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SETTLEMENT PATTERNS OF *CRASSOSTREA VIRGINICA* (GMELIN, 1791) LARVAE IN RELATION TO TIDAL ZONATION

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ABSTRACT Experiments were conducted to determine the settlement distribution of the oyster *Crassostrea virginica* (Gmelin) in relation to tidal zonation in an area where adult populations are largely confined to the intertidal zone. Hatchery-reared pediveliger larvae were interned in PVC tubes positioned at known tidal heights. The influence of non-tidal factors was limited: mesh covering the ends of the tubes prevented loss of larvae to dispersal or predation, the settling substrate was not colonized by competitors, and the effects of light and horizontal currents were minimized. Settlement was found to occur throughout the intertidal zone but predominated at the bottom of the tidal-depth gradient. Few oysters settled in the zone occupied by the adult populations, the intertidal position of which is hypothesized to be controlled by predation.

KEY WORDS: oyster, *Crassostrea virginica,* intertidal zonation, settlement, microcosm

INTRODUCTION

The zonation of organisms on hard intertidal substrates has long been of interest to marine ecologists. Rocky intertidal substrates have been especially well studied in this respect, and have proven useful for experimental testing of ecological and population biology hypotheses (Paine 1976, Lubchenco & Menge 1978, Menge 1983, Connell 1985). The distributions of marine invertebrates are generally conceded to be the result of complex interactions between biotic and abiotic factors which influence settlement success and post-settlement survival (Connell 1985). For sedentary organisms which disperse via planktonic propagules, the range of adults must obviously be some subset of the range of settlers. Mortality culls individuals which settle in unfavorable sites. Thus, the influence of larval settlement patterns on subsequent juvenile and adult distributions has received attention (Grosberg 1982, Keough & Downes 1982, Sousa 1984, Bushek 1988).

The location, duration, and magnitude of larval settlement onto substrates is influenced by a variety of factors. These factors include: temporal and spatial variability of larval abundances, caused by biologically, behaviorally, or physically mediated variations in larval supply or planktonic zonation (Grosberg 1982, Gaines et al. 1985, Gaines & Roughgarden 1987, Shanks & Write 1987, Roughgarden et al. 1988, Wolanski & Hamner 1988, Lipcius et al. 1990); enhanced settlement in response to chemical or physical environmental cues, including cues associated with the presence of conspecifics (Crisp 1967, 1976, Weiner & Colwell 1982, Hadfield 1984, LeTourneux & Bourget 1988, Raimondi 1988); and competitive responses to the settlement-inhibiting or predatory actions of established organisms (Mileikovsky 1974, Grosberg 1981, Young & Gotelli 1988, Osman et al. 1989). The relative importance of any of these processes on settlement may vary with organism and environment.

For organisms such as barnacles, serpulid polycheate worms, and oysters, which exist as permanently attached epibenthic individuals, settlement is a singular event which is initiated by the irreversible fixation of the larvae to the substrate. Concurrently, there is a permanent loss of pelagic mobility manifested during metamorphosis. Once physiologically committed to a site, the newly settled individual is termed a recruit. The survival of recruits is a function of post-settlement processes, such as intensity of predation and competition, or resistance to detrimental physical stresses. Thus, in a heterogeneous environment which varies in the severity of biotic and abiotic stressors, recruitment success can be determined largely by the site of settlement.

In the lower portion of the York River, Virginia, USA, pier pilings provide one of the few hard substrates spanning the tidal range which are available for larval colonization. On these pilings, populations of the American oyster *Crassostrea virginica* (Gmelin) are largely confined to the mid-intertidal zone (about 25–60% exposed). As part of a larger study on the growth and survival of intertidal and subtidal juvenile oysters, it was of interest to determine the settlement distribution of oyster larvae in relation to the ambient tidal oscillations. This note reports on experiments conducted to test the null hypothesis that oyster larvae settle uniformly along an exposure-depth gradient.

MATERIALS AND METHODS

Experiments were conducted in the York River, Virginia, USA, a major subestuary of Chesapeake Bay, during

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the late summer and autumn of 1988. The study site was located on a pier of the Virginia Institute of Marine Science at a position where water depth was about 0.75 meters below mean at low water (MLW). The tidal height, salinity, and air and water temperatures were continuously measured over the experimental period by automated sensors located less than 100 meters from the site.

At the study site, a vertically oriented wooden frame was permanently fixed to the pier, and the position of the frame was calibrated relative to MLW. Experimental units attached to the frame could then be secured at known tidal heights. The percentage exposure experienced at any given intertidal position was computed with hourly tidal heights recorded from the tide station. The computational algorithm allowed percent exposure per tidal position to be resolved to a scale of one day. The actual exposure/immersion curves for a given time frame could thus be established, which is not usually possible using predicted tidal heights. This was important since at this protected (low wave energy) site, atmospheric conditions could cause significant deviations from predicted tidal heights.

A microcosm system was constructed to examine settlement relative to tidal height while limiting the influence of non-tidal factors. Hatchery-reared *Crassostrea virginica* larvae were interned within tubes in which the internal water height was in equilibrium with tidal motion. These ''settlement tubes'' were constructed of 5.08 cm (2 in) diameter, opaque, PVC pipe cut into 150 cm lengths. The inside of each tube was completely lined with a clean, continuous Mylar sheet scaled into 10 cm intervals. The Mylar constituted the only substrate within the tube that was available for settlement. Both ends of the tubes were sealed with 202 μm Nitex mesh held in place with PVC ring connectors, and the ends of the Mylar strip protruded slightly from the ends of the tube thereby forming a close seal with the mesh. The mesh prevented the dispersal of the larvae or the introduction of predators. The tubes were conditioned in unfiltered flowing York River water for three days in the laboratory prior to initiation of the field experiments.

Oyster pediveligers, acquired from the Virginia Institute of Marine Science oyster hatchery, were filtered onto a 202 μm mesh sieve. Larvae were then scooped from the sieve to the bottom Nitex mesh of the microcosm tube with a 12 ml plastic measuring spoon, and the larvae-laden meshes were sealed into the tube with the PVC ring connectors. Approximately equal numbers of larvae (about 100,000) were volumetrically transferred into each of three replicate tubes per experiment. The settlement tubes were then secured with parachute line to a wooden rack, and the rack was deployed into the York River by attaching it to the permanent wooden frame. The rack was positioned vertically so that MLW corresponded to a distance of 50 cm above the bottom of the tubes. The tubes were thus suspended approximately 25 cm above the river bottom. Tidal fluctuations resulted in a minimum of a 50% water exchange per tube within a tidal cycle, and thus basic water chemistry parameters are assumed to have been ambient with river water and nonlimiting to larval performance. This orientation resulted in a gradation of exposure heights which varied from high intertidal to subtidal (an exposure-depth gradient). The actual exposure occurring at any tidal height, which varied throughout the experiments, was later determined by examining the tidal record. Horizontal currents in the tubes were greatly reduced over natural conditions.

After a period of three to six days, depending on the observed settlement progress of a larval subset monitored in the laboratory, the rack was recovered and the tubes removed. With the PVC rings and Nitex mesh separated, the Mylar linings were gently rinsed with fresh water to remove unattached individuals, and the sheets were removed from the tubes. Each sheet was then sectioned into the premarked 10 cm intervals, and the number of settled larvae per interval counted under a dissection microscope. Since the exact number of larvae added to each tube was not quantified, settlement per interval was evaluated as the percent of the total number of settled individuals per tube.

The experiment was repeated 4 times: the dates of initiation were 14 August, 23 August, 5 September, and 2 October, 1988 (this period encompassed part of the natural settling period of oysters in this area). The experiments were labeled Experiments S1 to S4, respectively. For each experiment, a one-way ANOVA was performed to test the null hypothesis that oyster larvae settle uniformly across the exposure-depth intervals. Proportional data was normalized with the angular transformation (Zar 1984).

RESULTS

The oyster larvae exhibited a strong preference for the bottom interval as a settlement site (Tables 1, 2, Fig. 1). Between 72 and 96% of the mean settlement occurred at the −50 cm interval, and most of that actually occurred within the bottom 5 centimeters of the tube. Larvae settled within this zone in extremely dense aggregations. Overall, settlement tended to increase with depth, and intertidal settlement was slight. Mean settlement in the intertidal zone ranged from 8 to only 0.5% of the total mean settlement per experiment. With the exception of Experiment S1, the intertidal settlement which occurred was mainly confined to aerial exposure heights lower than 30%. The presence of oysters that settled in areas of 100% emersion (Experiment S1) is an artifact which resulted from larvae stranding during the positioning of the tubes. All ANOVA tests resulted in highly significant F ratios (Table 3). The hypothesis that oyster larvae settle uniformly along the tidal-depth gradient is thus rejected.

DISCUSSION

The settlement pattern recorded during the microcosm experiments did not reflect the observed zonation patterns

TABLE 1.

Summary statistics for experiments S1 and S2.

	Experiment S1			Experiment S2		
Height	**%E**	**MPS**	**SD**	**%E**	**MPS**	**SD**
90	100.00	0.08	0.14	90.63	1.69	2.93
80	100.00	0.06	0.10	79.17	0.13	0.22
70	96.88	0.02	0.02	71.88	0.00	0.00
60	90.63	0.00	0.00	60.42	0.98	1.37
50	75.00	0.11	0.09	53.13	0.00	0.00
40	62.50	0.39	0.10	40.63	0.00	0.00
30	54.17	0.70	0.18	33.33	0.72	0.17
20	42.17	0.96	0.21	19.79	1.57	1.52
10	32.25	1.38	0.57	7.29	2.50	3.00
0	19.79	1.76	0.70	0.00	5.12	2.04
−10	7.29	1.91	0.78	0.00	3.83	2.59
−20	0.00	2.46	0.39	0.00	2.25	2.14
−30	0.00	2.39	0.28	0.00	3.96	2.13
−40	0.00	5.31	0.24	0.00	5.25	0.17
−50	0.00	82.48	2.61	0.00	71.55	4.10

Height: Tidal height (centimeters relative to MLW); %E: Percent aerial exposure; MPS: Mean percent set; SD: Standard deviation.

of adults at this locale. The settlement of the vast majority of the larvae in the lowest possible subtidal site within the settlement tubes suggests a behavioral tendency. In contrast, the adult oyster populations at the study site are mostly confined to the intertidal zone.

These results correspond well to the few previous studies which compared intertidal and subtidal recruitment of oysters on time scales short enough to distinguish between settlement and post-settlement mortality. (Many early studies sampled over monthly, or greater, time scales (Galtsoff & Luce 1930, Loosanoff 1932, Mackin 1946), and thus actually measured long term survival patterns.) McDougall (1942), in a study at Beaufort, N.C., evaluated settlement on ceramic plates over one to two week intervals and found subtidal settlement to be substantially greater than intertidal settlement, with the heaviest settlement occurring near the bottom. Chestnut and Fahy (1952, 1953) found similar results from week-long shellstring studies which measured settlement at depths between +3 to −15 feet relative to MLW at several sites in Bogue Sound, N.C. Nichy and Menzel (1967), in a recruitment study at Alligator Harbor, Florida, observed greater subtidal than intertidal settlement. Hidu and Haskin (1971), in Delaware Bay, found settlement patterns between inshore and offshore sites to be related to temperature and hydrographic processes. Intertidal settlement was very high at the inshore

TABLE 2.

Summary statistics for experiments S3 and S4.

	Experiment S3			Experiment S4		
Height	**%E**	**MPS**	**SD**	**%E**	**MPS**	**SD**
90	100.00	0.00	0.00	92.26	0.00	0.00
80	83.33	0.00	0.00	91.67	0.00	0.00
70	68.45	0.00	0.00	75.00	0.00	0.00
60	55.95	0.00	0.00	61.11	0.00	0.00
50	38.69	0.00	0.00	50.00	0.00	0.00
40	27.38	0.02	0.03	40.28	0.00	0.00
30	17.26	0.00	0.00	27.08	0.05	0.06
20	8.93	0.04	0.03	10.42	0.16	0.11
10	0.60	0.49	0.73	0.69	1.62	0.41
0	0.00	0.30	0.09	0.00	1.66	1.10
−10	0.00	0.35	0.08	0.00	2.45	1.18
−20	0.00	0.87	0.42	0.00	2.33	1.26
−30	0.00	0.95	0.18	0.00	3.00	0.20
−40	0.00	1.06	0.52	0.00	4.45	2.04
−50	0.00	84.28	4.79	0.00	95.91	0.88

Height: Tidal height (centimeters relative to MLW); %E: Percent aerial exposure; MPS: Mean percent set; SD: Standard deviation.

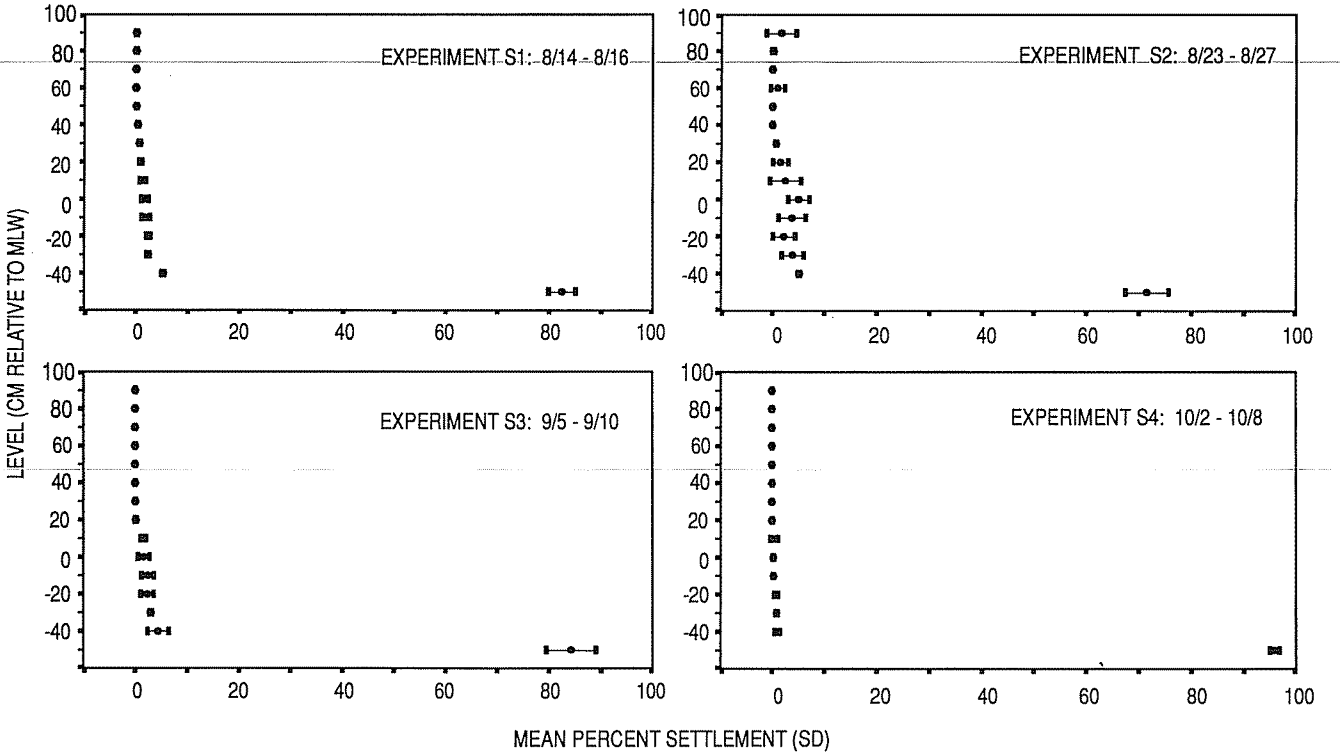

Figure 1. Mean percent settlement per experiment by tidal height (centimeters relative to MLW) ± SD. Experiments S1 to S4.

site where suitable subtidal habitats were scarce, but settlement was typically subtidal at the deep, off-shore sites. An exception to these results can be found in McNulty (1953), who found intertidal settlement to exceed subtidal settlement in two-week long shell bag experiments in Wadmalaw, S.C. At all of these sites adult populations occur in the intertidal zone.

The present study differed from those described above by the use of hatchery-reared larvae exposed to field conditions in microcosms, as opposed to relying on the presence of natural larval abundances. The use of cohorts of larvae spawned from known genetic stock and grown to a comparable developmental stage is advantageous for experimental research because biological variation is limited. The similarity of the results between experiments indicates little possibility of a cohort effect.

Several observations recorded during the data collection are of interest. First, growth, obvious as a "flattening out," or spreading of the posterior margin of the shell, was noted occasionally but the majority of individuals did not appear to have completed metamorphosis. Indeed, "eye spots," characteristic of the immediate presettlement larval form, were still visible in many settled individuals. This observation indicates that the recorded distribution of oysters probably reflects actual settlement patterns and not the effects of post-settlement mortality, which can rapidly alter initial distributions. The presence of metamorphosing

TABLE 3.

Statistical results. One-way ANOVA tables for each of the four settlement experiments. Transformed proportional settlement by tidal height.

Experiment S1					
Source:	df	SS	MS	F	P
Between	14	3.28	0.23	578.1	0.0000
Within	30	0.01	<0.01		
Total	44	3.30			
Experiment S2					
Source:	df	SS	MS	F	P
Between	14	2.56	0.18	41.5	0.0000
Within	30	0.13	0.04		
Total	44	2.69			
Experiment S3					
Source:	df	SS	MS	F	P
Between	14	3.61	0.58	293.0	0.0000
Within	30	0.03	0.01		
Total	44	3.64			
Experiment S4					
Source:	df	SS	MS	F	P
Between	14	5.04	0.36	1020.0	0.0000
Within	30	0.01	0.01		
Total	44	5.05			

df: Degrees of freedom; SS: Sum of squares; MS: Mean square; F: F ratio; P: F probability.

individuals with a growing margin was mainly confined to the subtidal zone. There also was a strong tendency for larvae to settle with the posterior margin of the shell pointing downward and the umbone region oriented up. It is uncertain if this orientation, which occurred at all heights, is indicative of some tube-related effect (i.e., water flow into the tube was from the bottom).

The exact influence of the microcosm tubes on the settlement behavior of the oyster larvae is unknown. Personal observations of the behavior of larvae in tubes in the laboratory do not reveal important detrimental factors other than some swimming inhibition at high larval densities. Conditions within the tubes differ from the natural environment in the lack of horizontal currents in the tubes. At the study site, these currents can approach 30 cm sec^{-1}. Barnacle cyprid settlement has been shown to be influenced by currents (Crisp 1976), and settlement patterns of *Mercenaria mercenaria* (L.) have been demonstrated to change in response to increasing flow velocities (Butman et al. 1988). There is also evidence that oyster larvae distinguish between hydrographic regimes (Hidu & Haskin 1971, Bushek 1988). Studies have indicated that larvae of many species may actively regulate their vertical position in the water column in accordance to tidally-forced changes in current velocity, salinity, or temperature (Wood & Hargis 1971, Mann 1986). Such a planktonic zonation may contribute to the estuarine retention of oysters (Pritchard 1952, Wood & Hargis 1971, Seliger et al. 1982, Andrews 1983, Mann 1988, Ruzecki & Hargis 1989) as well as possible site selection for settlement (H. Hidu, pers. comm.). In the shallow, well-mixed, and vertically homogeneous water column at the study site, larvae may not be able to vertically stratify in the water column until slack water. Turbulent flow may be an important factor for decreasing the sinking rate of negatively buoyant pediveligers. In contrast, the calmer conditions in the settlement tubes would allow the larvae to actively depth regulate by sinking or downward swimming. The observed distribution of settled oysters thus probably reflects larval behavior patterns and not those imposed passively by hydrographic conditions.

The consequence of the observed settlement pattern on the recruitment of oysters is significant. At the experimental locale, the preferred subtidal settlement sites are either not able to be colonized by larvae, perhaps because of competitive exclusion, or the sites are not compatible with oyster survival. On the pilings, the zonal position of the adult populations is relatively high in the intertidal (between about 25–60% exposed per year), while free space exists in the low littoral zone. Additionally, the mean growth rate of juvenile oysters is notably lower in the intertidal zone compared with subtidal locations (Roegner & Mann, in preparation) suggesting that oysters are restricted to a less than optimum habitat by post-settlement predation pressure. Susceptible recruits in the subtidal and low intertidal zones are eliminated from the substrate while individuals higher in the intertidal persist due to lower predation intensity. A number of significant oyster predators (the blue crab *Callinectes sapidus* Rathbun, the drills *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say), and the flatworms *Stylochus ellipticus* (Girard) and *Coronadena mutabilis* (Verrill)) are present at this site and undoubtedly contribute to the maintenance of the observed zonation.

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