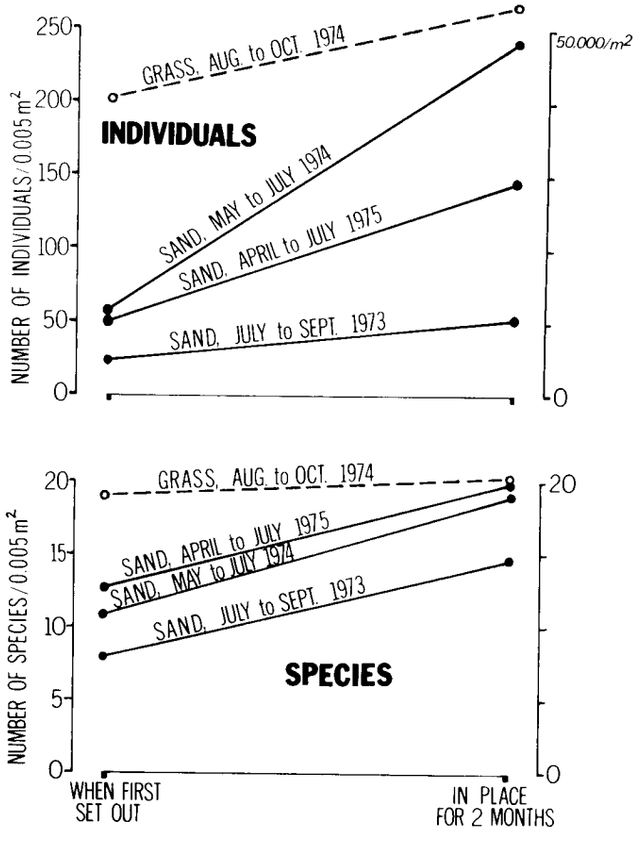


Figure 1. Mean numbers of individuals and species per 0.005 m² within 0.5 m by 0.5 m cages in place for two months. Dates of setting out exclosure cages are given in 1973, 1974, and 1975. York River, Virginia. Densities outside cages are not plotted, but remained relatively constant from start to finish during the course of each separate experiment.

no species declined in abundance inside cages, it was assumed that competition did not play a significant role in the natural community. Shown to be of major importance were two species of large motile predators, the blue crab *Callinectes sapidus* (Crustacea: Portunidae) and the spot *Leiostomus xanthurus* (Pisces: Sciaenidae).

In a nearby *Zostera marina* seagrass bed, infaunal densities were normally much higher than in adjacent bare sand patches (Orth, 1977). Infaunal densities inside cages within the seagrass bed increased significantly (Figure 1; Orth, 1977); however, this increase was smaller than that in the sand, implying that predation on infauna is less important in seagrass beds than in bare sand. Predation pressure on epifauna of seagrass beds is probably greater than on infauna.

Infaunal densities and species richness inside cages on sands with initially low infaunal density increased to levels similar to those found in nearby seagrass beds.

Indian River, Florida

The Indian River is a bar-built subtropical coastal lagoon on the southeast Florida coast. Except for the Intracoastal Waterway, the Indian River is shallow (mean depth < 1.5 m) with extensive seagrass beds. Salinity is near marine except during the summer-fall rainy season when salinities may drop to 17‰. This study and previous work (Young and Young, 1977; Young *et al.*, 1976) were done in pure stands of the seagrass *Halodule (=Diplanthera) wrightii*.

This earlier work had found no differences in density inside and outside cages, but small decapod crustaceans were suggested as important predators on the infauna.

The experiment using the large 2 m x 2 m cages was duplicated in bare sand as well as in the seagrass bed, and no differences were found inside and outside cages (Figure 2), nor were any differences found using the smaller 0.5 m x 0.5 m cages in the sand (Figure 3).

To test the hypothesis that small decapod crustacean predators found refuge and increased in density inside cages, cages were initially set up in both sand and grass and the entire 2 m x 2 m area sampled for decapods by dip-netting, digging out grasses and sediments to a depth of 15 cm, and dip-netting again until no further organisms were obtained. These entire cage contents were sieved through 12 mm mesh. Then after two months the experimental cages were dug up and sampled in the same manner. The number of decapod crustaceans increased by at least a factor of 3 inside cages (Figure 4). Approximately half of these decapods were blue crabs, *Callinectes sapidus,* shown to be an important predator on infauna in Chesapeake Bay (Virnstein, 1977; Woodin, 1978). These cages were obviously not effective in keeping out major predators.

In essentially the same experiment repeated in the spring, the smaller cages were used in both seagrass and sand. In this more carefully controlled experiment, predators were searched for and removed from the cages. However,

because of the refuge provided b
predators in the cage in the seagra

At the start of the experimen
2 x that in the bare sand. After tw
the cage in bare sand was 2 x that i
disparity was apparently still due t
removed from the cage in sand t
decapods in any of the samples fro
the seagrass cage contained at lea

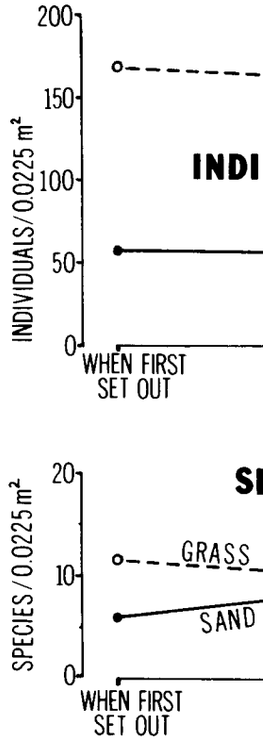


Figure 2. Mean numbers of indi
by 2 m cages set out i
Indian River, Florida.

assumed that competition
munity. Shown to be of
predators, the blue crab
pot *Leiostomus xanthurus*

unal densities were nor-
patches (Orth, 1977).
ed increased significantly
aller than that in the sand,
in seagrass beds than in
beds is probably greater

de cages on sands with
ar to those found in near-

al lagoon on the southeast
ne Indian River is shallow
. Salinity is near marine
nities may drop to 17‰.
977; Young *et al.*, 1976)
Diplanthera) wrightii.
lensity inside and outside
as important predators on

es was duplicated in bare
es were found inside and
found using the smaller

ustacean predators found
ere initially set up in both
led for decapods by dip-
of 15 cm, and dip-netting
entire cage contents were
e experimental cages were
r of decapod crustaceans
4). Approximately half of
shown to be an important
77; Woodin, 1978). These
jor predators.
n the spring, the smaller
more carefully controlled
from the cages. However,

because of the refuge provided by the seagrasses, it was difficult to find the predators in the cage in the seagrass bed.

At the start of the experiment, the infaunal density in the seagrass bed was 2 x that in the bare sand. After two months, the reverse was true: the density in the cage in bare sand was 2 x that in the cage in the seagrass bed (Figure 5). This disparity was apparently still due to the decapods, which were more effectively removed from the cage in sand than from the cage in grass. There were no decapods in any of the samples from the sand cage, whereas every sample from the seagrass cage contained at least two species of decapods.

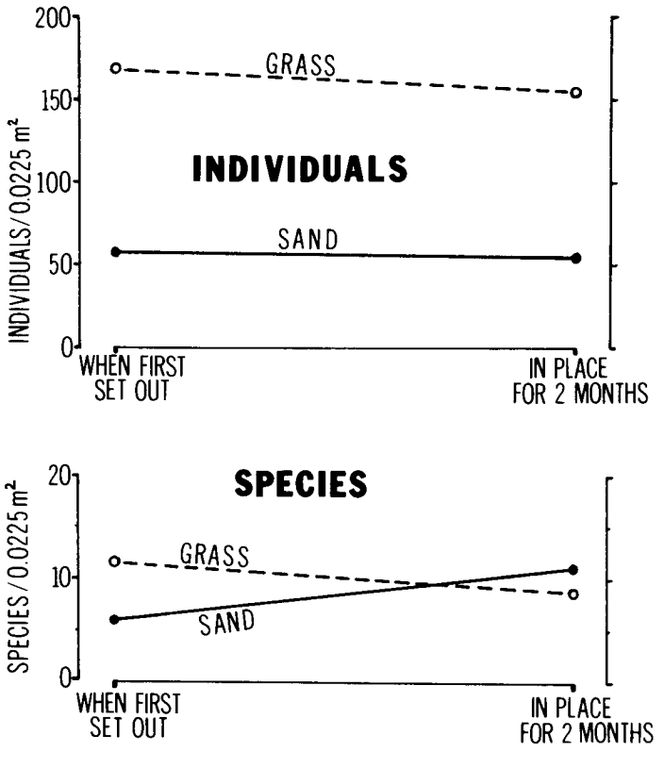


Figure 2. Mean numbers of individuals and species per 0.0225 m^2 within 2 m by 2 m cages set out in September and sampled in November 1976. Indian River, Florida.

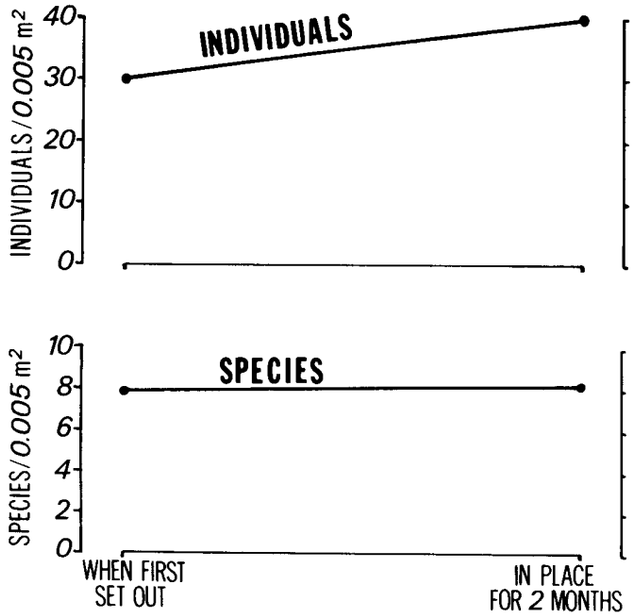


Figure 3. Mean numbers of individuals and species per 0.005 m^2 within 0.5 m by 0.5 m cages set out in September and sampled in November 1976. Sand bottom in the Indian River, Florida.

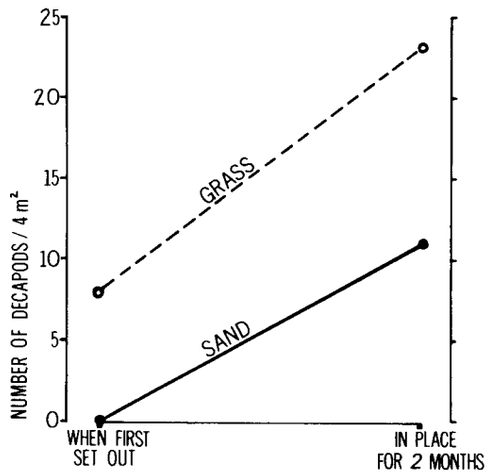


Figure 4. Number of decapod crustaceans within 2 m by 2 m cages initially (September) and after two months (November 1976). Indian River, Florida.

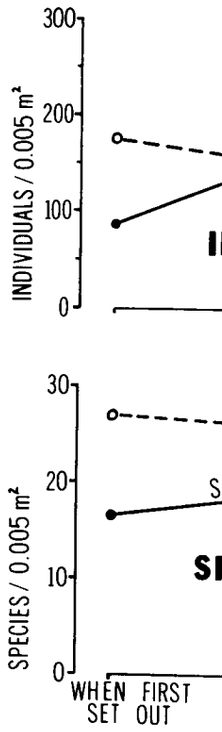
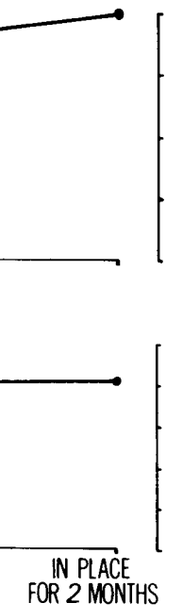


Figure 5. Mean numbers o by 0.5 m cages River, Florida.

Shallow continental she

The study area was a sa Pierce, Florida. Data are pre problems encountered.

After two and a half increase (Figure 6). Because edge of the mesh could not be easily burrow under the edge in place 20 weeks, I was able Foundation's submersibles, t serving as miniature artificial fishes, crabs, and starfish. W 35 fish. Each cage had at le picked up with the submersib two minutes two fish manage edges. The cages were obvio



es per 0.005 m² within 0.5 m
l sampled in November 1976.
da.

2 m by 2 m cages initially
vember 1976). Indian River,

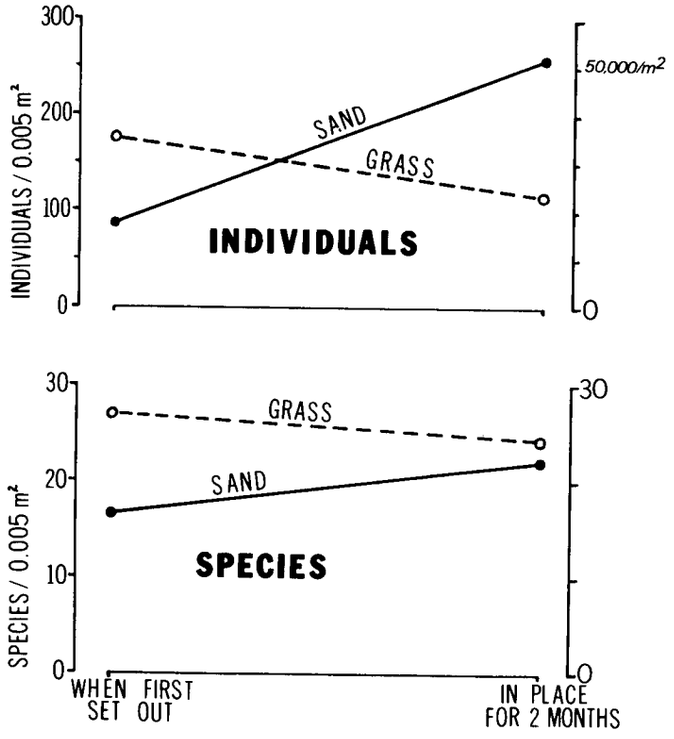


Figure 5. Mean numbers of individuals and species per 0.005 m² within 0.5 m by 0.5 m cages set out in April and sampled in June 1977. Indian River, Florida.

Shallow continental shelf

The study area was a sandy plain in 33 m of water 25 km offshore from Fort Pierce, Florida. Data are preliminary and are presented merely to illustrate the problems encountered.

After two and a half months, infaunal density inside the cage did not increase (Figure 6). Because cages were lowered from a surface ship, the bottom edge of the mesh could not be pushed into the sediment; therefore, animals could easily burrow under the edge of the cage and thus get into it. After cages had been in place 20 weeks, I was able to observe these cages from one of Harbor Branch Foundation's submersibles, the *Johnson-Sea-Link I*. The cages were obviously serving as miniature artificial reefs, providing structure and, I assume, refuge for fishes, crabs, and starfish. Within 2 m of each of the four cages, I counted 20 to 35 fish. Each cage had at least two fish inside it. After one of the cages was picked up with the submersible's manipulator arm and moved 1 m away, within two minutes two fish managed to get back inside the cage by wriggling under the edges. The cages were obviously not effective predator exclosures.

Figure 6. Number of individuals per 0.1 m^2 within 0.5 by 0.5 m cages set out in April and sampled in July 1977. In 33 m off the southeast Florida coast.

Problems Encountered

Besides the problem mentioned in the above paragraph, there are many other problems in field caging experiments. Many of these problems are related to the presence of a physical structure that has effects other than keeping out predators.

The unnatural presence of a physical structure can alter the physical nature and hydrodynamics of the caged area. Depending on currents, sediment load, and cage shape and orientation, cages can induce either scouring or increased sedimentation. Scouring around cages has been observed in Monterey Bay, California (L. Hulberg, pers. commun.) and on the shallow (33 m) shelf off southeast Florida (personal observation). D. Cunningham (pers. commun. from P. McCall) found increased densities of infauna near cage walls, both inside and outside of cages on an intertidal mud flat in Long Island Sound.

Cages may slow down currents within the cage, allowing suspended sediments to settle out. This increase in sedimentation may be small (Virnstein, 1977), or in waters with a high sediment load may be sufficiently large that the entire cage is filled with sediment (Naqvi, 1968; McCall, 1977; R. J. Diaz, pers. commun.). Large cages (3 m on a side) as used by A. F. Holland and N. Mountford (pers. commun.) may have avoided this problem, but presented other problems associated with handling such a large structure in the field. I am not convinced that larger cages have smaller physical effects, although a large cage would have a smaller ratio of cage surface area to area enclosed.

Planktonic larvae encountering a cage may be induced to set within the cage ("larval entrapment") due to: 1) a decrease in current velocity; 2) a

different sediment composition within the cage; or 3) contact with the cage surface. However, this effect may not be real and may instead be due to the increased survival of settling larvae inside the cage due to lack of predation. The 3 mm mesh cages used by Woodin (1974) selectively kept larvae of tube-building polychaetes from setting inside the cage because the larvae set and built tubes on the mesh of the cage.

The build-up of fouling organisms on cages can be expected to increase physical effects of the cage: change in currents and sedimentation, shading, and attraction of larger animals to feed on these fouling organisms. During summer in the York River, Virginia, cages needed scrubbing weekly. Instead of scrubbing, regular changes of the mesh on cages would be more satisfactory for the following reasons: 1) to temporarily remove fouling organisms; 2) to slow down fouling by providing new unconditioned surfaces; 3) to remove corroding surfaces; and 4) to avoid increasing the organic input into the cage (i.e., fouling organisms removed from the cage by scrubbing probably settle onto the sediment surface inside the cage). Reise (1977b) avoided fouling problems by adding several *Littorina littorea* to each cage; the snails grazed preferentially on the mesh.

Just as a natural reef provides structure and habitat for many animals, the presence of a cage in a generally structureless soft-sediment environment similarly attracts larger motile animals (also noticed by P. McCall, pers. commun.). The problem with the cages offshore was mentioned above. Arntz (1977) had a similar problem with cages on a mud bottom in the Baltic Sea. Starfish, crabs, and gobies were much more abundant inside his cages than outside. In a *Zostera marina* seagrass bed in the Chesapeake Bay, Orth (1975) had severe problems with oyster toadfish *(Opsanus tau)* digging next to cages, stakes, or any physical structure he set out. In the York and Indian Rivers, I have found that blue crabs are exceedingly difficult to keep out of cages, even when the bottom edge of the cage is pushed 5 cm into the sediment. S. A. Woodin (pers. commun.) has had this same problem with juveniles. When blue crabs molt, they are themselves temporarily very susceptible to predators and must seek cover at this stage. Small crabs may enter through the mesh, but after molting once, they may be too large to leave. The solution to complete exclusion of predators would seem to be the use of smaller mesh size, but: 1) there would be more problems of fouling and current effects; and 2) predators could still enter as juveniles or larvae and subsequently be protected from *their* predators during this critical phase, thus resulting in increased densities of predators inside cages. The existence of seasonal breeding migrations of predators and the use of appropriate seasonal timing may avoid this latter problem.

If seagrasses, marsh grasses, and drift algae are present, they may be trapped against the sides of cages, inhibiting current flow to the extent that Arntz (1977) found anaerobic conditions inside some of his cages. A fence surrounding the caged areas was proposed as a solution to the accumulation of drifting algae. I doubt that there is any caging study without problems; it is hoped that sufficient prior knowledge and careful planning will avoid many of these hazards.

Experimental Design Considerations

In designing a field caging experiment, there are several factors and choices that must be considered concerning predators, sampling schemes, type environment, and the cage itself. Some environments and communities are more amenable to caging experiments than others. Prior knowledge of the habitat and community is a prerequisite for anticipating field problems and limitations and for formulating testable hypotheses regarding potential predators and prey.

The cage itself should be designed to produce a minimum of disturbance effects other than the exclosure of predators. For example, if the predator size is known, then the mesh size should be just small enough to exclude this predator. Besides mesh size, the overall size, shape, and location of the cage need to be considered. To decrease edge effects and cage effects, bigger may be better, but the effect of cage size has never been tested. Larger cages could be sampled repetitively, but sampling disturbance would be too great in a cage less than several times the sample size. If cages are to be sampled over a time period, either repetitive samples can be taken from large cages, or enough smaller cages can be set out at the start of the experiment so that some cages are sampled after the first time interval, others sampled successively.

Replication of treatments is superior to replicate samples from only one replicate of the treatments. It has been my experience that variation between replicates is greater than the variation of samples within a replicate. This large between-treatment variability is likely due to the vagaries of initial colonization, and whether or not a small predator managed to get into the cage.

A "control" cage must be considered and attempted, although it is difficult to conceive of a cage that has all the physical effect of a cage but does not keep out predators. This control is essential to separate the effect of the cage from the effect of the predator. Topless, sideless, and two-sided cages have been used, but one must know their effects on animals and physical parameters to interpret them correctly.

The season during which a cage is in place can play a large role in determining the results (Virnstein, 1977). Many species spawn and recruit at certain times of the year only. If a cage is set out during this period, the larvae of these species are protected upon settlement and could successfully recruit within the cage at this time of the year but not at another time. Seasonal migration or activity patterns of major predators are common in estuaries. In Chesapeake Bay during the winter, when blue crabs and spot were absent from the system, cages produced no change in infaunal densities; during spring and summer, densities became much greater inside the cages (A. F. Holland and N. Mountford, pers. commun. of unpublished data).

If predators are to be enclosed inside cages, then the number of individuals, species, size, and possibly sex of the predator must be chosen. Some prior knowledge of the predator's normal range, behavior, and seasonal activity must enter into this choice. The behavior of a very active or swimming predator is probably altered by enclosure within a cage. A larger cage probably allows more

normal behavior. The density of preda
the number of predators within a cage
more than one species might be co
complex natural situation. Especially
important without there being one or
such a situation where many species o
caging any one species of predator in
the sum of all predators has a major e

A more restricted use of cages co
with a patch of potential prey to obse
prey, and to estimate feeding rates.

In all cases where cages are us
effects should be made to compare insi
tion, seston flux, current velocity, an

I recommend that extra cages b
allow for inevitable losses due to vand
and line or a vessel's anchor, and the oc
to get inside a cage.

As an alternative to caging, prec
e.g., chemical or scent barriers, or by p
are slow-moving (e.g., gastropods and
be preferable to caging because the
predators without any cage structure
method than field caging would be t
animals into aquarium systems, and the
others. This method allows the use of
artificial environmental constancy. It is
tal results also apply under natural fiel

Interpretation Considerations

The same caging experiment ca
effect in widely different situations. Th
Manipulating predator density can proc
abundance, e.g., there could result cl
abundance, size-class distribution, grow
ture and function. For example, if r
selective on the dominant species, remo
exclusion of non-dominant species (Pai
be expected to result in an increase
limiting. At increased population densi
limiting, causing the observed subseque
deposit-feeding species (Virnstein, 197
W. Young, pers. commun.). Such high