

## Limited transport and recolonization potential in shallow tidal estuaries

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### *Abstract*

Evidence of limited larval exchange and high levels of self-recruitment in marine populations continues to accumulate, implying that marine systems are not as open as we once believed. In estuaries, some organisms with long larval periods, such as crab and bivalve species, are capable of long-distance transport, while others, including many polychaete and gastropod species with crawling or brooded larvae, lack long-distance larval dispersal mechanisms and may disperse as juveniles and adults. To predict transport rates and colonization potentials of macrofaunal life stages transported in the water column, we use a combined hydrodynamic and particle tracking model. We vary particle release location to investigate how different habitats (i.e., main channel, lower sandflat, high sandflat, tidal creek) will contribute to the supply of colonists in different parts of the estuary. Most particles traveled short distances and settled within their release habitat. Slightly negatively buoyant particles (corresponding to small larvae) traveled much farther than more negatively buoyant particles (corresponding to larger, heavier larvae and juveniles). Particles released from high intertidal locations had lower rates of transport and transfer among habitats compared to lower intertidal sites. Other influences on organism transport include timing of release (with respect to tide), release location within the water column, tidal range, and magnitude of freshwater flood events. In general, estuarine communities dominated by organisms with limited dispersal periods are likely to be recruitment limited and limited in their ability to reach mature community states when subject to increasing frequencies or spatial extent of disturbance.

Evidence continues to accumulate supporting the hypothesis that marine systems are not as open as we have been led to believe (Sponaugle et al. 2002; Swearer et al. 2002). Environmental cues, larval behavior, larval life history, and hydrodynamic forces all influence the likelihood that a larval organism will return to its native environment (Butman 1987; Kingsford et al. 2002; Sponaugle et al. 2002). Physical forces affect recruitment ranging from boundary layer flows and small-scale turbulent processes (Butman 1987; Abelson and Denny 1997; Metaxas 2001) to larger oceanographic scale processes such as climatic conditions, flood events, and coastal upwelling (Sponaugle et al. 2002). Within estuaries, some benthic organisms spend long periods in the water column and are thus capable of being transported long distances to colonize far away habitats (McConaugha 1988). However, many other estuarine community members lack these long-distance dispersal mechanisms (Strathmann 1987; Shull 1997; Grantham et al. 2003), and dispersal within and among habitats is more limited as the amount of time an organism spends within the water column is reduced. Estuary-scale hydrodynamic processes may be particularly important for organisms with restricted dispersal because processes such as tidal currents and flood events influence the potential distance that an organism is transported after entering the water column. Hydrodynamic forces vary within an estuary, such that organisms may be subject to different transport rates

based on the location within the estuary where they enter the water column.

Different modes of transport of larval propagules and postsettlement juveniles strongly influence rates of colonization of disturbed areas in soft-sediment systems (Whitlatch et al. 2001). In hard substrate environments, mussels and barnacles, the most frequent model organisms, have long larval periods and colonization is relatively independent of local communities (Paine and Levin 1981; Caley et al. 1996; Grantham et al. 2003). In contrast, other organisms found in both hard (Olson 1985; Young 1986) and soft substrate (Thrush et al. 1991, 1996) environments have limited larval periods; in these situations, colonization is expected to be strongly influenced by local neighborhoods. Estuarine dispersal mechanisms are varied (Santos and Simon 1980; Thrush et al. 1996; Shull 1997; Turner et al. 1997; Beukema et al. 1999; Whitlatch et al. 2001; Norkko et al. 2002); colonists include settling larvae only in certain seasons, and initial recolonization is often by secondary settlement of juveniles and mobile adult species (e.g., thread-drifting juvenile bivalves [Sigurdsson et al. 1976; Beukema and de Vlas 1989; Cummings et al. 1993] swimming by adult polychaetes and oligochaetes [Dean 1978; Nilsson et al. 2000]). While there are certainly estuarine invertebrate species with long-lived larvae (e.g., most crab and bivalve species, some polychaete species), many estuarine species have short-lived, brooding, or crawling larvae that remain within the estuary throughout their larval life span and disperse relatively short distances, often only within meters of release (e.g., many polychaete species, some gastropod species) (Strathmann 1987; Shull 1997). Recent analyses of soft-sediment intertidal sites in California and Washington show that over 60% of species lack planktonic larval development (Grantham et al. 2003).

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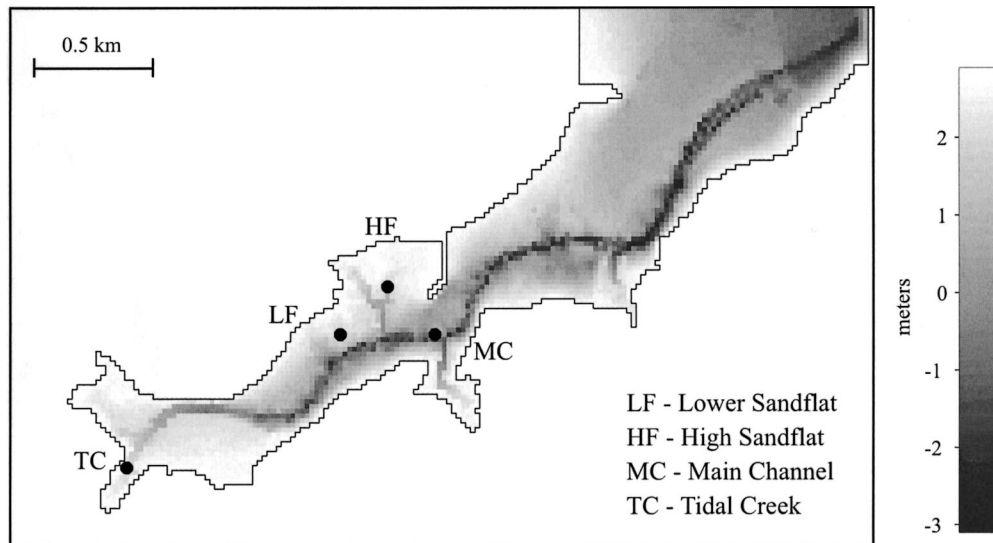


Fig. 1. Bathymetry of Okura estuary, North Island, New Zealand. Depths are relative to chart datum. Particle release locations are tidal creek (TC), lower sandflat (LF), high sandflat (HF), and main channel (MC).

Previous estuarine modeling studies examining larval dispersal and predicted transport in estuaries have focused on the population dynamics and recruitment of single or few species (e.g., Armonies 1996; Ellien et al. 2000). These studies have not examined species with shorter dispersal distances, such as many of the organisms that comprise the primary estuarine infaunal biomass (Grantham et al. 2003). Our goal is to present a broader community-based approach to estuarine transport, examining organisms with differing dispersal potential to evaluate the potential transport and recolonization by an entire community. We present results from a combined hydrodynamic and particle tracking model to illustrate transport differences of our community of dispersers. We demonstrate transport potential using three hypothetical types of dispersing larvae or juveniles to illustrate a range of possible dispersal distances within estuaries. Since disturbance processes such as sedimentation often disproportionately affect different habitats within an estuary, we also examine transport among and within different estuarine habitats.

## Methods

*Study site*—The model simulations were conducted based on the bathymetry of Okura estuary, a small estuary in New Zealand's North Island (36°40'S, 174°43'E) with a relatively simple hydrodynamic regime (Fig. 1). The bathymetry of the Okura estuary was obtained from echo-sounder field surveys, hydrographic charts, and aerial photos (Oldman and MacDonald 1999). The estuary is 600 m wide at the mouth and stretches 3.5 km inland. Okura has one primary tidal channel and is relatively protected from wind and waves. Tidal range is 2.0 m during neap tides, 2.4 m during mean tides, and 3.0 m during spring tides. Sediment grain size ranges from more than 90% fine and very fine sands (63 to 250  $\mu\text{m}$ ) and less than 5% silt and clay particles (<63  $\mu\text{m}$ )

at the mouth through midestuary to levels of up to 25% silt and clay particles closer to the site of freshwater influx (Oldman and MacDonald 1999).

*Hydrodynamic model*—The 3DD suite of computational models (Black 1995; Black et al. 1999, 2000) was used in this study. We used a two-dimensional depth-averaged Eulerian hydrodynamic model, computed on a 20 m by 20 m regular grid, to compute current velocities and water depth, since modifications to the three-dimensional version to allow for wetting and drying of the intertidal landscape were not available. Field CTD (conductivity, temperature, depth) measurements of the water column, demonstrating unstratified profiles with depth over a variety of climatic and tidal scenarios, confirmed that the two-dimensional hydrodynamic model was sufficient (Oldman and MacDonald 1999). To resolve vertical motion of larvae, we simulated three-dimensional movement of particles using POL3DD, a Lagrangian particle tracking model, which partitioned depth into 10 vertical layers. POL3DD calculates variable layer thickness based on tidal variations in depth. Each layer not adjacent to the sea bed is assigned a fixed thickness. The bottom layer thickness is calculated from the cell bathymetry, water level, and sum of the fixed layers above it.

Since the position of each particle is specified by its  $X$ ,  $Y$ ,  $Z$  coordinates, we converted the current velocity predicted by the two-dimensional depth-averaged Eulerian hydrodynamic model to current velocity at a specific elevation above the bed, assuming a logarithmic current profile (Black 1995; Oldman and MacDonald 1999);

$$U(z) = 5.75U_* \log_{10} \left( \frac{z}{z_0} \right) \quad (1)$$

where  $U(z)$  is the velocity at elevation  $z$  above the bed,  $U_*$  is the friction velocity, and  $z_0$  is the roughness length. The

depth-averaged mean velocity  $\bar{U}$  transferred from the two-dimensional hydrodynamic model occurs at 0.37 of the depth,  $h$ , thus,

$$\bar{U} = 5.75U_* \log_{10} \left( \frac{0.37h}{z_0} \right) \quad (2)$$

Substituting  $\bar{U}$  into Eq. 1 and rearranging gives

$$U(z) = \bar{U} \left[ \log_{10} \left( \frac{z}{z_0} \right) / \log_{10} \left( \frac{0.37h}{z_0} \right) \right] \quad (3)$$

The hydrodynamic model predicted depth-averaged current velocities and water depths throughout the estuary. At the open boundary of the model (the estuary mouth), water levels (boundary conditions) based on field measurements using DOBIE (NIWA Instrument Systems, Christchurch, New Zealand) pressure gauges were specified to account for tidal variation. Hydrodynamic model results were calibrated against field measurements from a range of DOBIE and current meter measurements (inside of the estuary boundary) interpolated on to the model grid. The model was calibrated by adjusting the friction coefficient such that measured current velocities matched model output over a range of hydrodynamic conditions, including variations in tidal range and magnitude of flood events (Oldman and MacDonald 1999).

The particle transport model used the velocity and water level fields predicted by the hydrodynamic model to track the movement of hundreds of particles, which represent hypothetical larval or juvenile recruits. Particle movement between grid cells and between vertical layers was calculated as a combination of (1) fall velocity of the particle being modeled, (2) horizontal and vertical water movement, and (3) random diffusion (Black 1995). Diffusion coefficients were estimated by running the model with a range of physically realistic diffusion coefficients to simulate an event during which CTD field measurements were made (Oldman and MacDonald 1999). Calibration of the particle tracking model was most sensitive to vertical diffusion coefficients, with the best fit between model and field data for values given in Table 1a. The model calibrated well against field measurements (using constant diffusion coefficients), often at greater than 90% agreement; thus, we did not include higher resolution field data incorporating tidal variability in diffusivity coefficients. The upper and bottom layers of the water column in the model were considered to be reflective bottom boundaries for random diffusion; thus, settlement does not include contact by turbulent (random) fluctuations, and particle deposition includes only those particles settling after reflection from the bottom layer.

Superposed onto the “random-walk” Lagrangian model is a particle fall velocity term. Different larvae and postsettlement dispersers were simulated by three fall velocities: (1)  $0.0001 \text{ m s}^{-1}$  (lower than reported settling velocities of most invertebrate larvae), (2)  $0.0010 \text{ m s}^{-1}$  (within the range of reported settling velocities of small invertebrate larvae such as polychaetes), and (3)  $0.0025 \text{ m s}^{-1}$  (at the lower range of reported settling velocities of larger invertebrate larvae, such as crabs and bivalves) (Chia et al. 1984). The highest settling velocity was also used to represent postsettlement organisms, e.g., secondary settlement by thread-drifting juvenile

Table 1. Model parameters for the hydrodynamic and particle tracking modules.

a. Constant across all simulations	
Vertical mixing	Well-mixed (unstratified)
Number of vertical layers	10
Maximum layer depth	0.3 m
Model duration	25 h (two tidal cycles)
Longitudinal diffusion coefficient	$0.1 \text{ m}^2 \text{ s}^{-1}$
Lateral diffusion coefficient	$0.1 \text{ m}^2 \text{ s}^{-1}$
Vertical eddy diffusivity	$0.0015 \text{ m}^2 \text{ s}^{-1}$
Uniform roughness length	0.001 m
b. Particle release options	
Particle fall velocity	0.0001 $\text{m s}^{-1}$ (small)
	0.0010 $\text{m s}^{-1}$ (intermediate)
	0.0025 $\text{m s}^{-1}$ (large)
Location of release	Lower Sandflat
	High Sandflat
	Main Channel
	Tidal Creek
Tidal range	Spring
	Mean
	Neap
Magnitude of freshwater inflow	High ( $1.1 \text{ m}^3 \text{ s}^{-1}$ )
	Mean ( $0.4 \text{ m}^3 \text{ s}^{-1}$ )
	Low ( $0.1 \text{ m}^3 \text{ s}^{-1}$ )
Release height (varying based on tidal height)	Lower 5% of water column
	Upper 5% of water column
	Randomly distributed within water column
Release time	High (slack) tide
	Flood tide (maximum incoming tidal current)
	Ebb tide (maximum outgoing tidal current)

bivalves with measured settling velocities of common size classes of drifting bivalves of up to  $1\text{--}2 \text{ cm s}^{-1}$  (Norkko et al. 2001). These fall velocities are referred to as small, intermediate, and large. Particles were considered as passive, i.e., larval behavior was not included in this version of the model, and also conservative, in that all larvae are competent to settle at all times (no larval mortality function was included). Resuspension of the particles from the bed was not included, i.e., once a particle made contact with the estuary floor, it was not able to return to the water column. Through this distinction we include larval release and active dispersal of postsettlement juveniles (e.g., bivalves releasing threads and thus actively entering the water column) but not passive resuspension of juveniles and adults. Particles moving beyond the model boundaries were assumed lost to the system, reflecting biological constraints of time to settlement.

Rather than release particles spread over the entire estuary and track relative percentages settling in each habitat, we instead released particles from various point source locations in order to identify both sources and sinks of colonists as well as to compare transport among habitats. The release points were (1) lower sandflat, (2) high sandflat, (3) main channel, and (4) tidal creek (site of primary freshwater inflow) (Fig. 1). The sites differ in tidal height, distance from

Table 2. Differences in hydrodynamic parameters between the four release locations simulated in the model.\*

Site	Lower Sandflat	High Sandflat	Main Channel	Tidal Creek
Depth above chart datum (m)	1.7	1.6	-0.6	1.2
Water depth (spring high tide) (m)	1.3	1.4	3.6	1.8
Max flood tidal current velocity (cm s <sup>-1</sup> ) (spring)	2.9	9.1	19.1	4.3
Max ebb tidal current velocity (cm s <sup>-1</sup> ) (spring)	3.7	3.5	13.9	2.4
Max flood tidal current velocity (cm s <sup>-1</sup> ) (neap)	1.2	5.7	9.7	1.9
Max ebb tidal current velocity (cm s <sup>-1</sup> ) (neap)	2.0	3.0	10.2	1.4
Mean inundation time, spring tide (%)	42	42	100	58
Mean inundation time, neap tide (%)	38	42	100	54

\* All parameters are averaged over 20 m × 20 m cells.

the estuary mouth and the main channel, and tidal current velocities (Table 2). To demonstrate differences in transport potential among habitats within the estuary for the three hypothetical organisms, we performed simulations of particles with each of the three fall velocities released at each of the four release points within the estuary. To represent sudden release from a point source (i.e., adult spawning, release of brooded larvae, postlarval movement from an unfavorable site), all particles were released instantaneously, during high tide, into the lower 5% of the water column. The movement of each individual was tracked for two tidal cycles (25 h). We monitored the distance moved and the settling location of all particles in each simulation. The settling location was classified into habitats based on estuarine depth (high intertidal, >2 m above chart datum; midintertidal, 1–2 m above chart datum; low intertidal, 0–1 m above chart datum; subtidal channel, below chart datum) in order to estimate relative transport among habitats within the estuary. These habitat classifications have biological relevance, since different communities are often found at different tidal heights within an estuary (Johnson 1970). All simulations were performed with identical conditions of spring tides and mean freshwater influx (0.4 m<sup>3</sup> s<sup>-1</sup>) in order to compare transport differences among all release sites.

To determine the relative effects of the other input parameters of the model on the transport of larvae and juveniles within the estuary, we varied additional aspects of particle release. Since tidal and freshwater flood-generated currents can carry larvae over longer distances and increase the amount of time spent in the water column through turbulent resuspension, we varied tidal range and the magnitude of freshwater flood events to determine the effects of meteorological and astronomical forcing on particle transport (Table 1b). All variations were simulated with an unstratified water column, since CTD field measurements confirmed that even during a large flood event, tidal mixing rapidly broke down stratification of the water column. To investigate the effect on particle transport of different current flow velocities and directions at the time of release and at different release heights (e.g., polychaete species that swim to the surface to spawn), we varied the height of particle release and the timing of release with respect to the tide (Table 1b). This mimics the variation in timing of release and height of release of larvae across species; for example, some species release larvae during ebb tides. Each of these simulations was per-

formed using the high sandflat site as a release point and illustrated using small particles.

## Results

*Lower sandflat*—Model simulations using spring tides and mean freshwater influx scenarios, with particles released into the lower portion of the water column at high (slack) tide, indicate that the majority of particles settled very close to their release points (Fig. 2). At all locations and for all fall velocities simulated, particles settled within one tidal cycle. Dispersion of particles increased with time from release; however, particles with higher fall velocities (intermediate and large) settled within shorter time frames than the small particles. For example, 93% of intermediate particles versus 22% of small particles settled within the first hour from release in this scenario (Fig. 2).

A comparison of the distribution of distances traveled at the lower sandflat site at all three buoyancies demonstrated that increasing fall velocities reduced both the mean distance traveled and the proportion of long-distance dispersers (Figs. 2, 3). The majority of the particles released from the lower sandflat site settled within the midintertidal habitat. Small particles (fall velocity = 0.0001 m s<sup>-1</sup>) were advected farthest ( $\bar{x}$  = 470.0 m,  $s$  = 672.5 m), with those particles remaining in the water column for longer periods of time settling in the subtidal channel and low intertidal habitats. Mean distance traveled was an order of magnitude lower for the intermediate particle (fall velocity = 0.0010 m s<sup>-1</sup>;  $\bar{x}$  = 47.1 m,  $s$  = 45.8 m) and large particle (fall velocity = 0.0025 m s<sup>-1</sup>;  $\bar{x}$  = 21.7 m,  $s$  = 26.4 m) simulations (Fig. 3).

*High sandflat*—Simulations with release points from the high sandflat site showed similar patterns with respect to buoyancy, with small particles dispersing farther than either the intermediate or large particles (Fig. 3). Distances traveled by particles for the small particle, high sandflat site simulation were slightly less than for the lower sandflat simulation, with a mean distance of 312.8 m traveled from the release point, compared to a mean of 470.0 m traveled by settling particles in the lower sandflat scenario (Fig. 3). Transport to other habitats was limited, with the majority of particles released from the high sandflat site settling within either the high intertidal habitat (approximately 50%, 70%,

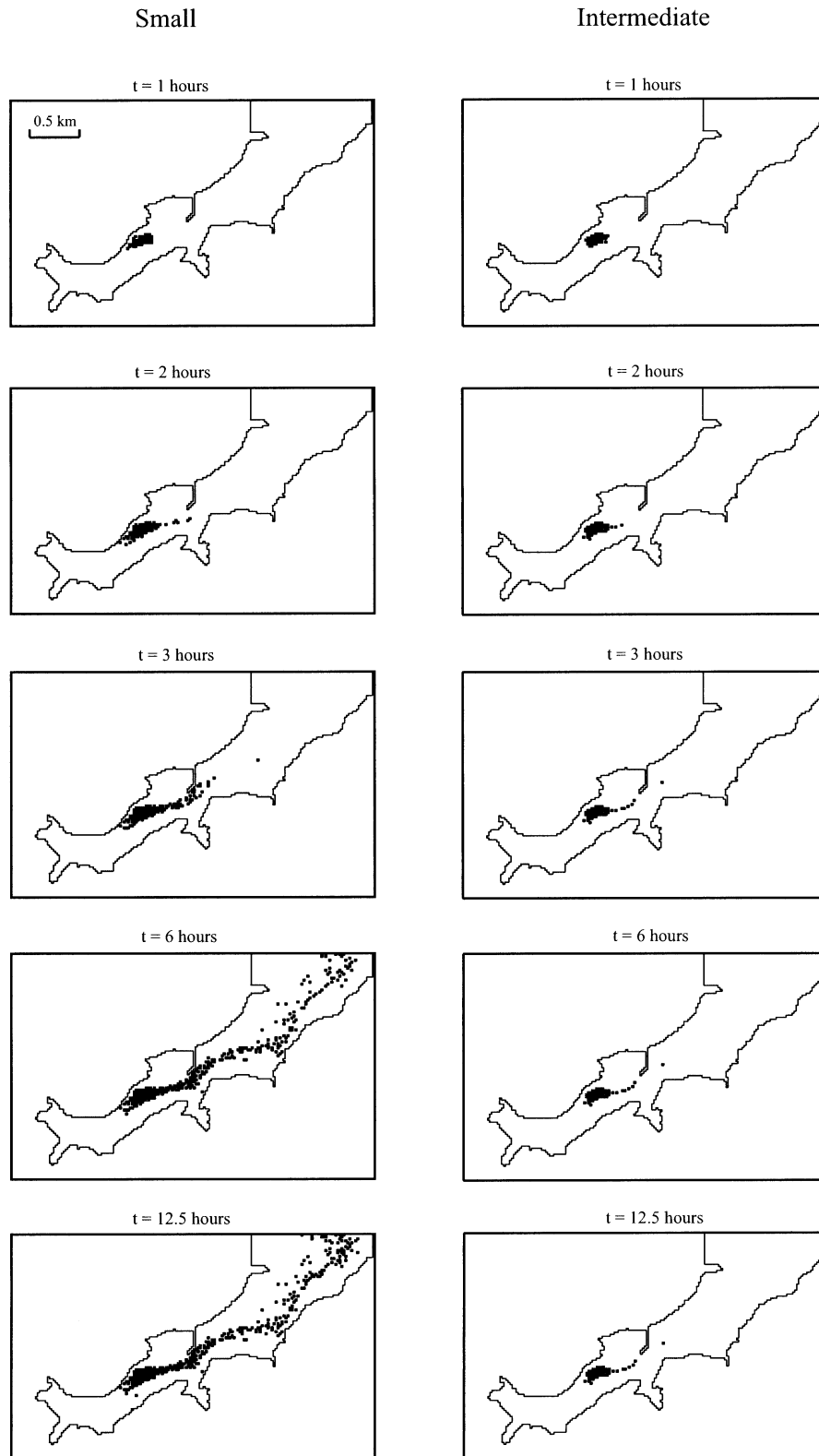


Fig. 2. Time series of a particle dispersion simulation. Particles released into the lower portion of the water column at the lower sandflat site during a spring high tide with mean freshwater inflow ( $0.4 \text{ m}^3 \text{ s}^{-1}$ ). Particles were tracked for two tidal cycles (25 h) using small and intermediate particle fall velocities.

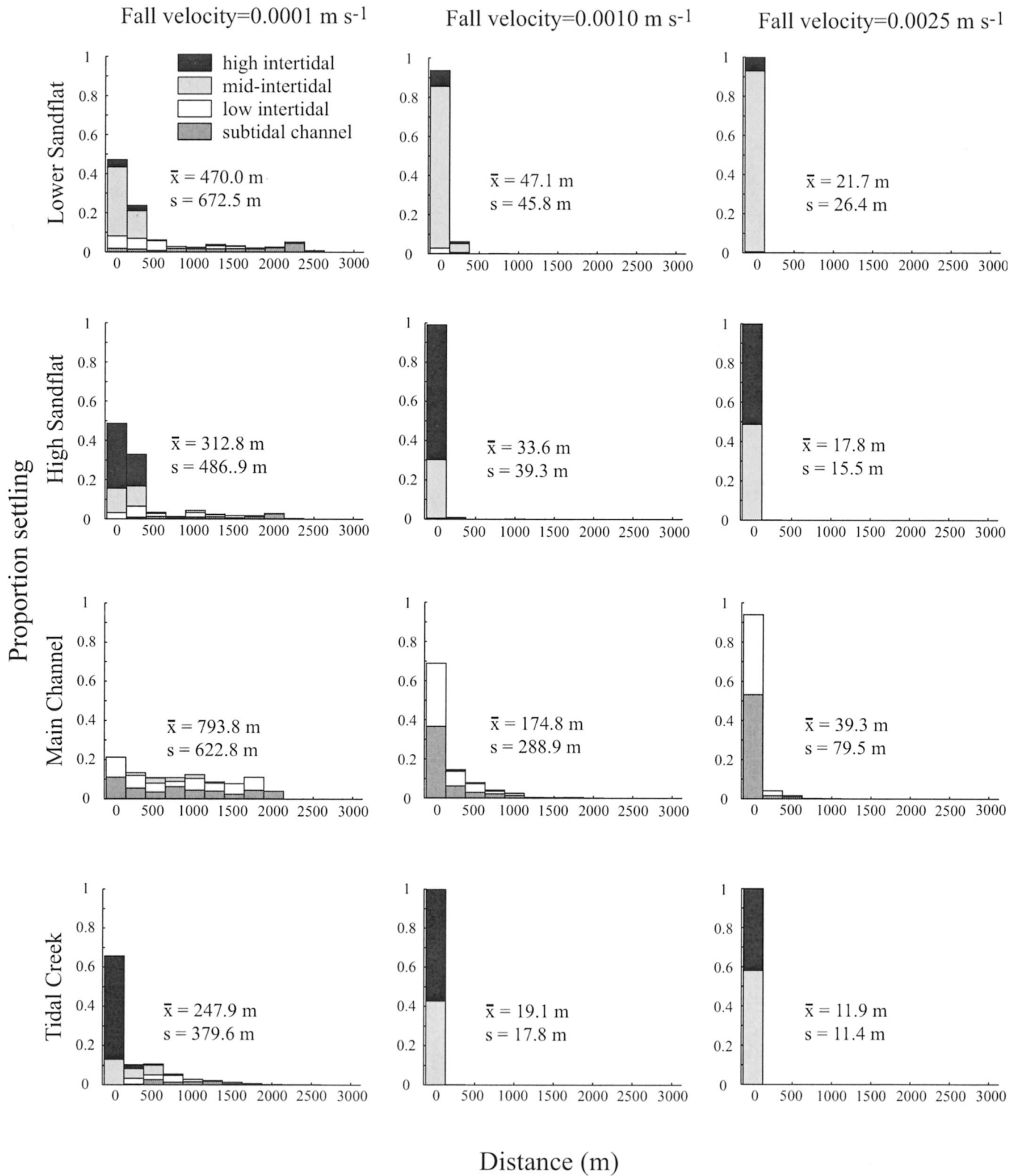


Fig. 3. Particle transport across habitats. Particles released into the lower portion of the water column at the lower sandflat, high sandflat, main channel, and tidal creek sites during a spring high tide with mean freshwater inflow ( $0.4 \text{ m}^3 \text{ s}^{-1}$ ). Particles were tracked for two tidal cycles (25 h) for small (fall velocity =  $0.0001 \text{ m s}^{-1}$ ), intermediate (fall velocity =  $0.0010 \text{ m s}^{-1}$ ), and large (fall velocity =  $0.0025 \text{ m s}^{-1}$ ) particles. Bar heights represent the proportion transported to each subenvironment, classified based on water depth (high intertidal,  $>2 \text{ m}$ ; midintertidal,  $1\text{--}2 \text{ m}$ ; low intertidal,  $0\text{--}1 \text{ m}$ ; subtidal channel,  $<0 \text{ m}$  chart datum).

Table 3. Results of small particle simulations at the High Sandflat site (HF) demonstrating the effects on distribution of distance traveled and proportion of particles transported among habitats for tide and flood conditions, release height, and release time.

	Tide	Flood event	Mean distance (m)	Standard deviation (m)	Median distance (m)	Maximum distance (m)	Proportion high intertidal (>2 m)	Proportion middle intertidal (1–2 m)	Proportion low intertidal (0–1 m)	Proportion subtidal channel (<0 m)
Tide and flood conditions										
Release height: bottom 5% High (slack) tide release time	Spring	High	436.3	552.8	141.4	2,058.5	0.37	0.27	0.11	0.25
		Medium	312.8	486.9	128.1	2,183.6	0.49	0.25	0.10	0.16
Mean	Spring	Low	319.9	514.7	121.7	2,141.4	0.49	0.27	0.10	0.14
		High	243.8	437.7	72.1	2,154.1	0.38	0.33	0.09	0.20
		Medium	141.5	343.1	44.7	2,164.8	0.52	0.32	0.06	0.10
Neap	Spring	Low	68.3	200.2	28.3	2,103.8	0.69	0.24	0.02	0.05
		High	290.9	507.6	82.5	2,047.9	0.37	0.33	0.11	0.19
		Medium	103.1	239.5	28.3	1,869.5	0.61	0.27	0.03	0.09
Low	Spring	High	64.5	155.7	28.3	1,830.5	0.72	0.21	0.02	0.05
		Medium	312.8	486.9	128.1	2,183.6	0.49	0.25	0.10	0.16
		Entire	309.1	494.0	126.5	2,257.4	0.48	0.27	0.10	0.15
Release height										
Spring tide, medium flood event		Bottom 5%	312.8	486.9	128.1	2,183.6	0.49	0.25	0.10	0.16
High (slack) tide release time		Top 5%	302.8	481.1	120.0	2,103.0	0.50	0.28	0.09	0.14
Release time (tide)										
Spring tide, medium flood event		High (slack)	312.8	486.9	128.1	2,183.6	0.49	0.25	0.10	0.16
Release height: bottom 5%		Flood	157.9	217.0	107.7	2,156.5	0.85	0.12	0.02	0.02
		Ebb	112.5	310.2	44.7	2,210.7	0.56	0.34	0.03	0.07

and 50%, for small, intermediate, and large particles, respectively) or the midintertidal habitat (approximately 25%, 30%, and 50% for small, intermediate, and large particles, respectively) (Fig. 3).

*Main channel*—Transport distances for particles released from the main channel site were substantially larger than those particles released from the two sandflat sites (Fig. 3). Less than 25% of small particles settled within the first 125 m of the release point. Dispersal distances were noticeably larger for intermediate and large particles compared to the two sandflat simulations with mean distance traveled of 174.8 and 39.3 m, respectively. However, transport among habitats again appeared to be limited, with most particles settling in subtidal channel and low intertidal habitats.

*Tidal creek*—The tidal creek simulations resembled the high sandflat simulations, with reduced dispersal distances and particle settlement limited to primarily the high intertidal and midintertidal habitats (Fig. 3). Over 65% of small particles, 99% of intermediate particles, and 100% of large particles settled within 125 m of the release point. Mean distance traveled for the three fall velocities in the tidal creek simulations was lowest of all release points, with values of 247.9, 19.1, and 11.9 m for small, intermediate, and large particles, respectively.

Comparing between the four release sites, intermediate and large particle simulations settled on average within less than 50 m of the release point, the exception being for intermediate particles at the main channel sites. Relative to the 600 m by 3.5 km dimensions of the estuary, small particles

were more widely dispersed, with mean distance traveled ranging from 247.9 to 793.8 m.

*Particle release options*—We present simulation results for small particles released at the high sandflat site to illustrate the differences in transport distance and among-habitat transport when varying biologically relevant particle release options (Table 3). Since the small particles spend the largest relative time in the water column of the three particle buoyancies simulated, these comparisons represent the maximum differences in distance traveled by particles among simulations. Meteorological and astronomical variations (combinations of three tidal conditions and three freshwater input levels) demonstrated predictable differences among simulations, with largest transport distances for spring tides and high flood events (Table 3). The range of mean travel distances (64.5 to 436.3 m) was higher than expected, with lowest mean values for low base flow discharge and neap tides and highest mean values for high flood events and spring tides. However, the range of median distance transported was substantially lower (28.3 to 141.4 m) and more representative of the distance traveled by most particles due to the highly skewed nature of the distribution. Effects of meteorological and astronomical conditions on among-habitat transport were generally small, with a minimum of 64% of particles settling within high intertidal and midintertidal habitats with release during spring tides and high flood events and a maximum of 93% of particles settling in high intertidal and midintertidal habitats with release during neap tides and low flood events.

The vertical location of release within the water column

had the smallest effect on transport of all variables tested, with a range in mean distance of less than 10 m and no apparent effect on transport among habitats (Table 3). The magnitude of the effect of release time was larger and similar to that of simulations with varying tidal and flood scenarios, with a difference in mean distance traveled of 200 m between particles released during high tide (slack water) and those released during ebb tide (Table 3). The smallest percentage (16%) of particles was transported outside of the high intertidal habitat when particles were released at flood tide (Table 3).

## Discussion

Estuarine communities include a variety of organisms with different dispersal modes and different subjectivities to transport (Santos and Simon 1980; Shull 1997; Grantham et al. 2003). While a few species have long-distance dispersing larvae, many are restricted in their dispersal abilities and are not readily transported out of the estuary. A community perspective of recolonization processes requires that we focus not only on the long-dispersing organisms, but also on the many shorter dispersers that form the basis for estuarine communities. Our model results imply that most soft-sediment organisms in estuaries and embayments are subject to local dispersal processes and that transport among habitats (i.e., channels, sandflats, tidal creeks) is limited.

Our results support recent studies of larval transport that indicate a high prevalence of self-recruiting populations even when the potential for long-distance transport is high (Swearer et al. 2002). Those sites with limited transport potential such as upper sandflats and tidal creeks are likely to have slow colonization rates for organisms even for small disturbances. Field recolonization experiments have demonstrated slower recovery at upper sheltered sites than exposed sites close to the mouth of Okura estuary (Norkko et al. 2002). For larger scale disturbances, with either a large spatial extent of disturbance or a high frequency of small disturbance events that reduces that proportion of habitat dominated by late successional stages or slowly colonizing species, recovery in the disturbed area will be slow and limited in extent, since all locations are impacted by depletion of the pool of local colonists (Thrush and Whitlatch 2001). The distance from a source of colonists is also predicted to have a substantial influence on the rate of colonization (Thrush and Whitlatch 2001). Sites that are particularly isolated from colonists may be subject to extremely long periods (years) before returning to initial community composition; this prediction has also been supported by field studies (Evans et al. 1999).

All models are a simplification of reality, and we used ours to illustrate general predictions about transport processes within small estuaries. One complexity omitted was that of larval behavior, which might act to increase the amount of time spent in the water column by dispersing larvae and juveniles and/or increase the likelihood of resuspension from unsuitable habitats (Kingsford et al. 2002). Sammarco and Andrews (1989) demonstrated differences in dispersal capabilities between coral species that they attri-

buted to different modes of coral reproduction. Models of the dispersal of coral larvae have also demonstrated differences in dispersal patterns based on the release depths of simulated larvae (reviewed in Sammarco 1994). While many larvae are capable of swimming to orient themselves vertically within different water masses and influence their horizontal transport, turbulent and advective processes dominate larval transport at horizontal scales (Metaxas 2001; Sponaugle et al. 2002). Other modeling studies of larval particles have assumed organisms (e.g., fish, crabs, and polychaete larvae) to behave as passive particles (Blanton et al. 1999; Quinlan et al. 1999). However, studies are accumulating that demonstrate the influence of behavior on larval transport (Kingsford et al. 2002), enhancing the need for more detailed studies of the effects of behavior on larval and juvenile transport.

Our research results support other studies that demonstrate the influence of meteorological and astronomical variables on organism dispersal (Sponaugle et al. 2002). Our model did not include wind-induced particle transport, since Okura estuary is relatively sheltered, resulting in very little wind-induced transport (Norkko et al. 2002). Studies of organism and sediment transport in larger estuaries that are subject to wind-wave disturbances have shown increased transport during periods of high wind-wave activity compared to calmer periods (Commito et al. 1995; Turner et al. 1997). Preliminary modeling of larger New Zealand estuaries, however, has shown similar expected transport distances of hypothetical organisms to that of the smaller Okura estuary, even with added hydrodynamic complexity (Lundquist unpubl. data).

Our approach provided a way to examine the recovery potential of an entire community where recovery is influenced by the supply of different life stages of colonists in the water column. Not surprisingly, dispersal mode (as mimicked by variations in the fall velocity of organism) is particularly important in influencing dispersal distance and individual recovery times of species. Many recolonization studies have shown seasonally delayed recovery of some species that recruit only by larval propagation (Norkko and Bonsdorff 1996; Beukema et al. 1999). The relative importance of nonlarval dispersal stage in estuarine recolonization experiments has been confirmed in numerous field studies, with nonlarval colonization modes including burrowing, adult and postlarval swimming, postsettlement drifting, and bedload transport (Beukema and de Vlas 1989; Cummings et al. 1995; Hewitt et al. 1997; Shull 1997). Understanding the interactions between larval mobility, location of the colonist pool, and connectivity between estuarine habitats is important as we continue to investigate the effects of disturbance at varying temporal and spatial scales.

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