



## CHAPTER 12

### POSTSETTLEMENT DISPERSAL AND DYNAMIC REPOPULATION OF ESTUARINE HABITATS BY ADULT *MERCENARIA MERCENARIA*, ST. CATHERINES ISLAND

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Jennings and Hunt (2009: 76) note that “post-larval or juvenile dispersal is important because for many species this is a last chance to migrate to their adult location (Hiddink and Wolff, 2002) as mobility often decreases with increasing size.”<sup>2</sup> Postsettlement passive transport and recruitment of nonsessile bivalves under rigorous hydrodynamic conditions is not a new observation, although it was little explored back in 1991 when Emerson and Grant described it for populations of *Mya arenaria* and when we initiated study of selected *Mercenaria mercenaria* populations on St. Catherines Island. Since the early 1990s, postsettlement dispersal has been documented in several other bivalve species, including *Macoma balthica*, *Gemma gemma*, *Corbicula japonica*, *Austrovenus stuchburyi*, and *Macomona liliana* (Gunther, 1991; Norkko et al., 2001; Hunt and Mullineaux, 2002; Petuha, Lundquist, and Pilditch, 2006; Bowen and Hunt, 2009, among others). These studies have documented postsettlement transport of juvenile bivalves (see discussion by Jennings and Hunt, 2009), either the result of resuspension in the water column or bedload transport (e.g., the dispersal of small juveniles of the New Zealand tellinid *Macomona liliana* over distances of several kilometers on a single spring tide and the bedload transport of larger juveniles over tens of meters on a single tide; Petuha, Lundquist, and Pilditch, 2006). Hunt, Fugate, and Chant (2009) noted that even bedload transport of juvenile bivalves could achieve, over time, cumulative net displacements of kilometers. Many studies have also noted that postsettlement dispersal of some bivalve species can also be influenced by morphology and

behavior, such as the depth of burrowing, the employment of byssal threads (Beukema and de Vlas, 1989), and the use of mucoid drogue lines (Prezant and Chalermat, 1984). Significant postsettlement dispersal of sedentary adult bivalves has seldom been reported, although as early as 1955 Dow and Wallace described storm-induced large-scale passive redistribution of intertidal populations of *M. mercenaria* in coastal Maine.

#### DYNAMIC REPOPULATION OF ESTUARINE HABITATS OF ST. CATHERINES ISLAND BY ADULT *MERCENARIA MERCENARIA*

Two decades ago we documented patterns of postsettlement transport and repopulation on St. Catherines Island by large adult clams inhabiting the Engineers Point West *Mercenaria mercenaria* populations in the fringing marsh adjacent to Walburg Creek and nearby Northwest Marsh, and within point bars along Long Creek (Prezant, Rollins, and Toll, 1990a, 1990b, 1992, 1997; Prezant et al., 1994a, 1994b; Rollins, West, and Busch, 1990; Rollins, Yu, and Busch, 1990; H.B. Rollins, Sandweiss, and J.C. Rollins, 1990; Rollins, Prezant, and Toll, 1990a, 1990b; 1992; 2008; this volume, fig. 12.1).

In 1989, we established along Engineers Point West three 3.5 × 6.0 m quadrats (A, B, C) that encompassed 60 m of an overwash area adjacent to a high-energy levee of Walburg Creek at the northwest margin of St. Catherines Island (figs. 12.2–12.4). All quadrats were at a midintertidal position and arranged sequentially, A–C, downstream from a small tributary channel draining



Fig. 12.1. Aerial photograph of Engineers Point West, St. Catherines Island. Map from Google Earth™, 2010.

Northwest Marsh. Elongated oyster patch reefs lined a significant portion of the Walburg Creek side but were never included within the quadrats. Specimens of *Mercenaria mercenaria* were abundant in the sand substratum aproning a dense stand of medium to tall fringing *Spartina alterniflora*. Clams were often several centimeters below the sand surface, sometimes nestled against dense *S. alterniflora* roots. During a single low tide interval in August 1989, each quadrat was mapped via laser level and elevations were recorded, at 0.5 m intervals, to the nearest centimeter below a U.S. Coast and Geodetic Survey benchmark. Twelve hours later each quadrat was totally defaunated of clams, also during a single low tide period. Following a complete tidal cycle, the quadrats appeared to have recovered from the collection efforts. Approximately 100 of the collected clams were marked, measured, and weighed, and then replaced randomly within each quadrat. The quadrats were revisited in January 1990, October 1990, and February 1991. During

the subsequent visits each quadrat was remapped, and all clams within the quadrats were harvested, measured, weighed, and aged (via annual growth ring counts). Recruits were sequentially numbered and replaced in each quadrat, along with those of the original and subsequent collections. To assess reproductive maturity, 20 clams were randomly collected during the August 1989 and January 1990 visits from areas adjacent to each quadrat. Gonads were examined by standard histological procedures, following fixation in Helly's fluid. Although all clams were removed from the quadrats during each visit and only marked individuals were replaced, all three quadrats contained unmarked adult clams at each harvest. We did not attempt to assess intraquadrat spacing and density of individuals. Numbered individuals were randomly replaced in the quadrats. Very few juvenile clams were collected at any of the quadrats during the harvests. Laser leveling data were used to construct contour maps of the substrata (contour interval = 2 cm). Isoleth maps



Fig. 12.2. Photographs, at low (left) and high (right) tides, of the fringing marsh along Walburg Creek and the Engineers Point West quahog-monitoring quadrats described in this study.

showing net changes in terms of erosion and aggradation were prepared for each quadrat (figs. 12.5–12.7). The isopleth maps display only the net gain or loss of substratum at the termination of the experiment and do not accurately describe the short-term dynamic changes of each quadrat. Table 12.1 presents the net change in population structure of each quadrat for the entire two-year study period. The cumulative mean length of clams from all quadrats increased over time. The mean size of harvested clams from all quadrats, as measured by total length, provided evidence of selective movement of smaller-sized adult hard clams. For all quadrats the mean length of immigrants was 49.36 mm and the mean length of emigrants was 56.17 mm. Individuals that remained within the boundaries of the quadrats for the duration of the study (statics) averaged 61.27 mm in length. Table 12.1 also records the demographic flux per quadrat. The greatest population loss, as assessed by a percent of the original population, occurred at quadrat C (emigration loss = 62%). Quadrat C also sustained dramatic substratum change during the course of the study due to erosional ravinement and loss of sand over about one-half of the surface. At this site an exposed oyster shell lag was impenetrable by infaunal clams. The lowest emigration loss (40%) was recorded for quadrat B. Although there was significant repositioning of the sand veneer at quadrat B, the substratum remained suitable for burrowing clams. Similar emigration loss (43%) occurred at quadrat A. Immigration gain, measured as a percent of recruits to the original

population, was 29%, 57%, and 74% at quadrats C, B, and A, respectively. Quadrat A represents the most southerly station and the closest to the tidal channel draining Northwest Marsh.

Analysis of variance (ANOVA) comparisons of total lengths of immigrants, emigrants, static individuals, and the original population, for all three quadrats, resulted in differences significant at or above the 95% confidence level between immigrants and emigrants, between immigrants and static individuals, between immigrants and the original population, between emigrants and static individuals, and between static individuals and the original population (table 12.2). Statistically significant differences were not demonstrated between the emigrants and the original population. The average number of individuals per quadrat at the end of the monitored interval (101.33) approximately equaled the original number of individuals (96.67) per quadrat. Note, however, that the final number of individuals at quadrat C was 64 compared to 129 at quadrat A (table 12.1).

Adult clams recovered adjacent to the quadrats were sexually mature and about equally divided between males and females at different stages of pre- and postspawning activity. Subsamples of recruits within the quadrats were also sexually mature.

Overall, quadrat A experienced aggradation of up to 20 cm of sand in spite of localized erosion and shoreward regression of *Spartina* cover concomitant with the development of increased ebb tidal drainage. Erosional scour of up to 20 cm of sand substratum in the southwestern por-



Fig. 12.3. Photograph of portion of Long Creek point bar at low tide, near quahog mark and recapture study site discussed in text.

tion of quadrat B was balanced by about 20 cm of aggradation in the northeastern portion. *Spartina* distribution was only slightly affected by these substratum changes. Quadrat C underwent major net change over the interval studied. Erosional scour was pronounced over the entire quadrat, denuding the western portion of sand and exposing an underlying oyster shell lag. Concurrently, the *Spartina* cover retreated shoreward.

Realizing that their observations at Engineers Point might be considered a localized anomaly associated with a rare confluence of hydrodynamic factors, Prezant, Rollins, Toll, and Skoog performed a comparable mark and recapture experiment over the same time period in Long Creek, on the eastern side of the island (Prezant et al., 1994a, 1994b). They used one of a sequence of point bars located in the ebb-flow dominated tidal creek (fig. 12.3). A runnel occurs on the marsh side of the point bar. Twenty-eight hard clams were collected from the runnel, marked, and replaced. An additional 51 clams were collected from the point bar surface, also marked and replaced. After five months, 65 of 79 clams were recovered; all losses were from the surface of the point bar and none was lost from the low-energy runnel. The latter represents a re-

gion of turbulent flow along the point bar and a likely “catchment” area. Tidal creek point bar sites typically have larger clams than the wash-over fringing marsh zones represented by Engineers Point, and are also subjected to strong channel-side tidal flows with ebb current velocities as high as 1.1 m per second (Howard and Frey, 1985). The average length of clams recovered from Long Creek point bar was 92.1 mm; those lost from the system averaged 86.6 mm in length; those adults recruited into the mouth of the runnel averaged 90.0 mm in length.

## DISCUSSION

As noted by Kraeuter et al. (2009: 273), “It is generally believed that hard clam recruitment ... is controlled by interactions between larval supply, post settlement predation, and substrate composition.” In fact, most traditional views of recruitment of benthic marine organisms involve the addition of larval or small juvenile cohorts to established populations with a focus on larval competence, metamorphosis, and ultimate settlement (Sale, 1990). This conventional model of recruitment does not satisfactorily account for the observations of hard clams at Engineers Point.



The rapid population replacement by adult clams following within-quadrat loss of adults demanded an explanatory model that involved wholesale movement of otherwise sedentary adult bivalves. Moreover, the agent(s) of dispersal had to be employed frequently. The relatively rare event of stochastic rafting via slumping along oversteepened tidal creek banks or by tidal current “plucking” of mud clasts did not adequately explain the rapid recolonization by only adult clams. Movement of blocks of rooted *Spartina alterniflora* substratum does occur sporadically on St. Catherines Island, in association with the larger ebb tidal deltas. Such so-called “peat reefs” could be involved with abortive recolonization of *Mercenaria mercenaria* on patches of relict marsh mud along high-energy beaches (West, Rollins, and Busch, 1990). In the experimental sites, the highest emigration and lowest immigration clearly occurred at quadrat C, which correspondingly experienced the greatest substratum change. It is more likely that the clams were transported in a saltational manner associated with specific hydrodynamic events such as episodic storms, probably in combination with the effects of dominant ebb tidal flow velocities. Rarely, marked clams were found entrapped within adjacent surface oyster bars, demonstrating the likely saltational redistribution of these adult bivalves. A number of recent studies have established that, for a given energy sys-

tem, there is a threshold size above which clams escape the combined effects of erosion, entrainment, and transport (Norkko et al., 2001; Hunt et al., 2007; Jennings and Hunt, 2009). For Engineers Point, that size is approximately 61 mm shell length. In higher energy regimes threshold sizes could be even larger.

Postsettlement transport and dispersal of bivalves (either juvenile or adult) invites discussion of potential adaptive strategies. Is postsettlement transport of clams obligatory or facultative? Or both? Consideration of potential adaptive strategies that might aid in postsettlement survival of infaunal bivalves has understandably focused upon depth of burrowing and shell size. Other factors (e.g., siphonal length and access to surface waters) notwithstanding, larger bivalves are generally presumed to burrow deeper than smaller bivalves, and thus are better able to escape predation, and, for many species, the degree of postsettlement mortality is assumed to be a major aspect of recruitment success or failure (Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Jennings and Hunt, 2009; Kraeuter et al., 2009). Jennings and Hunt (2009) point out that juvenile invertebrates are often vulnerable during early postsettlement and suggest that both vertical (burrowing) movement and horizontal (transport) movement at this time may afford critical opportunities for successful migration to adult

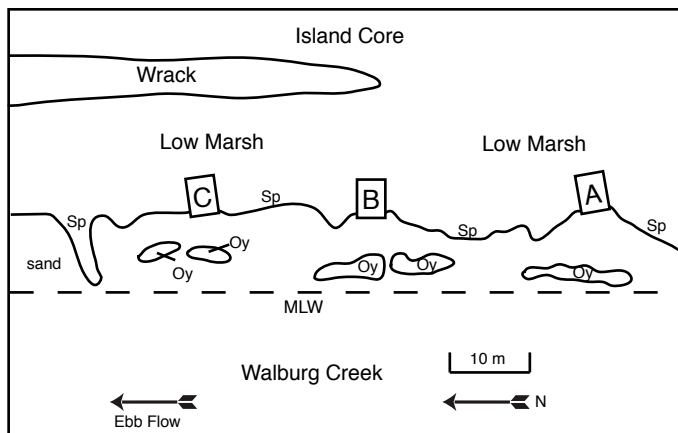
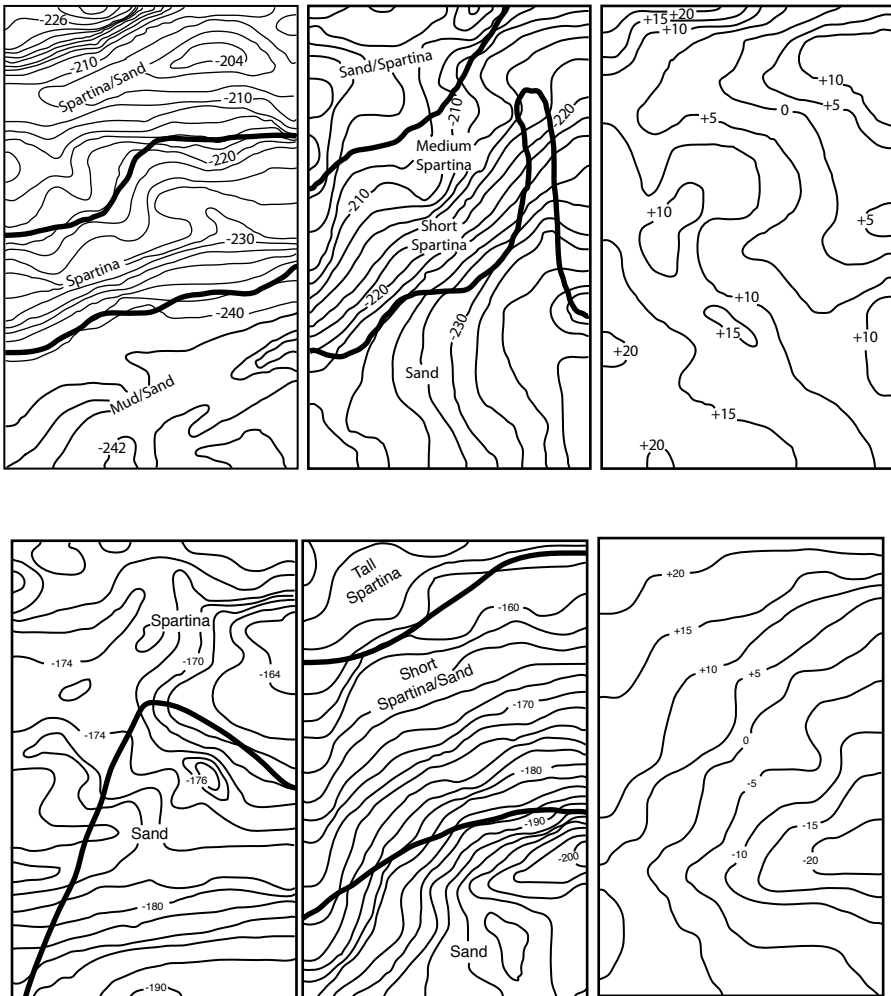


Fig. 12.4. Schematic map of Engineers Point West hard clam stations A, B, and C (adapted from Rollins, Prezant, and Toll, 2008).. Sp = *Spartina*; Oy = oyster patch; MLW = mean low water. Quadrats measure 3.5 x 6.0 m.

locations. In this regard, based on flume and field experiments, they demonstrated that “juveniles of several bivalve species are transported as bedload over distances up to tens of centimeters per hour” and noted differences in distance of juvenile dispersal related to differences in species hydrodynamic properties (e.g., density, fall velocity), but the results varied among experiments (Jennings and Hunt, 2009: 84). Uncertainty surrounding

the nature and potential adaptive significance of postsettlement transport of bivalves can be seen in a study by Huxham and Richards (2003). In an attempt to assess habitat selection by intertidal postlarval infaunal bivalves, they found that secondary settlement (i.e., relocation) by *Cerastoderma edule* and *Macoma balthica* demonstrated no ability to select sediment type, and therefore “must be related to other mechanisms,



Figs. 12.5, 12.6. Laser-level contour and isopleth maps showing substrate change at Engineers Point West *Mercenaria mercenaria* stations A and B, between Aug. 1989 (left) and Feb. 1991 (center). Figure 12.5 (top) details quadrat A, contour interval = 2 cm.; figure 12.6 (bottom) details quadrat B, contour interval = 2 cm. Contour interval of isopleths maps (right) = 5 cm..

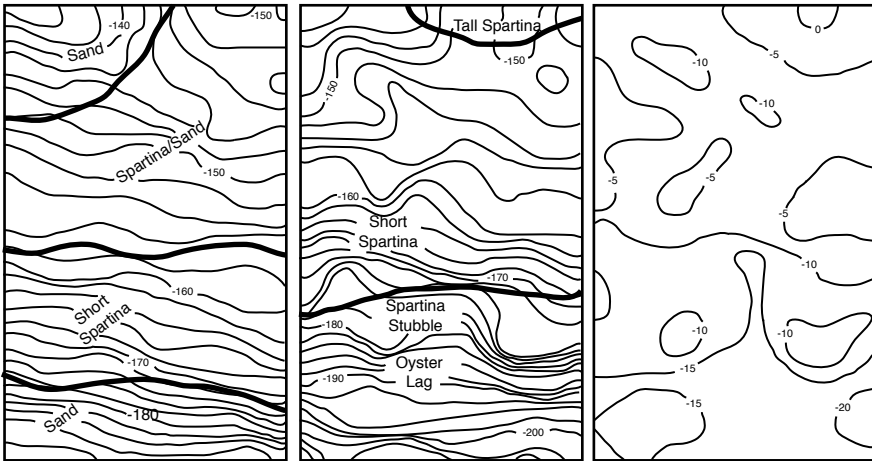


Fig. 12.7. Laser-level contour and isopleth maps showing substrate change at Engineers Point West *Mercenaria mercenaria* station C, between Aug. 1989 (left) and Feb. 1991 (center). Contour interval = 2 cm. Contour interval of isopleth map (right) = 5 cm.

possibly postsettlement predation ... and/or an ability to leave less-preferred sediments in a series of migrations until the preferred habitat is found” (Huxham and Richards, 2003: 279). We suggest that a more parsimonious explanation might be one focused upon repeated, but passive, hydrodynamic entrainment (i.e., obligatory, not facultative).

Petersen (1986: 200–201), in a study of *Mercenaria mercenaria* occupying seagrass beds in North Carolina, posed the question: “To what degree can a given biological pattern be explained as a passive response to physical phenomena without need to invoke an active biological mechanism?” and he attempted to help “resolve the controversy in marine benthic ecology over whether settlement or subsequent survivorship determines various population and community patterns.” He documented a statistically significant increase in the density of adult *M. mercenaria* individuals in seagrass beds compared to the settlement density (0-year-class recruits) of this species, and attributed this between-habitat density disparity to differential survival and not to physical transport and baffling by the seagrass beds. He speculated that differential survival was due to differential predation, stronger

in areas where the clams were not protected by vegetational root systems. Roberts et al. (1989) suggested that vertical migration, as seen in *M. mercenaria*, during ebb tides, could help prevent erosional exhumation of clams but those clams nestled among *Spartina* roots remain in place without deeper burrowing. Storm events and increasing pore water pressures, however, might bring clams to a shallower infaunal position, making them more vulnerable to entrainment and transport. Peterson’s argument against the efficacy of physical transport as an explanation for the observed pattern in density distribution hinged upon his evaluation of the hydrodynamic energy necessary to remobilize settled clams. He concluded that “physical transport of 5–25 mm clams in the Back Sound study site is highly unlikely,” citing Baggerman (1953) who “showed that physical transport of the bivalve *Cardium edule* virtually ceased when individuals reached a length of 2 mm in an intertidal locality of higher energy than the subtidal sites here.... The actual current velocities measured at the Back Sound study sites during spring tides peak at only 7 cm per sec...an order of magnitude less than the required velocities” (Petersen, 1986: 203).

Our survey of the literature revealed only

TABLE 12.1  
**Actual Numbers and Average Lengths of the Original, Static, Emigrant, and Immigrant Populations of Hard Clams in Individual Quadrats along Engineers Point West**

Quadrat	Immigrants		Emigrants		Statics		Original		Population total
	<i>N</i>	$\bar{x}$ mm	<i>N</i>	$\bar{x}$ mm	<i>N</i>	$\bar{x}$ mm	<i>N</i>	$\bar{x}$ mm	
A	73	55	42	57.9	56	65.5	98	58.2	129
B	54	45	38	54.5	57	58.9	95	56.1	111
C	28	48.1	60	56.1	36	59.4	97	56.6	64
$\bar{x}$	51.67	49.36	46.67	56.17	49.67	61.27	96.67	57.3	101.33

TABLE 12.2  
**Statistical Analysis of *Mercenaria mercenaria* – Engineers Point West  
 Post Hoc Analyses Performed on the Results of a One-Factor ANOVA  
 for Repeated Measurements ( $F = 23.926$ ;  $p < 0.001$ )**

Comparison of total length	Mean difference	Fisher PLSD	Scheffe F-test
Immigrants vs. emigrants	6.81	3.504 <sup>a</sup>	7.539 <sup>a</sup>
Immigrants vs. statics	11.91	3.504 <sup>a</sup>	23.06 <sup>a</sup>
Immigrants vs. original population	7.943	3.504 <sup>a</sup>	10.258 <sup>a</sup>
Emigrants vs. statics	5.1	3.504 <sup>a</sup>	4.228 <sup>a</sup>
Emigrants vs. original population	1.133	3.504 <sup>a</sup>	0.209 <sup>a</sup>
Statics vs. original population	3.967	3.504 <sup>a</sup>	2.558 <sup>a</sup>

<sup>a</sup>Significant at 95% confidence level.

one specific documentation of passive movement (and relocation) of fully grown adult hard clams, that of Dow and Wallace (1955). In 1949, they discovered two widely separated “residue” populations of the 1947 *M. mercenaria* recruitment in Maquoit Bay, Maine, and, in 1950 they initiated a detailed study of clam distribution in one of these populations. Detailed survey revealed marked redistribution of clams in the size range 27–56 mm (median diameter = 43 mm), correlated with patterns of storm activity. They noted that the remnant and redistributed population suffered 40.3% mortality over the study interval, but its areal coverage was enlarged from 3.28 acres to 6.81 acres.

Prezant, Rollins, and Toll (1990a, 1990b, 1997), Prezant et al. (1994a, 1994b) and Rollins, Prezant, and Toll (1990a, 1990b) suggested that

the hard clam repopulation dynamics presented above for Engineers Point and Long Creek might provide an additional explanation for some previous observations of the distribution and population structure of hard clams along coastal Georgia. In this region, population age class structure often lacks a range of year classes (Walker and Tenore, 1984; Walker and Rawson, 1985). This is particularly common along higher-energy habitats, such as fringing marshes along large tidal creek levees and the point bars in larger tidal creeks. Lower energy sites (e.g., ponded marsh habitats and small “gut” creeks) more often harbor cohorts with numerous age classes. Although missing year classes are generally attributed to either the vagaries of larval settlement or extreme selective harvesting/predation, Walker and Tenore (1984) suggested that passive movement



of larger adult clams, as observed in their study, may also be added to the list. It might be useful to consider the distribution of *Mercenaria mercenaria* on St. Catherines Island in terms of metapopulations and patch dynamics. *M. mercenaria* is widely distributed among different habitats on the island. Age classes differ among habitats with the oldest (and largest) clams in lower energy, muddy, larger tidal creeks. Younger and intermediate-sized clams are found along the higher energy and sandier intertidal stretches of fringing marshes. Lastly, hard clam populations along coastal Georgia have been reported to exhibit heterozygotic deficiency (Humprey, 1981), usually explained in terms of capricious larval dispersal and recruitment in a heterogeneous environment. These heterozygotic deficiencies, however, could be explained by stochastic adult repopulation without significant larval broadcasting, an extension of the fine-scale genetic heterogeneity noted by Johnson and Black (1984) in larval recruitment of the pulmonate limpet *Siphonaria jeanae*.

### CONCLUSION

The fate of postsettlement juvenile and adult bivalves under varying physical conditions has, we believe, significant meaning for the rather pervasive, if not reigning, paradigm of "supply-side" ecology (Lewin, 1987; Roughgarden, Gaines, and Pacala, 1987). Supply-side ecology predicts that larval recruitment would produce a series of age (size) classes reflecting the variable success of adult reproductive events. While certainly the dominant controlling factor for sessile biota, the numerous reports of recruitment patterns for several other sedentary (but not permanently attached) marine organisms document irregular or unpredictable settlement patterns that cannot be explained by small (planktonic) propagules (Sinclair, 1987; Beukema and de Vlas, 1989; Jokeil, 1989; Emerson and Grant, 1991; Gunther, 1991; Martel and Chia, 1991). General trends in recruitment as well as variability are discussed by Sale (1990) who emphasized that larval behavior, correlated with environ-

mental regime, largely controlled recruitment. The idea that ocean hydrodynamics can impact population distributions, especially of juvenile infaunal macrofauna, has more recently begun to be explored and there is now considerable evidence of the significance of postsettlement dispersal as a major influence on adult distribution of many groups, including bivalves (Armonies, 1994; Commito et al., 1995; Norkko, et al., 2001; Hunt, McLean, and Mullineaux, 2003; de Montaudouin, 1997; Petuha, Lundquist, and Pilditch, 2006; Bowen and Hunt, 2009).

As noted by Hunt (2005: 143), "Although the existence of juvenile invertebrate dispersal has been recognized for at least 50 yr (e.g., Baggerman, 1953; Smith, 1955), it has received much less attention than larval dispersal, and there are critical gaps in our knowledge of this process." We suggest, based on our studies of hard clam dispersal on St. Catherines Island, that one of the major gaps in our knowledge involves the role of passive dispersal of fully grown adults. In particular, these stochastically redistributed and reproductively mature bivalves can help support and sustain locally dispersed metapopulations. The relative roles of larval recruitment, postsettlement juvenile dispersal, differential survival, and adult movement (both passive and active) have yet to be assessed under varying hydrodynamic situations. As discussed by Emerson and Grant (1991) for the softshell clam *Mya arenaria* and by Rollins, Prezant, and Toll (2008) and Rollins and Thomas (chap. 16, this volume) for the hard clam *M. mercenaria*, the proportional efficacies of these processes also influence our assessments of overfishing and recovery (past and present) of these shellfish resources.

### NOTES

1. Authorship is alphabetical.
2. We thank C. Cleveland, J.C. Rollins, C. Rucker, and R.R. West for extensive assistance in the laboratory and field, Youping Chen for assistance with the histological analysis, and R. Hayes, St. Catherines Island Foundation, for his logistic support and advice. This research was supported by grants from the E.J. Noble Foundation, administered by the American Museum of Natural History.

