Settlement and early post-settlement survival in the recruitment of *Mulinia lateralis* (Bivalvia)*

Mark W. Luckenbach

Belle W. Baruch Institute for Marine Biology and Coastal Research
and
Department of Biology, University of South Carolina, Columbia, South Carolina 29208, USA

ABSTRACT: Recruitment of benthic invertebrates involves settlement and early post-larval survival. In soft-sediment habitats these 2 events generally have not been distinguished despite the fact that they may lead to different interpretations of the processes affecting recruitment. Settlement and early post-larval survival of the bivalve *Mulinia lateralis* (Say) in a natural infaunal community were recorded and the 2 phenomena distinguished. *M. lateralis* settled in large numbers (514 0.01 m^{-2}) into an intertidal infaunal community characterized by high but variable densities of the tubicolous polychaete *Diopatra cuprea* (Bosc). Settlement density was variable but did not differ between sites with and without *D. cuprea* tubes. Early post-larval (within 1 mo) survival/persistence was lower in sites with high densities of *D. cuprea* and in sites which were bounded by high densities of *D. cuprea* than in sites without *D. cuprea*. Rapid changes in *M. lateralis* abundance after settlement and differential survival between microhabitats led to distribution patterns which after 1 mo differed substantially from initial settlement patterns. Attempts to evaluate processes which lead to observed recruitment patterns must first distinguish between these 2 events.

INTRODUCTION

Recruitment patterns play an important role in determining community structure. The process of recruitment into a habitat consists of at least 2 components: (1) arrival in the habitat and (2) early survival in the habitat (Thorson, 1966). Only recently, however, has this distinction been made in data collection for sessile hard substrate benthos (Grosberg, 1981: Keough and Downes, 1982) and for mobile epibenthos (Fretter and Manly, 1977; Sarver, 1979; Cameron and Schroeter, 1980; Highsmith, 1982). Processes occurring during these phases generally have not been distinguished in marine infaunal communities, and recruitment has been defined operationally as settlement followed by post-settlement survival and growth to a size retained on a sieve, often ≥ 500 µm (but see Williams, 1980a, b for an exception in a gravel habitat). In order to understand processes which affect recruitment and subsequent population structure it is necessary to distin-

guish between patterns of settlement and early post-settlement survival.

Settlement of benthic invertebrates may be affected by several factors: (1) larval availability (Thorson, 1966; Hannan, 1981; Grosberg, 1982), (2) active selection by settling larvae (reviewed by Meadows and Campbell, 1972; Scheltema, 1974; Crisp, 1976; Lewis, 1977), and (3) passive accumulation and dispersion of settling larvae (Hannan, 1981; Eckman, 1983). Frequently, observed patterns of recruitment are attributed to settlement and inferences are made concerning one of these factors (but see Keough and Downes, 1982 for an exception). Sampling methods used are, however, seldom adequate to detect settlement events. Two conditions must be fulfilled in order to observe settlement patterns of benthic invertebrates (Williams, 1980a). First, settlement-sized individuals must be observed which, in soft sediments, requires that small sieve sizes be used. Second, the time between settlement and sampling must be small. Both of these conditions are met rarely in recruitment studies of marine infaunal benthos.

Mulinia lateralis (Say), a small infaunal bivalve, is an opportunist that has highly variable annual recruit-

ment (Boesch, 1973; Boesch et al., 1976; Virnstein, 1977). Such variability could result from year-to-year differences in larval availability and settlement, or in variation in post-settlement survival. Here I report on the recruitment of *M. lateralis* into a heterogeneous, intertidal, soft-bottom community and distinguish between the patterns of settlement and early post-settlement survival as a function of the heterogeneity

STUDY SITE

The study site was located on a low intertidal mud-flat along Debidue Creek in the North Inlet marsh near Georgetown, South Carolina, USA (33° 19′N, 79° 10′W). Surface salinity in Debidue Creek ranged from 30 to 35 ‰. The habitat into which this recruitment event was recorded is characterized by high but variable densities of the tube-building onuphid polychaete *Diopatra cuprea* (Bosc). The large, conspicuous tubes project above the sediment surface and add considerable structural heterogeneity to the habitat. A 10×50 m portion of the mudflat contains a large number of *D. cuprea* tubes ranging from 0 to 15 tubes 0.01 m^{-2}. The sediment is sandy mud with median grain size = 148 μm (2.76 phi); silts and clays (< 63 μm) comprise 12 % by weight. Because access to the marsh is limited, the study site was undisturbed.

INITIAL FINDINGS

Initial sampling revealed that juvenile *Mulinia lateralis*, ranging in shell length from 200 to 700 μm with a modal size of 350 μm, were less abundant at sites with *Diopatra cuprea* tubes than at sites without worm tubes. Sites with high densities of worm tubes ($\geq$ 10 · 0.01 m^{-2}) had a mean density of 22.3 · 0.01 m^{-2} ± 18.5 (SD) (N = 4) juvenile *M. lateralis* while sites without *D. cuprea* had mean densities of 145 · 0.01 m^{-2} ± 13.1 (SD) (N = 4) juvenile *M. lateralis* (Student's *t*-test, $p = 0.01$). The differences in abundances between the sites may reflect variation in settlement or in very early mortality. The goal of this research was to distinguish between these possibilities.

METHODS

Nearly 100 % of *Diopatra cuprea* tubes contain live worms, and old unoccupied tubes are easily recognized by color and texture (Mangum et al., 1968; own obs.). Tubes provide an accurate means of counting these worms, and hereafter, reference to tubes indicates occupied tubes. Four types of sites were selected

for sampling based upon the densities of *D. cuprea* (Fig. 1). Local sample sites were approximately 0.01 m^2 and contained either high densities of *D. cuprea* ($\geq$ 9

Fig. 1. *Diopatra cuprea* density treatments. LL: low regional, low local densities; LH: low regional, high local density; HL: high regional, low local densities; HH: high regional, high local densities

tubes) or no *D. cuprea*. The area of the sites are approximate because natural clumps of *D. cuprea* vary in size and shape. Sites were selected with clumps as close to 0.01 m^2 as possible. Subsampling procedure, described below, standardized estimates of post-larval densities within these sites. In addition, the 0.25 m^2 regions around these sites were characterized as having either high ($\geq$ 25 tubes) or low ($\leq$ 3 tubes) densities of *D. cuprea*. The combination of local density (high or none) with regional density (high or low) resulted in 4 treatments of natural densities of *D. cuprea* (Fig. 1). These 4 spatial arrangements of *D. cuprea* tubes were used to permit distinction between local and regional effects of the tubes on the settlement and survival of *Mulinia lateralis*. Ten regions of the mudflat with *D. cuprea* densities corresponding to each of the treatments were located and labelled in the spring of 1981 prior to the settlement of *M. lateralis*.

To detect settlement of *Mulinia lateralis*, plankton and benthos samples were taken beginning May 1981 at daily or not less frequently than 4d intervals. Two plankton samples, taken with 2 min oblique tows using a 102 μm mesh net (50 cm diam. mouth) were sorted for bivalve larvae. A malfunctioning flowmeter caused estimates of larval abundance to be qualitative only. Replicate samples of surface sediment, taken near the treatments, were sieved on 105 μm mesh screen and examined. Density estimates for larval and post-larval *M. lateralis* were based upon counts per subsample (replicate 2 ml aliquots for plankton and one 8.2 cm diam. Petri dish for benthos) and were ranked from 0 (none present) to 4 (very abundant). Since the intent of these samples was to reveal the time of settlement and not the relation between larval and post-larval abundances, relative density estimates were adequate.

Identification of post-larval *Mulinia lateralis* was accomplished by rearing field collected individuals in the lab until they were easily identifiable (> 500 μm). Attempts to maintain larvae through metamorphosis were unsuccessful. Pediveligers were identified by comparison with early post-larval bivalves and with

Chanley and Andrews (1971). Larval and post-larval identification was aided by low diversity of bivalves in the study area at the time.

Shortly after settlement (4 to 8 d), 5 replicates of each treatment were sampled to determine settlement abundances and distribution of *Mulinia lateralis*. All samples were taken from the central 0.01 m² region of the treatments using a 1.5 cm diam. core. Eight such cores were taken within each treatment replicate for a total of 40 cores treatment. One month after the initial sampling, the remaining 5 treatment replicates were sampled in the same fashion to determine early post-settlement survival. All samples were preserved in the field in 10 % buffered formalin with Rose Bengal stain. Samples were sieved on a 105 μm screen, and all *M. lateralis* juveniles were counted and measured to the nearest 40 μm with an ocular micrometer.

A 2-way nested analysis of variance (Sokal and Rohlf, 1969) was used to test the effects of local and regional densities of *Diopatra cuprea*. The combined treatment effect was represented by the cross term between the local and regional densities. Replicate cores were nested within treatments. Appropriate *F*-tests were determined using expected mean square errors derived by the method of Kirk (1982, p. 390). Where significant effects were observed, Scheffé *a posteriori* Multiple Contrast Tests (Sokal and Rohlf, 1969) were performed to identify significant differences among means.

RESULTS

Mulinia lateralis settlement occurred in a distinctive pulse of 1 to 4 d (Fig. 2). Larvae first appeared in plankton samples on May 30 and were among the most abundant members of the plankton in samples taken on May 30, June 1 and June 6. Benthic samples from June 1 until June 9 contained only occasional *M. lateralis*. Samples taken on June 13 had relatively
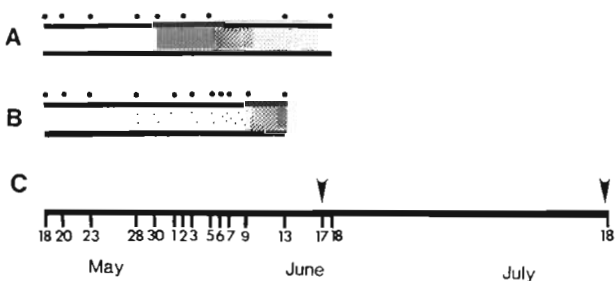

Fig. 2. *Mulinia lateralis*. Occurrence of larvae and post-settlement juveniles. (A) Planktonic larvae; ● actual sample dates; degree of shading: qualitative density estimates. (B) Benthic spat, same symbols. (C) Quantitative benthic cores; arrows: sample dates

lower densities of *M. lateralis* larvae in the plankton and high densities of metamorphosed juveniles (i.e. without velum) in surface sediments. Settlement of *M. lateralis* therefore occurred primarily between June 9 and June 13.

Half of the treatments were sampled on June 17, the first day after settlement with sufficiently low tides. These samples, taken within 4 to 8 d after settlement, had mean abundances of *Mulinia lateralis* within the treatments ranging from 488 · 0.01 m⁻² to 563 · 0.01 m⁻² (Table 1A). ANOVA indicated that there was

Table 1. *Mulinia lateralis* abundance (mean ± SD × 0.01 m⁻²) in each *Diopatra cuprea* treatment. (A) June 17, 4 to 8 d post-settlement; (B) July 18, approximately 35 d after settlement. Means based on 6 to 8 1.5 cm diameter cores per site at 5 sites per treatment for a total of N samples per estimate. In B, means connected by a vertical line are not significantly different by Scheffé *a posteriori* Multiple Contrast Test (*p* ≤ 0.05)

(A) Treatment-*Diopatra* density	*Mulinia* abundance	N
Low local Low regional	572 ± 312	39
Low local High regional	501 ± 293	39
High local Low regional	540 ± 254	33
High local High regional	496 ± 210	37

(B) Treatment-*Diopatra* density	*Mulinia* abundance	N
Low local Low regional	255 ± 77	40
Low local High regional	158 ± 25	40
High local Low regional	105 ± 33	40
High local Low regional	159 ± 34	40

no effect of treatment or its components, local and regional *Diopatra cuprea* densities, on *M. lateralis* abundance (Table 2A). However, there was a significant amount of variation between replicates of the treatments (Table 2A).

Modal size of *Mulinia lateralis* sampled on June 17 was 190 μm. This is assumed to be very close to the actual settlement size for 2 reasons: (1) very few smaller juveniles were ever collected, including the June 13 samples, and (2) pediveligers ranged from approxi-

mately 150 to 190 μm. There was no difference ($p > 0.1$, Kolmogorov-Smirnov test; Hollander and Wolfe, 1973, p. 219) in the size composition of *M. lateralis* within the treatments (Fig. 3). Size frequencies of *M. lateralis* within treatments with *Diopatra cuprea* were pooled and reported as 'High Density Diopatra' (Fig. 3) to facilitate comparisons with later abundance data.

Samples taken 1 mo later, on July 18, showed that *Mulinia lateralis* abundances had declined in all 4 treatments, with means ranging from $105 \cdot 0.01 \text{ m}^{-2}$ to $255 \cdot 0.01 \text{ m}^{-2}$ (Table 1B). ANOVA revealed a very significant ($p < 0.005$) effect of the local × regional cross term, i.e. the combined treatment term (Table 2B). Mean *M. lateralis* abundances in the three treatments with *Diopatra cuprea* differed from that in sites without *D. cuprea* ($p < 0.05$; Scheffé Multiple Contrast Test). In the 3 treatments containing *D. cuprea*, *M. lateralis* abundances averaged only 55 % of the abund-

Table 2. Modified 2-way nested ANOVA tables. trt: treatment or local × region cross term. Significance levels: ns $p \geq 0.05$; • $p \leq 0.05$; •• $p \leq 0.005$. (A) Analysis of data 4 to 8 d post-settlement. (B) Analysis of data approximately 35 d after settlement

(A) Source	df	Sums of squares	F	
Local density	1	7.38636	0.03	ns
Regional density	1	18.77778	0.27	ns
Local × regional	1	1.53436	0.01	ns
Replicates within trt	16	2016.77089	4.64	••
Error	139	3363.53214		

(B) Source	df	Sums of squares	F	
Local density	1	51.55507	0.96	•
Regional density	1	4.47619	0.08	ns
Local × regional	1	53.83789	12.89	••
Replicates within trt	16	66.82363	0.94	ns
Error	139	620.85714		

ance in the treatment with no *D. cuprea*. Variation between replicate treatments was not significant (Table 2B). Size frequency data revealed that growth in sites without *D. cuprea* and sites with *D. cuprea* (3 treatments with tubes pooled to reflect *M. lateralis* abundance differences) did not differ, modal size being 230 μm in each (Fig. 4). However, numbers in the smaller size classes were greatly reduced in the treatments with *D. cuprea* compared to treatments without *D. cuprea*.

DISCUSSION

Recruitment of *Mulinia lateralis* may be viewed in 2 phases in this study: (1) initial recruitment including settlement and a few days post-settlement, and (2) an early post-settlement period of 31 d. The distribution and abundance of *M. lateralis* at the end of the initial phase (4 to 8 d post-settlement) is presumed to be similar to that of settlement, suggesting that settlement abundance was unaffected by the presence of *Diopatra cuprea* tubes. Early post-settlement mortality was high in all treatments (Table 1), but greater in sites with *D. cuprea* than in site without *D. cuprea*. The result was a spatial pattern of recruitment substantially different from that at settlement.

Artificial and defaunated substrata have been used in recruitment studies (e.g Jackson, 1977; Sutherland and Karlson, 1977; Dean and Hurd, 1980; Kay and Keough, 1981; Eckman, 1983) to delimit the time of
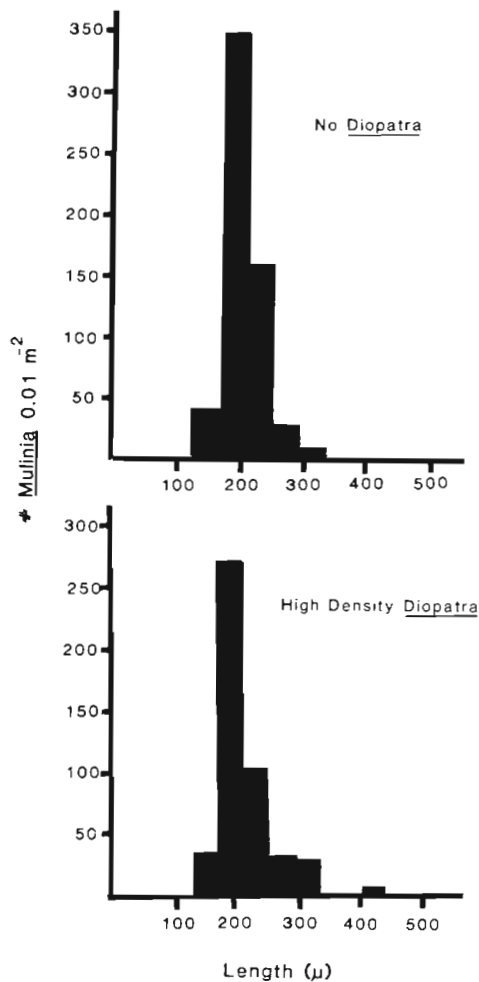

Fig. 3. *Mulinia lateralis*. Size-frequencies on 17 June, less than 1 wk after settlement. The 3 treatments containing *Diopatra cuprea* are pooled and reported as 'High Density Diopatra'

settlement (all recruits must have settled after introduction or defaunation of the substrate). The interval between introduction or defaunation and sampling is often 1 mo or more. Where shorter intervals have been used and the time of settlement more precisely established (McCall, 1977; Grosberg, 1981; Keough and Downes, 1982; Zajac and Whitlatch, 1982; Eckman, 1983) early post-larval mortality has been observed to affect recruitment patterns. Close observation of settlement into natural communities, however, requires fre-

Fig. 4. *Mulinia lateralis.* Size-frequencies on 18 July, 4 to 5 wk after settlement. The 3 treatments containing *Diopatra cuprea* are pooled and reported as 'High Density *Diopatra*'

quent sampling beginning prior to the settlement event.

Most *Mulinia lateralis* settlement in this study occurred between June 9 and June 13 (Fig. 2). Samples taken on June 17 are therefore a maximum of 8 and a minimum of 4 d post-settlement. Mean densities of 514 juveniles 0.01 m^{-2} over the 4 treatments indicate a substantial settlement of *M. lateralis* that was highly variable over the study site, leading to differences among the replicates. The variability was not associated with the presence of *Diopatra cuprea* tubes (Table 2A). Eckman (1979, 1983) found that simulated tubes, singly and in arrays, enhanced larval settlement as a result of hydrodynamic effects, a phenomenon that did

not occur with *M. lateralis* larvae around *D. cuprea* tubes.

The overall reductions in *Mulinia lateralis* densities observed approximately 1 mo after settlement (Table 1B) may be the result of mortality or emigration (passive and/or active movements). The decrease in *M. lateralis* density was accompanied by a reduction in the variability within a treatment, i.e. between replicate variance decreased (Table 2). Muus (1973) similarly found that spatial variation in the recruitment of several bivalve species leveled off after settlement. The reduced abundances of *M. lateralis* in the 3 *D. cuprea* treatments relative to abundances in the treatments without *D. cuprea* (an increase in between habitat variance) must result from processes subsequent to settlement. Whereas the actual magnitude of differences in *M. lateralis* abundances between treatments was small, these differences arose after only the first month post settlement. The data listed under 'Initial Findings' reveal that this pattern of differential abundances becomes accentuated with time.

The precise cause of the reduced *Mulinia lateralis* abundances in the vicinity of *Diopatra cuprea* tubes is not clear. *D. cuprea* itself is unlikely to be responsible, because the treatment containing no *D. cuprea* locally but with high regional densities showed the same reduced abundances of *M. lateralis* as did the treatments with high local abundances of *D. cuprea* (Table 1B). *D. cuprea* forages to a large extent on the epibiota of its tube cap (Mangum et al., 1968), and although individuals will sometimes feed on the sediment surface, this is unlikely to have accounted for the reduced *M. lateralis* abundances where *D. cuprea* is locally absent.

Explanations of community structure based on the effects of established community members on recruitment (Rhoads and Young, 1970; Woodin, 1976; Wilson, 1980; Watzin, 1983) have emphasized post-larval interactions. Virnstein (1977) demonstrated with the use of exclosures that the failure of *M. lateralis* to recruit at some sites in the Chesapeak Bay may result from post-settlement predation/disturbance rather than failure to settle. Poor survival of newly-recruited *M. lateralis* in the vicinity of *D. cuprea* tubes may have resulted from predation/disturbance by other infauna in the community. Alternatively, sites with high densities of tubes may be areas of reduced sediment stability (Eckman et al., 1981), leading to resuspension and washout of small juvenile bivalves in such areas.

The above findings show the hazard of inferring settlement patterns based upon the distribution of early-stage juveniles. The rapidity with which abundance patterns changed indicate not only that young, small individuals must be observed, but also that the time of settlement must be known if we wish to distinguish
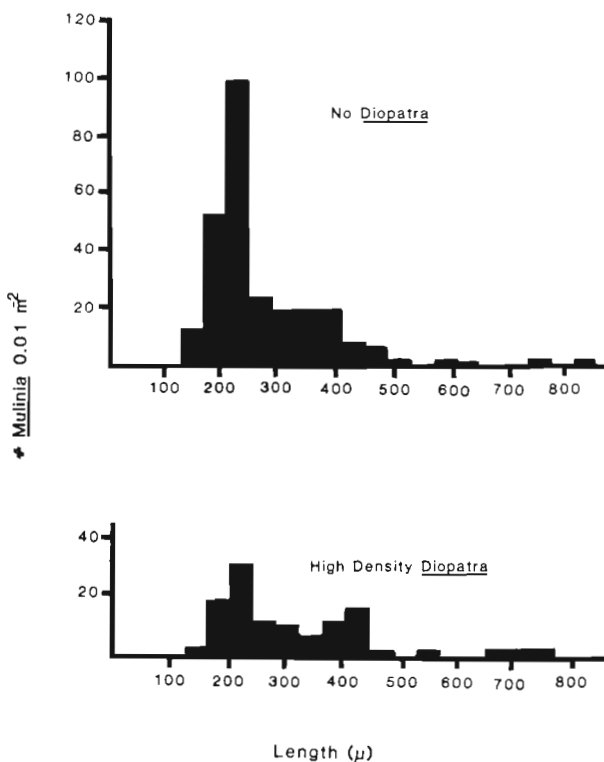
between settlement and post-settlement processes and to discern their effects on subsequent populations structure.

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