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ENHANCEMENT OF SUBTIDAL EASTERN OYSTER, *CRASSOSTREA VIRGINICA*, RECRUITMENT USING MESH BAG ENCLOSURES

FRANCIS X. O'BEIRN,[1,*] RANDAL L. WALKER,[1] AND PETER B. HEFFERNAN[2]
[1]*University of Georgia*
Shellfish Aquaculture Laboratory
20 Ocean Science Circle
Savannah, Georgia
[2]*Marine Institute*
80 Harcourt Street
Dublin 2, Ireland

ABSTRACT Eastern oysters, *Crassostrea virginica*, in the southeastern United States are found predominantly in the intertidal zone. In this study, mesh bags (3 and 6 mm) were deployed over collecting frames, and the patterns of oyster settlement on these collectors were compared against unmeshed controls at three tidal heights (intertidal, low water, and subtidal) over three sampling regimes (biweekly, monthly, and seasonal) at two sites. Within the biweekly sampling regime, the meshed collectors and controls had similar patterns of settlement at the respective tidal heights. For monthly samplers, mesh treatments maintained higher settlement subtidally whereas controls had highest settlement on the collectors at mean low-water level. Controls had highest recruitment intertidally for seasonal collectors, whereas mesh treatments had higher recruitment lower in the intertidal zone. Conclusions from this experiment were that the use of mesh-covered collectors enhanced subtidal oyster recruitment. Causes of observed increases in subtidal settlement in mesh collectors over unmeshed controls over time could be the result of a combination of factors: predator exclusion, larval entrainment, or reduced desiccation, which seemed to overcome the detrimental effects of increased fouling, resulting in reduced flow and possible hypoxic conditions within the mesh bags. Given the degree of recruitment and the sizes of the recruits attained within the mesh bags, the use of these methods to attain juveniles for commercial purposes would appear to be both feasible and viable, particularly for long periods (up to 6 mo) of deployment.

KEY WORDS: *Crassostrea virginica*, mesh excluder, oysters, predation, recruitment

INTRODUCTION

The range of eastern oyster, *Crassostrea virginica* (Gmelin), extends from the Gulf of St. Lawrence south along the eastern seaboard of the United States and throughout the Gulf of Mexico (Galstoff 1964). Within this range, the oyster is found predominantly in the subtidal zone. However, in the southeastern United States, and specifically in South Carolina and Georgia, the majority of oysters are intertidal.

The primary reasons given for the lack of subtidal oysters have been disease, mismanagement of the resource, competition from other epibionts, and predation (Harris 1980, Ofiara and Stevens 1987, Michener and Kenny 1991). Macropredators are numerous and include mammals, fish, crustaceans, and molluscs (Linton 1968, Walker 1981, Walker 1993). However, relatively little is known concerning the effect of these predators on newly settled oysters. Predation on young oysters by blue crabs, *Callinectes sapidus*, was identified as a contributing factor in the 1946 failure of oyster recruitment in South Carolina (Lunz 1947). Galstoff (1964) observed that many young oysters were adversely affected by crabs feeding on larger oysters on which larvae had settled and attached.

Recruitment studies by O'Beirn et al. (1995 and 1996) suggested that events shortly after oyster settlement and metamorphosis may contribute to the confinement of oysters intertidally in coastal Georgia. It was observed that oyster numbers recorded on collectors were significantly higher in the subtidal than intertidal environment over short periods of sampler deployment (i.e., 2 wk and 1 mo), with the reverse observed for longer periods (up to 7 mo). Furthermore, it was suggested that with greater duration of deployment and consequently the submergence of subtidal collectors, the potential for predation or other mortality factors (such as competition or exposure to pathogenic organisms) on oysters was increased. We describe a field study to evaluate oyster settlement using protective mesh bags that in theory would allow oyster larvae to set on collectors while limiting the access of potential predators. Also, we anticipated that the use of protective meshes would increase the potential to harvest adequate numbers of spat from the subtidal zone in the southeastern United States.

STUDY SITES

The work was carried out from April to November 1993 at two sites and April to September 1994 at one site (for logistical reasons), in Wassaw Sound, GA (Fig. 1). The two sites were: House Creek, a sheltered tidal creek near the mouth of the sound; and Skidaway River, a less sheltered site located on the Intracoastal Waterway. A more detailed description of the hydrographic characteristics of the sites can be found in O'Beirn et al. (1995). The two sites have been used to monitor oyster recruitment since 1991 (O'Beirn 1995, O'Beirn et al. 1995, O'Beirn et al. 1996).

METHODS

The sampling apparatus and methods of deployment were similar to those already used in the established monitoring programs in coastal Georgia (O'Beirn 1995, O'Beirn et al. 1994, O'Beirn et al. 1995, O'Beirn et al. 1996). Briefly, longitudinally grooved poly-

*Corresponding Author; Present Address: Dept. of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0321.

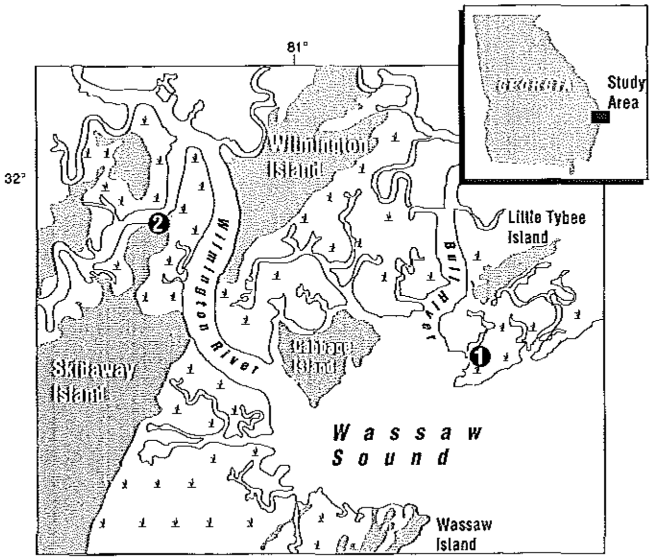

Figure 1. Map of sampling area in Wassaw Sound, GA, indicating the two sampling sites used throughout the study: (1) House Creek and (2) Skidaway River.

vinylchloride (PVC) tubing embedded with chips of calcium carbonate was used for collecting spat. A 12-cm section of tubing on each collector provided a sampling area of approximately 100 cm^2. Three collectors were arranged vertically on a sampling unit; each collector was exposed to one of three tidal heights (subtidal, mean low water, and intertidal). Four replicate sampling units were attached to a portable frame, which in turn was attached to a fixed frame (Fig. 2). After return to the laboratory, each collector was rinsed to remove extraneous material and examined with a binocular microscope at 10× to enumerate the number of oysters on each collector.

Collecting frames with four replicate sampling units were covered with 3- and 6-mm mesh bags (see Fig. 2). The open end of each bag was sealed, folded, and inserted into a PVC pipe that had been slit longitudinally. Hereafter, the 3- and 6-mm mesh bag–covered frames shall be referred to as the 3- and 6-mm treatments, respectively. An exposed control frame was also placed at each site. Collectors were retrieved and replaced at the two sampling sites on a biweekly and monthly basis. Thus, every 2 wk and once monthly, three frames (i.e., two mesh treatments and one control) were taken from each site and evaluated for spat. A separate set of

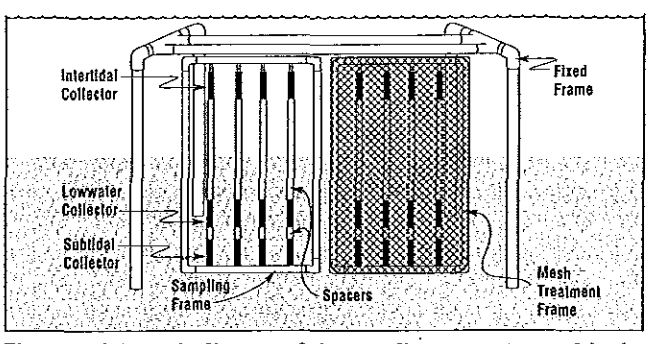

Figure 2. Schematic diagram of the sampling apparatus used in the study. For the 3- and the 6-mm treatments, mesh bags were slipped over the sample frame.

seasonal collectors was also deployed at the two sites. These were left on site for the duration of the study. These seasonal collectors gave an estimate of the overall recruitment of oysters for the entire spawning season. The experiment was repeated in 1994 at the Skidaway River site only.

STATISTICAL ANALYSIS

The enclosure of each of the treatment frames within a mesh "bag" would result in some problems of analysis relating to pseudoreplication (Hurlbert 1984). Therefore, data at each tidal height, within each sampling period, were pooled and each period was then used as a replicate with which to carry out the analysis. The substantial variation in oyster numbers retrieved on the collectors throughout the study necessitated the log transformation [ln(x + 1)] of these values within each of the data sets retrieved. To evaluate the patterns of settlement within each treatment, one-way analysis of variance (ANOVA) and the Tukey Studentized Range Test (when appropriate) were performed on these transformed data with tidal height as the main effect. Separate ANOVAs were performed on the data for each mesh treatment, within each sampling regime at each site, and in the case of the Skidaway River, each year. The primary goal was to evaluate the patterns of settlement within each treatment. It was hypothesized that the mesh treatments would retain proportionally greater numbers of spat, subtidally over time, than the unmeshed control. A standard significance level of 5% was chosen for all statistical tests ($\alpha = 0.05$).

RESULTS

Overall, oyster recruitment in Wassaw Sound in 1993 was considerably lower than that in 1991 and 1992 (O'Beirn 1995, O'Beirn et al. 1996). At House Creek, recruitment on the biweekly control collectors was first observed in late May 1993. However, peak settlement did not occur until late September ($\bar{x}$ = 7.4 spat/0.01 m^2; Fig. 3A). At the Skidaway River site in 1993, levels were extremely low until peak settlement in late September ($\bar{x}$ = 63.2 spat/0.01 m^2; Fig. 3B). Settlement was high on the monthly control collectors at House Creek early in the 1993 season, after which, settlement dropped off and showed no appreciable increase over the rest of the season (Fig. 4A). Peak monthly settlement on the intertidal collectors occurred in May at the House Creek site ($\bar{x}$ = 225.6 spat/0.01 m^2). Similar patterns were observed at the Skidaway River site; peak settlement occurred early in the 1993 season, followed by low settlement levels throughout the year. Peak settlement at the Skidaway site was on the low-water collectors in June ($\bar{x}$ = 154.4 spat/0.01 m^2; Fig. 4B). Oyster settlement on the biweekly subtidal collectors at the Skidaway River site in 1994 commenced in mid-May and increased to a peak in mid-June ($\bar{x}$ = 5.75 spat/0.01 m^2; Fig. 3B). Monthly settlement values had peak settlement on the low-water collectors in July ($\bar{x}$ = 26.3 spat/0.01 m^2; Fig. 4B).

Results of the ANOVAs on the transformed biweekly, monthly, and seasonal data from House Creek and Skidaway River are presented in Table 1. For the biweekly data at both sites in 1993 and at Skidaway in 1994 (Table 1), controls tended to retain greater number of oysters than both of the treatments. The lack of significance of many of the tests indicated no distinct patterns. The highest settlement was achieved on subtidal and low-water collectors for both treatments and controls at Skidaway in 1994 (Table 1).

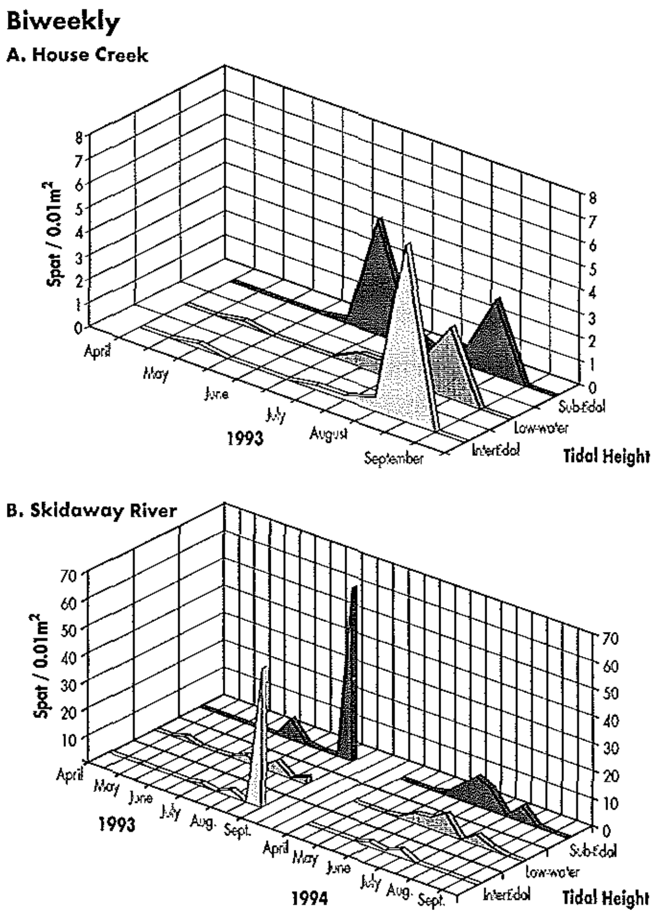

Figure 3. Mean number of spat per 0.01 m^2 from biweekly recruitment onto control collectors at (A) House Creek (1993) and (B) Skidaway River (1993/94).

The monthly data also tended to have substantially higher numbers of oysters on control collectors than treatment collectors (Table 1). Significantly higher oyster numbers were maintained on subtidal than on intertidal collectors on the Skidaway 3-mm treatments in 1993 and 1994 ($p = 0.0007$ and 0.0015, respectively). Neither differed from the low-water collectors. Control frames at Skidaway in 1994 did have significantly higher numbers of oysters on the low-water collectors ($p = 0.0003$; Table 1) than the other tidal heights.

The seasonal data did reveal some divergence in patterns of recruitment between control and treatments, particularly at the Skidaway site (Table 1). Controls had predictably higher recruitment intertidally. Treatments at House Creek in 1993 closely mimicked the pattern observed in the controls, i.e., higher numbers of intertidal oysters (Table 1). Skidaway River, although having highest recruitment intertidally on control frames in both years, did have highest recruitment lower in the intertidal zone on treatment frames. In 1993, both treatments had higher numbers of oysters on the low-water collectors than the controls. In 1994, the 3-mm treatment had highest recruitment subtidally, whereas the 6-mm treatment had highest recruitment on the low-water collectors.

Analysis of the size data (Table 2) detected no substantial differences among treatments and controls at each tidal height and site for the biweekly regime. However, for the monthly sampling regime, treatment frames tended to have larger oysters than controls, particularly at the lower tidal heights. For seasonal returns, the 3-mm-treatment consistently had larger oysters at the two sites and at all tidal heights (Table 2).

DISCUSSION

The successful collection of wild molluscan spat for maricultural purposes is dependent on a consistent supply of larvae as well as a high rate of their settlement and subsequent survival. These latter two factors have been enhanced by the development of efficient means for collecting spat from natural spawning events in a number of bivalve species. Such means include monitoring adult gametogenesis, predicting times of larval availability, and deploying suitable collecting apparatus with which to collect spat.

In the study described here, oyster settlement on collectors covered with mesh bags was compared with that on uncovered control collectors. It was anticipated that subtidal recruitment would be enhanced on the mesh-covered collectors. For the biweekly sampling regime, no differences in patterns of settlement among the tidal heights were apparent at either site in 1993 and at Skidaway River in 1994 (Table 1). Some divergence was observed between the control and the 3-mm treatment for the monthly sampling regime at the Skidaway site in 1993 and 1994 (Table 1) whereby the treatment frames retained greater proportions of oysters subtidally.

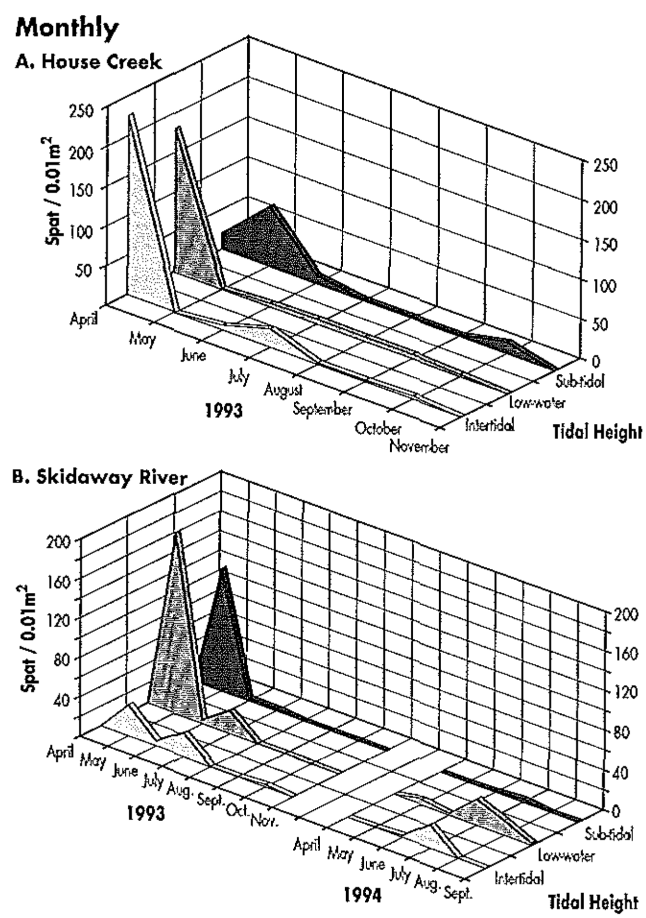

Figure 4. Mean number of spat per 0.01 m^2 from monthly recruitment onto control collectors at (A) House Creek (1993) and (B) Skidaway River (1993/94).

TABLE 1.

Biweekly, monthly, and seasonal mean oyster numbers from the two sites in 1993 and Skidaway River in 1994.

	Biweekly			Monthly			Seasonal		
Year/Group	SUB	LOW	INT	SUB	LOW	INT	SUB	LOW	INT
1993									
House Creek									
Control	1.1	0.6	1.0	35.7	29.9	18.5	1b	2.6b	63.8a*
3 mm	0.2	0.1	0.1	1.6	10.3	1.6	0c	16.0b	57.0a*
6 mm	0.1	0.2	0.1	0.8	5.0	0.5	1.8b	3.3b	20.3a*
Skidaway River									
Control	8.0	1.5	6.0	9.2	26.0	18.5	0.6b	0.04b	17.8a*
3 mm	0.2	0.1	0	1.6a	0.7ab	0.1b*	14.3b	43.5a	37.0a*
6 mm	0.8	0.6	1	0.4	0.4	0.2	14.5b	47.0a	12.8b*
1994									
Skidaway River									
Control	4.7a	3.1a	0.8b*	5.3b	10.2a	1.0b*	0.3b	3.1b	11.8a*
3 mm	1.8a	0.9a	0.1b*	6.8a	3.1ab	1.0b*	32.8	17.8	24.8
6 mm	1.9a	1.5a	0.3b*	1.3	0.9	0.3	13.8	30.3	23.3

Given are the outputs from the Tukey test. Tidal heights with the same letter designation were not significantly different, * $p < 0.05$. SUB, subtidal; LOW, low water; INT, intertidal; 3 mm, 3-mm mesh bag treatment; 6 mm, 6-mm mesh bag treatment.

At the Skidaway River site, recruitment patterns observed on the seasonal collectors (Table 1) tended to support the overall theory that an external mortality factor on newly settled oysters results in their confinement to the intertidal zone. Although the control frame displayed higher recruitment intertidally, both of the treatment (3 and 6 mm) frames tended to have higher recruitment subtidally or at low water in both 1993 and 1994 (Table 1).

Both the 3- and the 6-mm seasonal frames from House Creek in 1993 developed tears in the mesh and were heavily inundated with silt below the low-water mark. Siltation was a result (in part) of the lower end of the frames resting on the bottom and, thereby, trapping silt in an area with high sediment loading (Virnstein 1978, Peterson 1979). A similar problem was encountered on the 3-mm seasonal frame at the Skidaway River site in 1993. Caging artifacts unfortunately were present, and consequently, the treatments were not maintained throughout the study. Despite this, the seasonal results from 1993 and 1994 at the Skidaway site indicated that the placement of mesh over collectors had an effect on the recruitment patterns of oysters. These data suggest that even with the problems encountered (siltation, torn mesh bags, and low recruitment), the "bagging" manipulation altered the distribution of oysters, such that survival tended to be higher below the low-water mark relative to controls.

The degree of variability in settlement patterns exhibited by biweekly and monthly data impedes the interpretation of observed trends. However, as already stated, more consistent trends were observed from the seasonal returns at the Skidaway River site. Factors affecting postsettlement oyster survival (e.g., predation) appear to take more than 1 mo to overcome the patterns set by "short-term" recruitment events. The bags may have other effects besides excluding potential predators and could be responsible for much of the inconsistencies observed over the shorter time scales.

TABLE 2.

Mean sizes of oysters (mm) from treatments and control collectors over the three sampling regimes at the three tidal heights.

	Biweekly			Monthly			Seasonal		
Sampling Area	3 MM	6 MM	CON	3 MM	6 MM	CON	3 MM	6 MM	CON
Intertidal									
House Creek	2.6a	1b	2.2a*	2.1ab	2.6a	1.5b*	45.1a	16.1c	37.9b*
Skidaway River	—	—	—	—	—	—	44.7a	46.5a	14.5b*
Skidaway River ('94)	2.7a	3.5a	0.9b*	5.3a	3.3ab	1.2b*	18.2a	17.0a	6.6b*
Low water									
House Creek	2.6	2.0	3.2	1.4b	1.1b	2.5a*	27.5	18.1	22.7
Skidaway River	5.3	5.6	2.6	2.2ab	3.7a	1.7b*	56.3a	61.0a	16.0b*
Skidaway River ('94)	2.6	4.2	3.4	5.2	5.8	4.2	23.9a	13.7b	8.4b*
Subtidal									
House Creek	2.7	2.6	1.7	1.4ab	1.0b	2.4a*	—	—	—
Skidaway River	2.5ab	0.7b	2.6a*	1.7	2.2	2.5	39.3a	33.5a	18.0b*
Skidaway River ('94)	2.3	3.2	2.6	5.6	5.8	4.3	27.0a	20.2a	8.3b*

Also given are the outputs from the Tukey test. Treatments with the same letter designation were not significantly different, * $p < 0.05$. 3 MM, 3-mm mesh treatment; 6 MM, 6-mm mesh treatment; CON, control.

For example, the shading effects of the bags (a combination of the mesh itself with fouling that was observed) on intertidal collectors may reduce mortality and stress on newly settled oysters due to desiccation and temperature extremes (Roegner and Mann 1995). Consequently, this would obscure emerging differences resulting from higher survival on the subtidal collectors.

Negation of differences among the tidal heights in the treatments might also occur if water flow was restricted within the bags, resulting in hypoxic conditions, particularly at the lower tidal heights, where fouling was greatest. Hypoxia and anoxia have been shown to retard development and result in increased mortality of young oysters (Widdows et al. 1989, Baker and Mann 1994). It is assumed, however, that some oysters can survive these apparent stresses, and the cumulative effect of their settlement and survival results in the patterns observed on the seasonal collectors. Water flow restriction might also result in larval entrainment within the bags.

Neither the 3- nor the 6-mm meshes exclude predators such as flatworms, *Stylochus* sp., and juveniles of the oyster drill, *Urosalpinx cinerea*. Both had been observed on collectors inside the mesh bags, and their presence did coincide with low oyster numbers on the collectors. Also, holes characteristic of oyster drills were observed on many small oysters (ca. 5 mm). Both of these predators have been observed to prey voraciously on juvenile oysters elsewhere (Newell et al. 1991, Spencer et al. 1986). Other potential predators might be juveniles of known predators before an ontogenic shift to a larger food source, as is the case with blue crabs, *Callinectes sapidus* (Laughlin 1982), and the predatory drill, *Thais haemastoma* (Garton 1986). Blue crabs have been shown to prey heavily on juvenile (15 mm in shell height) oysters, *C. virginica* (Eggleston 1990). Other possible candidates include species of commercial penaeid shrimp as well as the grass shrimp, *Palaemonetes* sp. In studies with another bivalve, *Mercenaria mercenaria*, grass shrimp were shown to prey heavily on clams <0.6 mm in length (Uguccioni and Posey 1992). Also, Posey and Hines (1991) demonstrated that grass shrimp can prey on other thinner shelled bivalves such as *Mulinia lateralis* and *Macoma mitchelli* (up to 1 mm in shell length).

The enclosure of collecting materials (cultch) within plastic or wire meshes would serve two primary purposes: it retains the cultch in one cohesive unit, thus reducing the costs of subsequent handling, and it would protect newly settled oysters from some predatory organisms. Results from this study suggest that the recruitment of oysters lower in the intertidal zone (subtidally and/or at the low-water mark) can be enhanced by the use of mesh enclosures with the collecting apparatus. This is particularly apparent for collectors deployed for the duration of the sampling season. This would result in a high yield of oysters that are comparable in size to those found intertidally and larger than those found on collectors without mesh covers (Table 2). A combination of collecting strategies, whereby covered cultch is deployed subtidally and uncovered cultch is deployed intertidally, would yield high numbers of recruiting oysters with minimal effort and cost, thus, making oyster culture in the southeastern United States a more attractive venture.

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