



Distances of dispersal of juvenile bivalves (*Mya arenaria* (Linnaeus), *Mercenaria mercenaria* (Linnaeus), *Gemma gemma* (Totten))

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ABSTRACT

Although it is recognized that many species of benthic invertebrates continue to disperse after settlement, particularly in soft-bottom habitats, the scale over which movements of juveniles occur is not well known. This study combined laboratory flume experiments assessing the effects of clam size, species, and water velocity on rates and distances of dispersal of three species of juvenile bivalves with field measurements of loss rates and distances of dispersal of transplanted bivalves in the Navesink River estuary in New Jersey, USA. Dispersal distances measured in the laboratory ranged from an average of 1.6 to 40 cm h⁻¹ depending on clam size, species, and flow speed. Distances and likelihood of dispersal were generally greater for *Mya arenaria* than for *Mercenaria mercenaria* or *Gemma gemma*, although differences between species were not consistent. As predicted, smaller (1.3 mm) *M. arenaria* tended to disperse more than larger (3.7 mm) ones, although no significant differences were detected between two sizes (1.8 and 3.4 mm) of *M. mercenaria*. The similarity of the erosion thresholds of dead clams across sizes and species suggests that burrowing behaviour plays an important role in determining variation in dispersal due to clam size and species. In the field, densities of clams (*M. arenaria* and *M. mercenaria*) were reduced to half of that in controls after 3.5–5 h, indicating high levels of dispersal and/or mortality. Some individuals were recovered up to 50 cm away from their initial locations. Overall, our results suggest that dispersal distances of these three species due to bedload transport are likely to be on the order of centimeters per hour. Although these dispersal distances are small, such movements are likely to occur frequently due to tidal currents and, consequently, may have profound impacts on patterns of abundance and distribution.

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1. Introduction

Early post-settlement events can change the patterns of distribution and abundance of juvenile invertebrates that are set up at the time of settlement (Hunt and Scheibling, 1997). While mortality is a major early post-settlement event that is often examined (e.g. reviews by Gosselin and Qian (1997) and Hunt and Scheibling (1997)), post-larval dispersal of individuals also has the potential to influence recruitment patterns. While dispersal can occur at various times during the life cycle, 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. Post-larval dispersal is likely to be particularly important in soft bottom habitats where organisms cannot anchor themselves to a fixed substrate.

It was recognized over 50 years ago that bivalves experience dispersal after settlement (Baggerman, 1953). While some bivalves are known to actively promote dispersal during the juvenile stage by

using byssus threads to increase drag and cause resuspension into the water column (e.g. Sigurdsson et al., 1976), juvenile bivalves also may be involuntarily moved to a new place as the sediment in which they are living is eroded. Erosion of sediment and transport of the organisms living within it is influenced both by flow speed and by factors influencing the erodability of the sediment: grain size, cohesion of the sediment, presence of biogenic structures and vegetation (Le Hir et al. 2007). Rates of post-larval dispersal of bivalves will further be influenced by their behaviour (burrowing or active emergence, production of threads), which is likely to lead to differences in rates of post-larval transport between species (e.g. Lundquist et al. 2004). Burrowing depth of bivalves is generally negatively correlated with size (Zwarts and Wanink, 1989), increasing the vulnerability of small juveniles to transport. Depending on the bottom shear velocity and the settling velocity of the individual, juvenile bivalves may either be resuspended into the water column (e.g. Sigurdsson et al., 1976; Beukema and de Vlas, 1989; Cummings et al., 1993) or transported as bedload (e.g. Emerson and Grant, 1991).

Large changes in the population dynamics of bivalves can be attributed to post-larval transport (Emerson and Grant, 1991). In a number of systems, rates of turnover of juvenile bivalves due to post-larval dispersal are similar to the ambient density of bivalves, resulting

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in turnover of individuals within one to several days (Armonies, 1994; Commito et al., 1995a; Norkko et al., 2001; Hunt et al., 2007). Frequent dispersal of juveniles also has been observed for other groups of macrofauna such as oligochaetes and polychaetes (e.g. Commito et al., 2005) and meiofauna such as copepods and nematodes (e.g. Commito and Tita, 2002).

Although rates of post-larval dispersal have been described for a number of systems, very little is known about the distances over which bivalves or other benthic invertebrates can disperse as juveniles. Measuring dispersal distances of small individuals in the field is very difficult. Norkko et al. (2001) made field measurements of dispersal distances of juveniles of the cockle *Austrovenus stutchburyi* and the tellinid *Macomona liliana*. The bivalves in their study dispersed at the scale of meters within a tidal cycle on an intertidal sandflat in New Zealand. Scale of dispersal will be affected by whether a particular species is resuspended into the water column (e.g. drifting using threads) or is transported as bedload along with the sediment. For example, Petuha et al. (2006) estimated that, on a spring tide, continually drifting juvenile *M. liliana* could travel up to 3.3 km compared to <80 m for those traveling in bedload. However, even dispersal as bedload is predicted to result in net displacement of kilometers over longer time periods (Hunt et al., in press).

The goal of this study was to examine the likelihood of dispersal and scale of movement of juvenile bivalves in laboratory and field experiments. The three species examined were the gem clam *Gemma gemma*, the hard clam *Mercenaria mercenaria*, and the soft shell clam *Mya arenaria*. These species are common on the eastern coast of North America (Sellmer, 1967; Newell and Hidu, 1988; Kraeuter and Castagna, 2001) and have been noted to disperse as juveniles (e.g. *G. gemma*: Rankin et al., 1994; *M. mercenaria*: Dow and Wallace, 1955; *M. arenaria*: Emerson and Grant, 1991; Günther, 1992; Hunt and Mullineaux, 2002). Juveniles of these species generally disperse as bedload, with transport initiated by sediment erosion (Commito et al., 1995a; Hunt, 2004, 2005; Hunt et al., 2007). Rates of post-larval dispersal are known to be affected by a variety of factors, such as flow speed and sediment characteristics, and to vary between species (e.g. Hunt, 2004). Differences between species may arise both from variation in the physical characteristics of the bivalves (shell shape and weight, fall velocity) and burrowing behaviour. Individuals that do not burrow into the sediment will be entrained at flow speeds lower than the erosion threshold of the sediment, while the likelihood of transport of burrowing individuals will depend both on depth of burial and on speed of burrowing as surrounding sediment erodes. Dispersal is predicted to decrease with increasing bivalve size as individuals become less vulnerable to entrainment by flow (effect of particle size on entrainment threshold: Miller et al., 1977) and burrow deeper in the sediment (Zwarts and Wanink, 1989). Laboratory flume experiments were carried out to measure distances and rates of dispersal of *M. arenaria* and *M. mercenaria* under a variety of flow speeds and for several different sizes of juveniles; *G. gemma* dispersal was compared to that of the other species at a single flow speed. The laboratory experiments were coupled with field transplant experiments using *M. arenaria* and *M. mercenaria* in the Navesink River estuary, New Jersey, USA to assess rates of loss in the field and determine whether individuals could be recaptured to estimate dispersal distances. The laboratory experiments allowed us to test cause–effect relationships under controlled conditions, while the field experiments provided a context of actual rates of dispersal of the same species observed in the field (Friend and Amos 2007).

2. Methods

2.1. Study site

The study site was located in the Navesink River, a 10 km long flood-dominated estuary south of Sandy Hook, New Jersey, USA. A

detailed description of the hydrodynamic regime and biological characteristics of the field sites used in this project is provided in Hunt et al. (2007). The laboratory experiments used sediment from Site 3 while field transplantation experiments were carried out at Sites 2 and 3. The sediment at Site 3 has a mean grain size of 427 μm and an average organic content of 0.80% while Site 2 had a mean grain size of 182 μm and an organic content of 1.5% (Hunt et al., 2007). *G. gemma* made up the majority of juvenile bivalves at Site 3 while 7–83% of small bivalves (<10 mm) in sediment cores collected at Site 2 in 2002 and 2003 were *G. gemma* (Hunt et al., 2007). A variety of other bivalves were found at the sites, including juveniles of *M. arenaria*, *Tellina agilis*, *Lyonsia hyalina*, and *M. mercenaria* (Hunt et al., 2007). In June 2002, mean densities of total bivalves in 2-cm deep cores used to quantify recruitment ranged from 1000 to 55,000 ind. m^{-2} at Sites 2 and 3 (Hunt et al. 2007).

2.2. Clams

M. arenaria, *M. mercenaria*, and *G. gemma* were chosen for use in the laboratory and field experiments. All three species are commonly found in the Navesink estuary. Juvenile *M. arenaria* were obtained from Sandy Cove Hatcheries in Harrington, Maine, USA, while juvenile *M. mercenaria* were obtained from Biosphere Inc. in Tuckerton, New Jersey, USA. Juveniles of *G. gemma* were obtained by collecting sediment from the Navesink estuary, sieving it on a 1 mm sieve, and sorting the remaining material under a dissecting microscope. Prior to experiments, clams were held in plastic containers with 180 μm mesh on the bottom filled with 1 μm filtered seawater at 20 °C in a controlled environment room. The seawater was changed every third day and the containers were constantly aerated. Clams were fed daily with *Isochrysis* sp. and *Tetraselmis suecica* originally obtained from the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP) at Bigelow Laboratories, ME. The algae were cultured in sterilized seawater enriched with Kent ProCulture F/2 algal culture medium.

2.3. Flume

Experiments were carried out in the racetrack flume at the Institute of Marine and Coastal Sciences at Rutgers University, New Jersey, USA (described in Hunt 2004, 2005) during the summers of 2003 and 2004. The oval shaped flume is 620 cm long with a 70 cm wide channel with flow driven by paddles. The flume was filled to a depth of 14 cm with 5- μm filtered seawater at 20 °C and a salinity of 30. Flow speed was measured with a 2-axis (measuring the downstream horizontal and vertical components of the velocity) laser Doppler velocimeter (LDV). For each flow profile, shear velocity (u_*) was estimated from the slope of the vertical profile in the log layer (as predicted by the ‘law of the wall’, Vogel, 1994), as determined from velocities measured at 11–14 heights between 1.8 and 5.0 cm above the bottom. Twenty two flow profiles for free stream velocities of 16–40 cm s^{-1} were used to develop a regression of the relationship between velocity at 9 cm above bottom and shear velocity. This regression was used to convert free stream velocity for each flow speed treatment to shear velocity.

2.4. Critical erosion velocities of clams

Critical erosion velocities of bivalves in the absence of burrowing behavior were determined for three sizes of *M. arenaria*, two of *M. mercenaria*, and one of *G. gemma* (see 2004 flume experiment for sizes of bivalves) by observing erosion of bivalves killed by ethanol. Five clams of each species and size (30 clams total) were dropped through a cylinder onto a flat bed of sediment. Free stream velocity was increased from 10 to 34 cm s^{-1} at 2 cm s^{-1} intervals every 2 min. Clams were considered to have been transported when they rolled out of the circular

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