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Performance of cages as large animal-exclusion devices in the deep sea

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ABSTRACT

Sedimentary, deep-sea communities include megafaunal animals (e.g., sea cucumbers, brittle stars, crabs) and demersal fishes, collectively termed the large, motile epifauna (LME). Individuals of the LME are common, and their biomass approximates that of the macrofauna. Based on analogies with shallow-water animals, they are likely to be sources of mortality for the infauna and to create spatial and temporal heterogeneity in the community. Given present theories of deep-sea community organization, such effects could be important. Unfortunately, this hypothesis has not been tested because of the difficulty of conducting experiments in the deep sea and because tools for manipulating the LME have not been developed. We studied the suitability of exclusion cages for this purpose at 780 m depth in San Diego Trough. We placed 16 cages of two mesh sizes for 4.5 months over regions of the seafloor that appeared free of LME. Time-lapse photographs of a cage and a control plot coupled with observations of all cages at the end of the experiment indicated that small (1.27-cm × 1.27-cm square)-mesh cages were effective at excluding LME. Further, the cages were essentially free of cage artifacts that have been reported in shallow-water studies. Large, mobile and disruptive animals (e.g., fishes, crabs) did not establish long-term residence adjacent to or on the cages. Bio-fouling slightly reduced the open surface area of the cage mesh, potentially reducing flow through the cage, but the composition of surface sediments in terms of organic C and N, phytoplankton-derived pigments, and grain size was indistinguishable between cages and control areas. Activities of excess ^{234}Th were significantly higher (average = 37%) inside of small-mesh cages, which might suggest enhanced particulate deposition inside cages. However, this measurement was an artifact of experimental manipulation. Particles that accumulated on the cage during the experiment were dislodged and settled to the seafloor when the cage was opened just prior to sampling. These particles would have been highly enriched in ^{234}Th, and their inclusion in core samples artificially inflated the calculated sediment accumulation rates inside cages. Therefore, the cages performed well; they excluded the targeted LME without causing artifacts and thus should be useful for experimental study of a group of animals that may have substantial impact on the structure and organization of deep-sea communities.

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1. Introduction

Large, motile animals often play an important role in soft-bottom communities. For example, when rays dig feeding pits, they displace the resident fauna, create a disturbed patch, cause drifting food to become concentrated in the feeding depression, and initiate a succession (VanBlaricom, 1982). The rays, thus, create ecologically important heterogeneity in space and time that has profound effects on the community. While not all large animals have such dramatic impacts, their actions as predators, disturbers, and creators of physical heterogeneity in the habitat are often of considerable consequence (e.g., Woodin, 1978, 1981; Reidenauer and Thistle, 1981; Oliver *et al.,* 1985).

In the deep sea, an equivalent role may be played by the epibenthic megafauna (e.g., sea cucumbers, snails, brittle stars) and bottom-feeding fishes (Bright, 1970; Sedburry and Musick, 1978; Mahaut *et al.,* 1990). Several lines of evidence suggest that these large, motile epifauna (LME) could be important in the organization of deep-sea communities. Photographs show that LME can be common (LaFond, 1967). Haedrich and Rowe (1977) report that the biomass of LME can be comparable to that of the macroinfauna. Smith (1983) has shown that the metabolic activity of the LME can equal that of the infauna and the sedimentary microbes combined. In terms of theory, the LME could generate the patches central to the patch-dynamic theories of deep-sea community organization (Grassle and Sanders, 1973; Grassle, 1989; Snelgrove *et al.,* 1992; Rice and Lambshead, 1994). The LME could be an important source of the mortality required by Dayton and Hessler's (1972) cropping theory (see also Rex, 1976, 1983). In sum, the LME are likely to be major players in the organization of deep-sea communities, but their effects are essentially unknown because they have not been studied experimentally in the deep sea.

To do so, the abundances of the LME must be manipulated so the responses of the local community can be used to infer their role (Paine, 1980; Hall *et al.,* 1990). In the deep sea, such an experiment must involve simple tasks because of the modest dexterity of remotely operated vehicles and research submersibles. Exclusion experiments with cages are ideal from that perspective, but artifacts can trouble caging experiments. Therefore, we conducted a study to determine if cages could be used to exclude LME in the deep sea without inducing the artifacts that have compromised the use of cages in many shallow-water experiments (Virnstein, 1978; Peterson, 1979; Dayton and Oliver, 1980; Hulberg and Oliver, 1980; Reise, 1985; Kennelly, 1991; Peterson and Black, 1994). In particular, we examined: (1) the alteration of flow through cages by the cage mesh (especially after fouling) and the potential change in deposition rates of particles used as food, (2) the attractiveness of cages to motile animals (e.g., fishes, crabs) that could take up semi-permanent residence adjacent to or on cages and could alter conditions in the cages (e.g., by dropping things inside), (3) the infestation of cages by small, motile predators that could enter the cage and accumulate because they are protected from their predators (Young *et al.,* 1976; Arntz, 1977), and (4) the unintentional entrapment of fauna targeted for exclusion (e.g., subsurface burrowing megafauna).
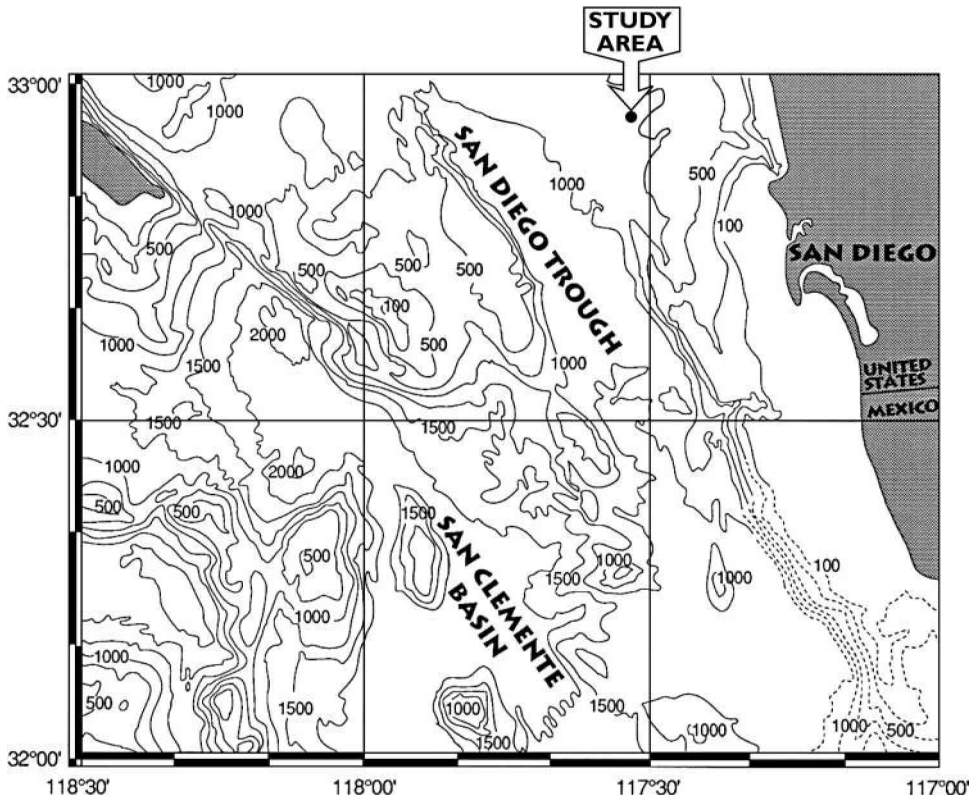
Figure 1. Chart of San Diego Trough showing study site (●).

2. Study site

The study site was in San Diego Trough (=SDT) at 32° 57.3′N: 117° 32.2′W at a depth of 780 m about 25 km off the coast of southern California (Fig. 1). The sediment was a pelletized, hemipelagic green mud. Surface features included burrow openings made by hagfish (*Eptatretus deani*) and various invertebrates, large arborescent foraminiferans, tracks, and mounds. Between 2 April and 26 August 1998, bottom-water temperature averaged 4.8°C. The average current speed measured 10 m above bottom was 4.8 cm s^{-1}, with a maximum recorded speed of 17.7 cm s^{-1}. The most conspicuous LME at this site are listed in Table 1.

3. Methods

a. Cage description

Cages (Fig. 2) were 75 cm × 75 cm × 50 cm (length: width: height) in outside dimension. A frame of 1.9-cm × 1.9-cm stainless steel angle bar was covered by square-mesh stainless steel wire (1.20 mm diameter). The sides of six cages had mesh

Table 1. Large, motile epifauna common at the study site in San Diego Trough.

| Common descriptor	Taxonomic descriptor	Feeding mode
Invertebrate:		
Anemone	?	suspension feeder
Gastropod	*Bathybembix bairdii*	deposit feeder
Gastropod	cf. *Phymorhynchus*	carnivore
Ophiuroid	*Ophiomusium lymani*	deposit feeder
Ophiuroid	*Ophiolepididae* sp.	deposit feeder/omnivore
Holothurians	*Synallactes, Pannychia*	surface deposit feeder
Asteroid	*Solaster borealis*	opportunistic feeder
Decapod (stone crab)	Lithodidae	carnivore/scavenger
Vertebrate:		
Rockfish	*Sebastolobus* spp.	carnivore
Sablefish	*Anoplopoma fimbria*	carnivore
Hagfish	*Eptatretus deani*	scavenger
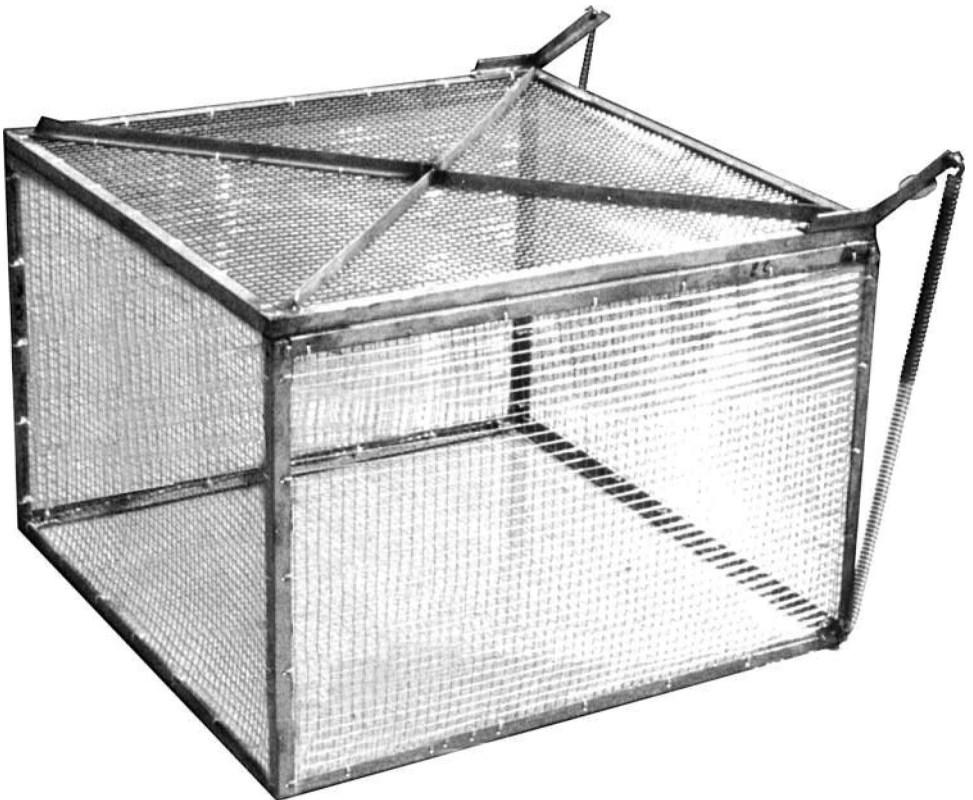
Figure 2. A cage showing its construction of wire cloth on a 75-cm × 75-cm × 50-cm frame. This image is of the small-mesh version.

measuring 24.5 mm from the centers of adjacent parallel wires (=large-mesh cages, surface area 90.4% open); the sides of ten cages had 12.7 mm center-to-center distances (=small-mesh cages, surface area 82% open). The lids of all cages were made of small mesh. Cage lids were spring loaded and would open without aid when the submersible pilot released a catch.

b. Deployment of cages and time-lapse cameras

Between 2 and 3 April 1998, we used DSRV *ALVIN* to establish paired cage and control plots (forming a block) at 16 haphazardly chosen locations within a 600 m × 400 m area. Control plots were unmanipulated regions of seafloor located near a cage (see below). The minimum distance between blocks was 34 m. The cages were pushed at least 9.2 cm into the sediment but no more than 19.3 cm (distances measured by the amount of mesh visible in video records of the cage). We knew from previous work in SDT that the narrow depression along the cage perimeter caused by inserting the cage into the seabed would disappear in a matter of days by gravitational slumping of the loosely consolidated sediment.

We deployed two time-lapse-camera systems at our site. Each consisted of a Benthos 372A camera and a Benthos 382 flash (adapted for long duration). The camera and flash were mounted on a stainless steel quadrapod and pointed 35° below horizontal. This angle was chosen so that a cage 2 m from the quadrapod would be in focus, completely visible and would occupy ≈1/3 of the horizontal span of the photo. Each quadrapod was fitted with a releasable 36-kg weight and sufficient syntactic foam so that the ensemble was 23 kg heavy in water and thus could be positioned by the submersible. The cameras fell freely from the sea surface to the seafloor and were then repositioned by *ALVIN*. One camera was placed with a small-mesh cage in its field of view. To ensure correct positioning, a 2-m-long aiming rod that extended from the camera frame was centered on one face of the cage. The rod was removed after 24 h. The second camera was placed 23.5 m away such that it looked at an unremarkable (control) portion of the seabed. The cameras took one photograph every 8 h with ASA 200 Ektachrome film. At the end of the field study, *ALVIN* attached a float to each quadrapod and released its 36-kg weight, allowing the quadrapod to float to the surface for recovery. The film was processed and duplicated for analysis.

c. Sampling of cage and control plots

Between 20 and 26 August 1998, we returned to the site, recovered the time-lapse cameras, and sampled the cage and control plots. Cages were therefore deployed from 140–146 d, and for convenience we refer to this aspect of the experiment as having lasted 4.5 months. All photographs from each camera did not contain clear images for the entire 4.5 months of deployment, and paired comparisons of cage and control photographs, therefore, did not cover the entire 4.5 months. For each comparison discussed, the exact duration of each useful camera record is noted below.

ALVIN approached each cage or control plot from down current. On approaching a cage,

ALVIN stopped about 1.5 m from it and videotaped a portion of the cage mesh with a high-resolution (zoom) camera. It then moved nearer and made a video recording of the sediment surface around the cage's exterior margin. The cage lid was then opened by using the submersible's arm to release a catch. The resulting agitation of the cage frame and walls and swing of the cage lid mobilized particles that had deposited onto the structure during the 4.5 months of deployment. These particles fell to the seafloor, including the sediment surface within the cage. The sediment surface inside the cage was videotaped with the high-resolution, zoom, video camera mounted on *ALVIN*'s arm. A 6.7-cm diameter tube corer (with custom-designed head to minimize the pressure wave preceding the corer) was used to collect a core that was used for analysis of sediment grain size, phytoplankton-derived pigments, organic C, and organic N. One to three Ekman cores were also taken within each cage. All cores were inserted into the sediment before any were removed. Our Ekman corer contained four 58-cm^2 subcores. One subcore from a single Ekman core was used for ^{234}Th measurements. The remaining subcores were used to search for buried megafauna to 10 cm depth.

The control plot was examined and sampled in a comparable manner. Control plots were unmanipulated regions of seafloor located an average of 16.2 m from a cage (range of 5.0–34.4 m). The orientation of the control plots relative to its paired cage was chosen haphazardly with the constraint being that the first of each paired cage-control plot sampled was down-current of the second.

d. Analysis of time-lapse photographs and video

To investigate the efficacy of cages in excluding LME, we used the time-lapse images from the control series to estimate the number of times animals visited an area the size of a cage. To do so, we projected images from the control series onto a chalk board on which we had marked an area equal to that a cage would have occupied in the image. We counted all LME that were photographed with any portion of their body in the cage-sized area as LME that would have been excluded by the cage, reasoning that if a cage had been present, these visitors would have been diverted by its walls. We examined a 137-d record (411 images).

The time-lapse photographs were also used to determine if the cages were used as habitats by animals, as has been noted in shallow-water caging experiments. From the time series of photos of the cage, we counted all individuals that were on the cage (=on) or within one body width (=near) as potential residents and noted the duration of their presence. From the time series of control photos, we counted as "near" all individuals that were within one body width of the perimeter of an area of seafloor equivalent in size to that a cage would occupy and that would have been visible if the cage had been present. To make the comparison fair, we omitted animals that had entered the zone around the cage from "inside" because there is no equivalent possibility for cages. For the controls, "on" visitors were individuals of groups that had been seen on the cages and that were >50% inside the imaginary cage. We examined 342 photographs from each time series.

Video images of cage mesh were analyzed to assess the degree to which fouling caused a

reduction in mesh openings, as an indicator of the potential of fouling to reduce flow through and alter particulate deposition within cages. (We also have direct measurements that bear on these potential effects of cages, see below.) A print was made of a close-up video image (containing $\approx$16 mesh squares) of cage wall from 15 of 16 cages (one cage was heavily disturbed by *ALVIN* during approach and was not sampled). Ten randomly chosen coordinates were selected within each image. For five of these coordinates, measurements were made of: (1) the wire diameter nearest the coordinate, (2) the distance between centers of adjacent horizontal wires nearest the coordinate (i.e., the wire spacing), and (3) the maximum opening (i.e., open distance between wire edges fouled by hydroid colonies or attached bio-films) along the same line segment measured by (2). We used the other five coordinates to make identical measurements between adjacent vertical wires. From these measurements, we calculated percent open space of unfouled and fouled mesh and the reduction in open space caused by fouling. The effects of mesh size (large vs. small) and wire orientation (horizontal vs. vertical) on percent reduction of mesh opening by fouling was analyzed by 3-factor, mixed model, partially hierarchical ANOVA (Winer, 1971), where "orientation" and "mesh size" were fixed, crossed factors, and "replicate cage" was considered a random factor nested within mesh size.

e. Analysis of excess ^{234}Th activity

One subcore from one Ekman core taken within each control plot and cage was used to determine inventories of excess ^{234}Th. This isotope of thorium, which has a 24.1 d half-life, is scavenged rapidly onto particles upon production from its parent ^{238}U, which is soluble in seawater. Sediment "excess" ^{234}Th activity (unsupported by ^{238}U within the sediment) reflects short-term rates of particulate deposition (e.g., Bruland *et al.,* 1981; Smith *et al.,* 1993; Murray *et al.,* 1996; Shaw *et al.,* 1998).

The upper 5 cm of each subcore was extruded and dried on board ship and then shipped back to the laboratory immediately upon arrival at the pier. Preliminary measurements in our laboratory on a core from the San Diego Trough, and previous work by Smith *et al.* (1993) on Santa Catalina Basin sediments, indicated that 90–100% of the ^{234}Th inventory was contained in the upper 3 cm, so the 5-cm interval we chose to analyze should have included nearly the entire sediment inventory of this isotope. A syringe subcore was collected from each sample for determination of bulk density by evaluation of water content and grain densities (measured via a pycnometer). Bulk densities, as well as ^{234}Th activities, were corrected for salt.

Sediment samples were thoroughly homogenized and packed into plastic containers for measurement of excess ^{234}Th activities with an intrinsic germanium detector. An initial measurement of the 63.2 keV photopeak was made as soon as possible upon delivery of the sediments to the laboratory and a second measurement was made about 100 d later to assess the ^{238}U-supported ^{234}Th. The detector was calibrated with a natural-matrix sediment standard (IAEA-300) packed in the same type of container as these samples. Sample-dependent differences in self-absorption of the low-energy γ-ray were corrected for by use

of a direct-transmission measurement from an external source that contains ^{238}U-^{234}Th (Cutshall *et al.,* 1983; Burnett *et al.,* 1993).

f. Analysis of carbon, nitrogen, and phytoplankton-pigment concentrations

In the ship's laboratory, the top 2 mm of sediment in each tube core was excavated and subdivided randomly into quarters. One quarter was archived and a second quarter was evenly subdivided into two combusted glass vials, which were then frozen and stored at $-70°C$. One of these subsamples was subsequently freeze-dried for 24 h and analyzed in duplicate for total (organic plus carbonate) C, organic C, and organic N content on a Fisons Model NA-1500 Series 2 elemental analyzer, using a modification of the Verardo *et al.* (1990) method. The other subsample was analyzed fluorometrically for chlorophyll *a* and pheopigment concentrations according to Parsons *et al.* (1984). Differences between cage and control plots in organic C and N, chlorophyll *a,* and pheopigments were evaluated separately for each cage mesh size with paired *t*-tests (Sokal and Rohlf, 1981).

g. Analysis of sediment grain size

The remaining two quarters of the 0–2 mm layer from the tube core were used to measure sediment grain size. Samples were preserved in a solution of 3.5% saline and buffered formalin such that the final formaldehyde concentration was 4%. In the laboratory, each sample was separated into two fractions with a 62-µm sieve. The >62-µm fraction was wet sieved at half-ϕ intervals from 1–4ϕ ($\phi = -\log_2 D$, where *D* is the grain diameter in mm). The sieve fractions were concentrated onto pre-weighed Whatman GF/D filters. The <62-µm fraction was filtered on a pre-weighed "sandwich" consisting of a Whatman GF/D filter and a 0.1-µm membrane filter. Each filter (or sandwich) was dried for >12 hrs at 60°C and cooled in a desiccator before weighing.

4. Results

a. Exclusion of LME and their responses to cages

Table 2 lists the LME noted within a cage-sized area in the control time-series photographs. These results show that a cage-sized area in this region of San Diego Trough was exposed to the influences of several common members of the LME. Rockfish, holothurians, and hagfish would have been excluded by cages on many occasions over a 4.5-month period, and other LME would have been interdicted as well, though less frequently.

A *Sebastolobus* was found inside one of the five large-mesh cages upon return after 4.5 months of deployment. There were no obvious indications of entry via burrowing beneath the perimeter of the cage (i.e., the sediment around the cage margin appeared undisturbed). Close-up video revealed that the fish was narrow enough in cross section to pass through the mesh of this large-mesh cage. We conclude that the large-mesh cage will allow passage of small rockfish, a species we wished to exclude.

Table 2. LME excluded by cages. LME that visited an area of seafloor equivalent in size to that enclosed by a cage, thus animals that would have been excluded by a cage. Data are from time-lapse photographs (8-h interval; 137-d record).

Common descriptor	Taxonomic descriptor	Number of visits	Feeding type
Holothurians	*Synallactes, Pannychia*	16	surface deposit feeder
Rockfish	*Sebastolobus* spp.	14	carnivore
Hagfish	*Eptatretus deani*	6	scavenger
Brittle star	*Ophiolepididae* sp.	3	deposit feeder/omnivore
Gastropod	*Bathybembix bairdii*	2	deposit feeder
Gastropod	cf. *Phymorhynchus*	1	carnivore
Burrowing Anemone	?	1	suspension feeder

One *Bathybembix* was noted inside one of the nine small-mesh cages. This animal was too large to have passed through the mesh, yet, as with the rockfish in the large-mesh cage, there were no obvious indications of entry via burrowing beneath the perimeter of the cage. We conclude that the gastropod was not seen by the pilot when the cage was placed on the seafloor and could not escape during the 4.5-month study.

Table 3 lists animals that were photographed perching on or adjacent to the cage and the duration of their presence. Three types of visitors (rockfish, hagfish, and holothurians) were photographed near the cage about as frequently as near the control, although a rockfish remained adjacent to the cage for 40 h on one occasion. Five taxa used the cage in

Table 3. Analysis of LME perching on or abutting cages. Comparison of visitors between a cage and a control plot in a 114-d series of time-lapse photographs (8-h interval between photographs). For cages, we distinguished visitors that were on the seabed within one body width of the perimeter of the cage ("near") from those that were on the cage. For controls, "near" visitors were within one body width of the perimeter of an area of seafloor equivalent in size to the cage and that would have been visible if the cage had been present. For controls, "on" visitors were individuals of groups that had been seen on the cages and were >50% inside the imaginary cage. Entries indicate the duration of each visit (number of consecutive photographs).

Common descriptor	Taxonomic descriptor	Control	Cage
A. Near			
Rockfish	*Sebastolobus* spp.	1, 1, 1, 1	1, 5, 1, 1, 1, 1
Holothurian	*Synallacties, Pannychia*	1, 1, 1, 1, 1	2
Hagfish	*Eptatretus deani*	—	1
Snail	*Bathybembix bairdii*	1	1
Starfish	*Solaster borealis*	2, 1	6
B. On			
Stone crab	Lithodidae	—	3, 3, 1, 2, 1, 1
Brittle star	Ophiolepididae	7	1
Starfish	*Solaster borealis*	—	45
Starfish	5-armed	—	27
Anemone	?	—	66

Table 4. Analysis of variance and summary statistics for impacts of bio-fouling on mesh size after 4.5 months of deployment of cages.

Source of variation	d.f.	SS	MS	F	p
Mesh	1	1645	1645	13.6	0.003
Orientation	1	59.6	59.6	0.89	0.36
Mesh × Orientation	1	17.29	17.29	0.26	0.62
Cage × Orientation	13	867	66.7	1.4	0.17
Cage (within Mesh)	13	1570	121	2.53	0.004
Error	120	5736	47.8		

Mesh size	n	Mean open space before fouling (%)	Mean open space after fouling (%)	Mean % reduction	St. dev.	Minimum % reduction	Maximum % reduction
Small	9	80.3	71.5	10.96	1.43	5.9	18.9
Large	6	88.8	85.1	4.1	0.56	2.7	6.0

a unique fashion (i.e., without parallel in control photos) by crawling over it or perching on it. Several visits of comparatively short duration (up to 24 h each) were made by stone crabs, and a single visit by a brittle star (lasting <16 h) was noted. On three occasions, an animal (two asteroids, one anemone) perched on the cage and remained on it continuously for up to 22 d.

b. Mesh fouling

ANOVA shows that the reduction in open space caused by fouling of cage wires varied significantly between cages having different mesh size (Table 4, $p = 0.003$). Large-mesh cages declined from having a mean 88.8% open space at deployment (calculated from video images) to having a mean 85.1% open space after 4.5 months (a 4.1% change). In contrast, small-mesh cages declined from having a mean 80.3% open space at deployment to a mean 71.5% open space (an 11% reduction). There was significant variability among replicate cages of both mesh sizes in the impacts of fouling (Table 4, $p = 0.004$). Other factors in the ANOVA were not significant.

c. Excess ^{234}Th accumulation

As expected, activities of excess ^{234}Th were similar in control plots paired with large-mesh cages (7.04 dpm cm^{-2}) and those paired with small-mesh cages (6.32 dpm cm^{-2}) (Table 5). These two values were statistically indistinguishable ($t_9 = 0.519$, $p > 0.50$). In contrast, for both small- and large-mesh cages, activities of excess ^{234}Th inside cages tended to be elevated relative to paired control plots. There was substantial variability among cage-control pairs in the magnitude of the apparent increase in excess ^{234}Th activity inside of cages (Table 5). However, the average increase was 37% inside small-mesh cages and 29% inside large-mesh cages. The increase inside of small-mesh cages was statistically significant (paired t-test, $t_6 = 2.59$, $p < 0.05$), but the increase inside of large-mesh cages

Table 5. Inventories of excess ^{234}Th in top 5 cm of sediments from paired cage and control plots. Values and summary statistics are listed separately for small- and large-mesh cages.

Cage no.	Cages inventory excess ^{234}Th (dpm cm^{-2})	Controls inventory excess ^{234}Th (dpm cm^{-2})	Difference (dpm cm^{-2})	% Change from control
Small Mesh				
1	11.41	5.75	5.66	98.5
3	6.02	4.28	1.74	40.7
4	6.24	4.61	1.63	35.4
6	8.83	5.12	3.71	72.4
8	10.07	8.26	1.81	21.9
11	10.83	10.19	0.64	6.3
13	5.21	6.05	−0.83	−13.7
Mean	8.37	6.32	2.05	37.4
St. Dev.	2.53	2.15	2.10	38.3
Large Mesh				
2L	6.50	4.82	1.68	34.8
7L	7.46	6.99	0.48	6.8
14L	9.68	10.38	−0.70	−6.7
15L	10.80	5.99	4.81	80.2
Mean	8.61	7.04	1.57	28.8
St. Dev.	1.98	2.39	2.37	38.4

was not ($t_3 = 1.32$, $p > 0.2$). However, given that the mean increase in excess ^{234}Th activities was similar for both large- and small-mesh cages, the lack of significance for the large-mesh test was probably caused by the lower statistical power (fewer samples) more so than by any lack of an effect.

d. Organic C and N, phytoplankton-derived pigments, and grain size

The upper 2 mm of sediments at the study site contained an average 3.83% organic C by mass and 0.44% organic N (Table 6). As expected at a deep-sea site, pheopigment concentrations in surficial sediments (41–51 μg g^{-1}) far exceeded concentrations of chlorophyll a (1.1–1.4 μg g^{-1}). There were no obvious or detectable changes in concentrations of any of these parameters inside of cages (of either mesh type) relative to paired control areas (Table 6).

There was no significant difference in the weight of the silt-clay fraction between small-mesh cages and paired control plots (Table 6); the ranges overlapped extensively (range in cages = 63.9%–81.4%; range in control plots = 64.1%–77.7%). The mean calculated dry bulk density for all cage sediments is 0.32 ± 0.01 g cm^{-3} and for all control samples is 0.33 ± 0.03 g cm^{-3}.

Table 6. Summary statistics and results of paired *t*-tests for comparisons between cage and control plots of concentrations of organic C and N, chlorophyll *a*, pheopigments, and mass percentage of particles smaller than 62 μm, in the upper 2 mm of sediments. Results are presented separately for small- and large-mesh cages.

	% Org. C		% Org. N		Chlorophyll *a* (μg g^{-1})		Pheopigments (μg g^{-1})		Mass (% <62 μm)	
	Cage	Control	Cage	Control	Cage	Control	Cage	Control	Cage	Control
Small Mesh										
Mean	3.75	3.83	0.44	0.44	1.08	1.11	43.8	50.6	76.3	72.2
St. Dev	0.34	0.22	0.01	0.01	0.38	0.35	13.4	16.9	6.2	5.0
n	9		9		9		9		9	
Paired *t*	−0.98		−0.13		−0.17		−0.89		1.36	
p	>0.2		0.9		>0.5		0.4		>0.2	
Large Mesh										
Mean	3.91	3.82	0.44	0.43	1.37	1.08	51.6	41.5		
St. Dev	0.18	0.13	0.02	0.01	0.73	0.58	29.8	19.5		
n	6		6		6		6			
Paired *t*	0.95		0.99		0.97		0.73			
p	>0.2		>0.2		>0.2		0.5			

5. Discussion

The time-lapse photographs indicate that small-mesh cages are effective at excluding targeted LME from regions of the seafloor. On multiple occasions during the 4.5-month deployment, cages excluded animals from enclosed areas of seafloor (Table 2). Interdicted individuals included carnivores (the rockfish *Sebastolobus,* and a gastropod cf. *Phymorhynchus*), deposit feeders (the holothurians belonging to *Synallactes* and *Pannychia,* an ophiuroid in the *Ophiolepididae,* and the gastropod *Bathybembix bairdii*), and hagfish (*Eptatretus deani*), which create burrows in the seafloor (Table 2). These large, motile animals all might affect macro- and meio-infauna.

It is important to note that very few individuals were observed in successive frames in either the cage or control time series. This circumstance indicates that most individuals traversed the photographed regions of the seafloor ($\approx$1.5 m in minimum horizontal span) in less time than that between successive photographs (8 h). From this observation, we deduce that many visitors to the areas photographed would not have been recorded on film. Therefore, we have underestimated both the number and probably the variety of LME excluded by cages. Thus, the small-mesh cages were effective exclusion devices in this study area.

It is noteworthy that the large-mesh cages were less than 100% effective in excluding small *Sebastolobus* from the interiors of cages. Because this species was one of the primary targeted LME, we consider the large-mesh cages to be suboptimal for use in caging studies at our study site. We, therefore, focus further discussion on the efficacy of the small-mesh cages.

Caging experiments in shallow water have been plagued because large, mobile, and disruptive animals (e.g., fishes, crabs) establish long-term residence adjacent to or on the cage (Virnstein, 1978). The primary concern is whether these animals alter conditions inside the cages, for example, by dropping things inside or by disrupting sediments at the cage margin with effects that subsequently penetrate into the cages. In the time-lapse records, LME individuals visited the cage perimeter at similar frequencies and for similar durations as they did a control region of the seafloor. Of the taxa on the cage and absent from equivalent areas of the controls, stone crabs made fleeting visits. In contrast, two starfish and an anemone perched on a cage continuously for 1–3 weeks (Table 3). When close-up video recordings of the sediment surface inside and outside the cage that was in front of the time-lapse camera were consulted, no obvious effects of the perching visitors were noted. For example, there were no piles of empty shells around the cage, such as we have observed occasionally at our study site around large sponges used as perches by crabs. In fact, video records of the sediment surface around all 15 cages sampled provide no indication that the peripheries of the cages were disrupted by activities of LME, and there was no indication that animals used cages to perch for feeding. The anemone noted in the time-lapse photographs was a suspension feeder. It and the starfishes noted in the time-lapse photographs (Table 3) were positioned on the cage well above the sediment and thus were unlikely to influence the benthos except perhaps by depositing feces inside the cage. We have direct measures of surficial sediment properties inside and outside cages that bear on this possibility, which are discussed below.

Most of the remaining artifacts that have compromised the use of cages in shallow water are important because they restrict flow through the volume enclosed by the cage and, therefore, might change the deposition rates of larvae and suspended particulates (a potential rich food resource). Such changes could affect the fauna inside the cage for reasons that have nothing to do with the exclusion of the LME and so must be guarded against.

Our observations and results that bear on this possibility indicate that the cages performed well in terms of these potential artifacts. No material drifted against the side of the cage we monitored with the time-lapse camera, nor did we observe drift material against the sides of any of the cages at the end of the experiment. After 4.5 months, the open area of small-mesh cages decreased by an average of 11% because of bio-fouling (colonization of wires by hydroid colonies and the accumulation of an organic film). The only macrofaunal fouling we found were anemones (one or two) near the lid of each of 7 of the 15 cages examined.

There is little evidence that these cage effects had any detectable impact on the properties of surficial sediments to which potential colonizing infauna might respond. The composition of surface sediments in terms of organic C and N, phytoplankton-derived pigments, and the weight percentage of fine sediment particles was indistinguishable between cages and control areas (Table 5). In particular, chlorophyll *a* and pheopigments, which derived from phytodetrital falls or settled fecal pellets of zooplankton that fed in the

upper water column, have degradation half lives shorter than the period of deployment of our cages (Westrich and Berner, 1984, see their Table 1; Lochte and Turley, 1988; Smith *et al.,* 1993, see their Table 5; Sun *et al.,* 1993a,b; Poremba, 1994; Stephens *et al.,* 1997). Therefore, concentrations of these pigments may be considered reasonable indicators of any changes by cages in particulate deposition within cages. No differences were observed in their concentrations between caged and control plots, providing evidence that cages performed well and without obvious artifact in this regard.

In contrast, the activity of excess ^{234}Th was significantly higher inside small-mesh cages than in control plots (average of 37% above controls), raising the possibility that this sensitive indicator of short-term particulate deposition detected an important impact of cages on flow and deposition. Unfortunately, our measurements of ^{234}Th accumulation inside cages were compromised by experimental artifact. As noted above, despite the care taken by the *ALVIN* pilots in opening cage lids, there was some agitation of the cage frame and walls. This shaking plus the dislodgement of particles from the cage lid as it swung open resulted in a "rain" of particles that had deposited onto the lid and walls during the 4.5 months of cage deployment onto the seafloor including the sediment surface within the cage. Because these particles had been exposed to flowing seawater in the bottom boundary layer while on the cage lid and walls, they continued to scavenge freshly produced ^{234}Th. In the control plots, the equivalent particles reached the seafloor, and a portion were mixed below the surface, isolating them from the high flux of freshly produced ^{234}Th in the water column. Thus, deposition of the ^{234}Th-rich particles from the walls and lid inside cages only moments before coring artificially inflated the difference in deposition rate calculated between sediments in control plots and cages. Moreover, there would have been considerable variation among cages in the degree of agitation by the submersible and the resulting deposition of ^{234}Th-rich particles before sampling, and this may help explain the comparatively high standard deviation in the difference of excess ^{234}Th activity between cages and control plots (i.e., standard deviation of the difference approximately equivalent to the mean difference—Table 5). Therefore, based on the data available to us, we conclude that the cages had no detectable impacts on the rate of particulate deposition or the quality of surficial sediments presented to residents or potential recruits.

One final potential artifact of cages deserves consideration, the potential for flow alteration by cages to affect fluxes of larvae or other potential recruits that disperse through the benthic boundary layer to sediments inside cages. Data that would bear directly on this potential artifact, *in situ* measurements of flow speed and turbulence intensities inside of cages (and controls), are not available. Moreover, direct measures of flow would not by themselves provide the required information, because the central issue is possible effects of cages on rates of contact of particles with the bed (McNair *et al.,* 1997; Eckman and Duggins, 1998). Unfortunately, the ^{234}Th data, which might have provided insight, are biased by the artifact associated with the opening of cages. The phyto-detrital pigment data, which also should have reflected particulate deposition to cage and control sediments,

indicate no impact of cages. Therefore, although we cannot assign a numerical value to this potential artifact of cages, related data suggest that such an effect would be small.

We conclude that the small-mesh cages worked effectively as devices for excluding LME from areas of the deep-sea floor and were effectively free for 4.5 months of other troublesome cage artifacts that have compromised cages in many shallow-water studies. These devices should serve as excellent tools for studying effects of LME on infauna in deep-sea environments, so long as care is taken to assess potential cage artifacts.

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