

TWO SPECIES OF OYSTER LARVAE SHOW DIFFERENT DEPTH DISTRIBUTIONS IN A SHALLOW, WELL-MIXED ESTUARY

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ABSTRACT The vertical distribution of late stage, or pediveliger, larvae of several bivalve mollusks was examined in a west Florida estuary. The study site was an artificial canal, and the water was shallow (1.5 m) and well mixed, with only modest currents. Pediveligers of three bivalve taxa were collected: the eastern oyster *Crassostrea virginica*; the crested oyster *Ostrea equestris*; and unidentified shipworms (Teredinidae). Despite the shallow and well-mixed water column, larvae exhibited vertical zonation, with most larvae of all three species collected from lower in the water column. The larvae of *C. virginica* and shipworms showed no significant effect of time of day, but larvae of *O. equestris* reversed their distribution pattern at night, with most larvae being near the surface. Pediveliger larvae were not behaving as neutrally buoyant particles but appeared to regulate their depth even in this well-mixed and shallow water column. Given that the larvae of the two oyster species were probably competent to settle, their vertical distribution patterns do not fit what has been reported about their adult depth distribution.

KEY WORDS: *Crassostrea virginica*, estuary, larvae, *Ostrea equestris*, pediveliger, plankton, Teredinidae

INTRODUCTION

A variety of studies over the years have attempted to address the issue of whether larval distribution in estuaries is controlled mainly by hydrologic forces, or whether there is a significant larval behavioral component that also affects distribution. For some crustacean larvae, the case seems to be fairly well made that behavior plays a large part in planktonic distribution, usually (but not always) for late-stage larvae or post-larvae (Shanks 1986, 1995, Benfield & Aldrich 1992, Gherardi 1995).

Bivalve mollusks also have been the focus of studies on larval distribution in estuaries, but there is no consensus in the literature on whether bivalve veligers are distributed as neutrally buoyant particles or whether behavior significantly affects their distribution. Like crustacean larvae, bivalve larvae clearly exhibit oriented swimming, at least in the laboratory (Feeny 1984, Hidu & Haskin 1978). Some field studies have appeared to show nonrandom bivalve larval distribution, relative to hydrodynamic processes (Tremblay & Sinclair 1990, Shanks et al. 2002, Baker & Mann 2003). Compared with crustacean postlarvae, however, bivalve pediveligers are small and slow swimming, and Banse (1986) questioned whether the weak swimming rates observed for these larvae are sufficient to produce distribution patterns. The distribution of bivalve larvae in estuaries may be attributed to hydrodynamic processes alone in some cases, if larvae are treated as neutrally buoyant particles (Wood & Hargis 1971, Mann 1988).

This author examined the above question (i.e., does bivalve larval distribution in an estuary have a behavioral component?) under the most restrictive conditions possible for an estuarine system. The estuarine system in question was simple in shape (an artificial inlet), very shallow, and well mixed throughout the study, although it was a low-energy system. Only late-stage bivalve larvae were included in the study. If bivalve larvae behave as neutrally buoyant particles, their distribution should be fairly even throughout the water column (allowing for boundary-layer effects), and the species should have similar distributions.

MATERIALS AND METHODS

Research was conducted at the Harbor Branch Oceanographic Institute, near Fort Pierce, FL, in May 1993. The study site was about halfway along a 1-km artificial canal that opened into the Indian River Lagoon. The sides of the canal were concrete and steel seawalls, heavily fouled by eastern oysters, *Crassostrea virginica*, and the mean water depth at the wall were about 1 m, gradually increasing toward the center of the canal. The observed currents were mostly tidal, with velocities near the seawalls of 1 to 3 cm s⁻¹, and the tidal range was up to 0.5 m.

Plankton was sampled with two modified 12-V bilge pumps, each rated at 1800 L h⁻¹. Power came from a standard 110-V outlet with a transformer to regulate voltage. Pumps were suspended about 2 m out from the canal wall, where the mean water depth was about 1.5 m. One pump was maintained at a depth of about 20 cm above the bottom, which was determined by preliminary samples to be the maximum depth achievable without entraining significant quantities of sediment. The other pump was adjusted for each sampling episode to a depth of about 20 cm below the surface. Mann (1986) and Møhlenberg (1987) found no avoidance of a plankton pump intake by bivalve mollusk larvae, which swim slowly compared with many zooplankton.

Water from each pump was delivered by a garden hose to a separate sieve on the banks of the canal. Each sieve consisted of a 400- μ m coarse filter and a 150- μ m final filter on which the sample was retained. Plankton was sampled twice daily, at mid-morning (full daylight) and mid-evening (after nightfall), for about 2 h at a time. The volume sampled at each depth was calculated from the time, to the nearest minute, multiplied by the mean pumping rate. The pumping rate was estimated before and after each sample, for each pump, by the time required to fill a 20-L container. (If sampling episodes included high or low water, the pumping rate measurements also were taken then and factored into volume calculations.) Samples were taken into the laboratory, and bivalve larvae were counted and identified to the lowest possible taxonomic level.

The identification of oyster pediveligers (*C. virginica* and *Ostrea equestris*) was verified by collecting newly settled juveniles on shell-strings (Haven & Fritz 1985) that had been immersed at the study site for <24 h, marking individuals, and letting them grow in the canal for several weeks. By the end of this time, *O.*

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equestris shells had developed the diagnostic dorsal-marginal dentition, or chomata (Galtsoff & Merrill 1962).

Only samples that had six or more pediveligers of a given taxa from the two pumps combined were used in the analysis. Data for each pump were converted to proportions of total larvae of a given species collected in a sampling episode and were arcsine-square root-transformed prior to statistical analysis (Zar 1996). Analysis of variance tests were used to test null hypotheses of equal proportions of larvae collected by either pump (top vs. bottom) at either time of day (morning vs. evening), with no interaction (Zar 1996).

RESULTS

Two species of oyster larvae were collected in plankton samples on the majority of days sampled: the eastern oyster, *C. virginica*; and the crested oyster, *O. equestris*. Pediveligers, or late-stage larvae, of these species could be distinguished on the basis of shape (*O. equestris* pediveligers were nearly identical to those of *C. virginica* in size but were more rounded, with a broader, less pronounced umbo). Living pediveliger larvae were clearly distinguishable on the basis of color. *C. virginica* pediveligers at this site were tan to brown and opaque, while *O. equestris* pediveligers were transparent except for their visceral masses, which were green to brown. The only other common bivalve larvae were shipworms (Teredinidae) of unknown species, which were treated in this study as if they were a single taxon. Unidentified pediveligers of other bivalve taxa were occasionally collected.

The abundance of all three species was highly variable, but fairly low. *C. virginica* and *O. equestris* reached peak densities of just over 12 per m³, but teredinids peaked at less than half of that. All three taxa showed peak densities near the beginning of the study. Density data for all three taxa from the lower intake are shown in Fig. 1.

The plankton pumps at the two sample depths did not collect equal densities of larvae, for any species. About 85% of *C. virginica* pediveligers and 75% of teredinid pediveligers were collected from the bottom pump, and time of day had no significant effect. During the day, the distribution patterns for *O. equestris* pediveliger larvae appeared to be similar to the above taxa, but at night 61% of *O. equestris* pediveligers were collected by the near-surface pump. Thus, for *O. equestris*, abundance differed significantly for neither time of day nor depth, but the interaction of depth and time of day was significant at $\alpha = 0.05$. The proportions for each species collected for each time and daylight treatment are presented in Table 1, and the results of the analysis of variance are presented in Table 2.

DISCUSSION

The above study rose serendipitously from an attempt to locate an estuarine environment in which oyster pediveliger larvae (*C. virginica*) were randomly distributed throughout the water column, for a separate study (Baker 1993). Clearly, nonrandom distribution complicates the effort to quantify the larval supply. Yet, even in this highly simplified estuarine environment, in <2 m of water, all three bivalve taxa exhibited strong vertical distribution patterns. The vertical distribution patterns from this study were similar to those observed for *C. virginica* and teredinid larvae in a more complex estuarine environment in Virginia (Baker 1993). The major difference noted from that prior study was the effect of time of day on the distribution of *O. equestris* larvae; no effects of time of

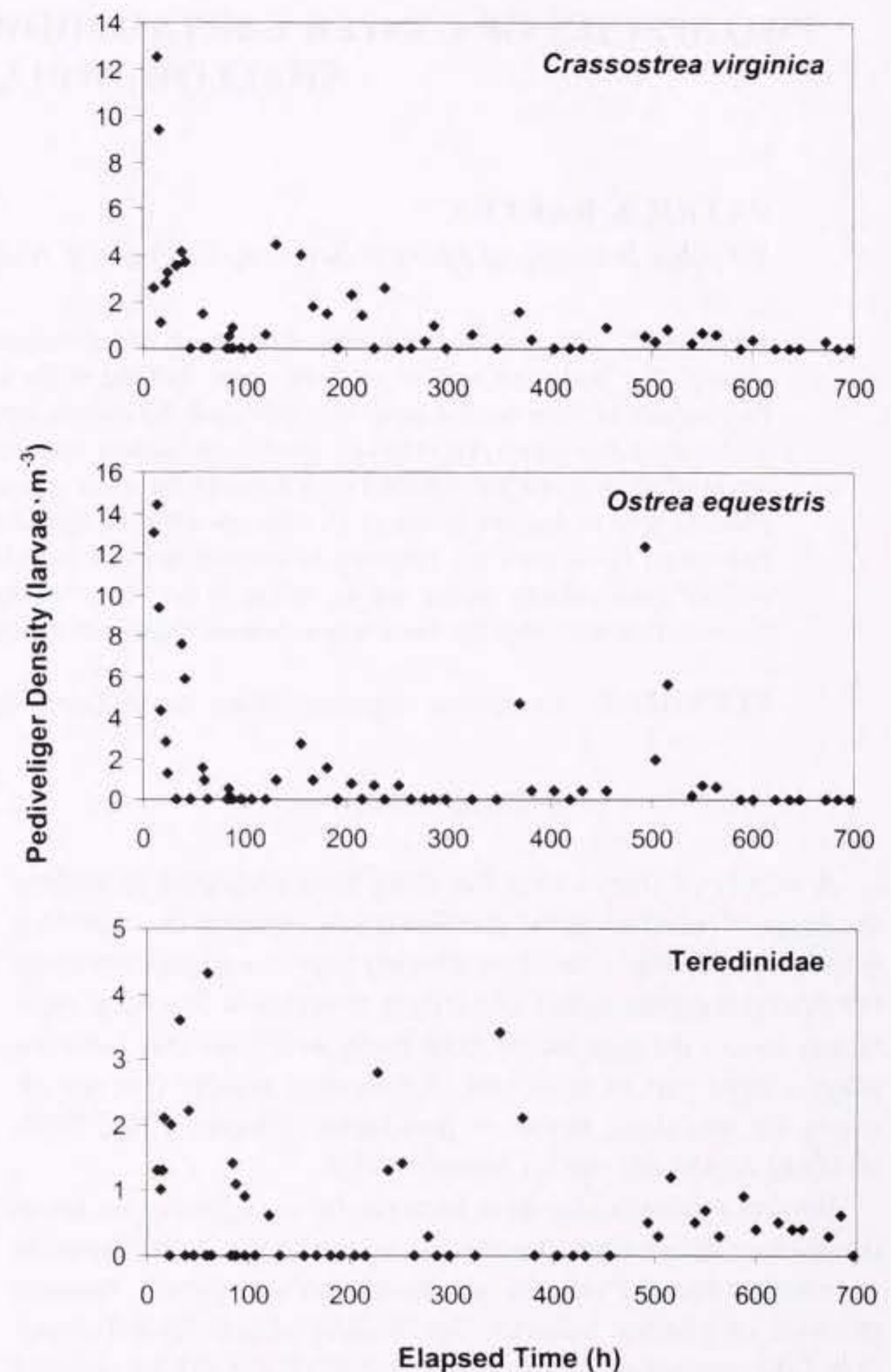


Figure 1. Abundance (density per cubic meter) of three taxa of bivalve pediveligers at the Harbor Branch Oceanographic Institute canal during May 1993, from the near-bottom plankton pump.

day were reported for any species in the Virginia study. The sparseness of pediveliger larvae also was noted by Carrier (1951), who collected only 56 pediveligers from >14,500 *C. virginica* larvae across six samples.

TABLE 1.

Mean proportional (%) abundances of three taxa of bivalve pediveligers at two times (morning vs. evening) and two depths (top vs. bottom) in the Harbor Branch Oceanographic Institute canal during May 1993.

Taxon	Depth	Morning	Evening	All Times
<i>C. virginica</i>	Top	14.6 (18.8)	16.8 (30.3)	15.5 (24.5)
	Bottom	85.4 (18.8)	83.2 (30.3)	84.5 (24.5)
		(n = 19)	(n = 13)	(n = 32)
<i>O. equestris</i>	Top	18.6 (29.4)	61.0 (41.9)	33.2 (38.6)
	Bottom	81.4 (29.4)	39.0 (41.9)	66.8 (38.6)
		(n = 19)	(n = 10)	(n = 29)
Unidentified teredinids	Top	23.2 (39.1)	26.8 (33.4)	24.2 (38.3)
	Bottom	76.8 (39.1)	73.2 (33.4)	75.8 (38.3)
		(n = 20)	(n = 8)	(n = 28)

SDs are given in parentheses.

TABLE 2.

Summary of analyses of variance for the effects of time of day (morning vs. evening) and depth (top vs. bottom) on proportional abundance of three taxa of bivalve pediveligers in the Harbor Branch Oceanographic Institute canal during May 1993.

Source	DF	Seq SS	Adj SS	Adj MS	F Value	P Value
Analysis of variance for <i>C. virginica</i>						
Time of day	1	7.779	7.779	7.779	1.89	0.174
Depth	1	46.685	36.225	36.225	8.81	0.004
Time × depth	1	7.967	7.967	7.967	1.94	0.169
Error	58	238.417	238.417	4.111		
Total	61	300.848				
Analysis of variance for <i>O. equestris</i>						
Time of day	1	10.701	10.701	10.701	1.39	0.244
Depth	1	41.905	15.269	15.269	1.98	0.165
Time × depth	1	52.386	52.386	52.386	6.80	0.012
Error	54	416.069	416.069	7.705		
Total	57	521.062				
Analysis of variance for teredinids						
Time of day	1	0.0161	0.0161	0.0161	0.02	0.898
Depth	1	16.6334	10.9201	10.9201	11.26	0.001
Time × depth	1	0.7875	0.7875	0.7875	0.81	0.372
Error	52	50.4180	50.4180	9.9696		
Total	55	67.8550				

Seq SS = sequential sum of squares; Adj SS = adjusted sum of squares; Adj MS = adjusted mean square.

Several authors have reported the vertical stratification of bivalve larvae in estuaries (Nelson 1927, Perkins 1932, Wood & Hargis 1971, Sekiguchi et al. 1991), although they did not attempt to demonstrate that this was due to larval behavior. Vertical stratification or the migration of bivalve larvae also has been observed in the absence of estuarine stratification (Tremblay & Sinclair 1990, Raby et al. 1994), but those studies were in systems significantly deeper than 1.5 m.

Deksheniaks et al. (1996) modeled *C. virginica* larval distribution in the water column of a well-mixed estuary, and predicted, as observed here, that the majority of late-stage larvae would be within a meter of the benthos. As larvae grow, they sink faster (due to an increased shell/cilia ratio), and the swim-sink behavioral pattern observed for this species by Hidu and Haskins (1978) would result in a net sinking rate for older larvae, according to the model (Deksheniaks et al. 1996). The above model, however, does not include bottom avoidance; larvae must either increase swimming rates in response to the benthos or spend a certain amount of time resting on the benthos. The latter behavior (except for benthic explorations by competent-to-settle larvae: Prytherch 1934, Cranfield 1973) has not been reported, and increased contact with the benthos also exposes the larva to a new guild of predators (Breese & Phibbs 1972, Steinberg & Kennedy 1979, Cowden et al. 1984, Osman et al. 1989, André et al. 1993). It is likely, therefore, that size-related sinking/swimming ratios provide only a partial explanation for pediveliger distribution in *C. virginica*, *O. equestris* pediveligers, which in this study were about the same size as *C.*

virginica pediveligers, were not constrained to the lower reaches of the water column by the weight of their shell, at least not during the night.

If pediveliger larvae were no more than negatively buoyant particles, they could not remain in the water column in a low-energy environment. If they were neutrally buoyant particles, they would be distributed evenly in a well-mixed water column. None of the species observed in this study were evenly distributed, and one species (*O. equestris*) differed from the others, altering its depth distribution on a diurnal cycle. Thus, while neutral buoyant models may be sufficient to describe broad distribution patterns (Wood & Hargis 1971, Mann 1988), ciliated larvae are clearly not inert particles, and species-specific larval behavior must be invoked to describe at least some scales of distribution.

ACKNOWLEDGMENTS

Funding for this study was provided by the Commonwealth of Virginia through the Virginia Institute of Marine Science Bivalve Ecology program. The Smithsonian Marine Station (then at Linkport) and the Harbor Branch Oceanographic Institute (HBOI) graciously provided us with the use of their facilities for this study. Technical assistance was provided by Sherry Reed and other members of the Smithsonian Marine Station staff. Gratitude is also expressed to the alligators in the HBOI canal for restraining their territorial and predatory tendencies when I had to enter the water at night to service equipment.

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