



12-1995

# Dispersal Dynamics in a Wind-Driven Benthic System

John A. Commito  
*Gettysburg College*

S. F. Thrush

R. D. Pridmore

*See next page for additional authors*

Follow this and additional works at: <http://cupola.gettysburg.edu/esfac>

 Part of the [Environmental Sciences Commons](#)

**Share feedback about the accessibility of this item.**

---

Commito, J., et al. Dispersal Dynamics in a Wind-Driven Benthic System. *Limnology and Oceanography*. 1995. 40(8): 1513-1518.

This is the publisher's version of the work. This publication appears in Gettysburg College's institutional repository by permission of the copyright owner for personal use, not for redistribution. Cupola permanent link: <http://cupola.gettysburg.edu/esfac/24>

This open access article is brought to you by The Cupola: Scholarship at Gettysburg College. It has been accepted for inclusion by an authorized administrator of The Cupola. For more information, please contact [cupola@gettysburg.edu](mailto:cupola@gettysburg.edu).

---

# Dispersal Dynamics in a Wind-Driven Benthic System

## **Abstract**

Bedload and water column traps were used with simultaneous wind and water velocity measurements to study postlarval macrofaunal dispersal dynamics in Manukau Harbour, New Zealand. A 12-fold range in mean wind condition resulted in large differences in water flow (12-fold), sediment flux (285-fold), and trap collection of total number of individuals (95-fold), number of the dominant infaunal organism (84-fold for the bivalve *Macomona liliana*), and number of species (4-fold). There were very strong, positive relationships among wind condition, water velocity, sediment flux, and postlarval dispersal, especially in the bedload. Local density in the ambient sediment was not a good predictor of dispersal. Results indicate that postlarval dispersal may influence benthic abundance patterns over a range of spatial scales.

## **Keywords**

Wind-Driven Benthic System, Bedload, Postlarval

## **Disciplines**

Environmental Sciences

## **Authors**

John A. Commito, S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings

## Dispersal dynamics in a wind-driven benthic system

**Abstract**—Bedload and water column traps were used with simultaneous wind and water velocity measurements to study postlarval macrofaunal dispersal dynamics in Manukau Harbour, New Zealand. A 12-fold range in mean wind condition resulted in large differences in water flow (12-fold), sediment flux (285-fold), and trap collection of total number of individuals (95-fold), number of the dominant infaunal organism (84-fold for the bivalve *Macomona liliana*), and number of species (4-fold). There were very strong, positive relationships among wind condition, water velocity, sediment flux, and postlarval dispersal, especially in the bedload. Local density in the ambient sediment was not a good predictor of dispersal. Results indicate that postlarval dispersal may influence benthic abundance patterns over a range of spatial scales.

The mechanisms of postlarval meiofauna and macrofauna dispersal have not been extensively studied (Palmer 1988). Active crawling and burrowing occur on the bottom (Kukert and Smith 1992), but passive transport in the bedload may be even more important, particularly for small or postlarval stages (Emerson and Grant 1991; Commito et al. 1995). In the water column, both active swimming (Varon and Thistle 1988) and passive transport (Cummings et al. 1993) have been reported, although the distinction between the two modes has yet to be fully elucidated (Smith and Brumsickle 1989; Armonies 1992).

In spatially heterogeneous soft-bottom habitats, dispersal from high-density areas into low-density patches created by small-scale disturbance events can affect local species distribution and abundance patterns. Small-scale events often fail to produce long-term effects because high rates of movement, especially of postlarval stages, can quickly smooth out small-scale patchiness, thus homogenizing densities over large areas (Thrush et al. 1991; Commito et al. 1995). In mathematical models, active and passive dispersal can stabilize some populations (Hastings 1993)—even chaotic populations within a metapopulation (González-Andujar and Perry 1993). Thus in some soft-bottom habitats, postlarval dispersal may play an important role in regulating populations and communities.

Studies at Manukau Harbour (Auckland, New Zealand) have demonstrated postlarval dispersal in response to disturbance (Thrush et al. 1991; Pridmore et al. 1991). Bivalves in particular move actively or passively in the bedload or water column in this harbor (Cummings et al. 1993) and other sandflat environments (Emerson and Grant 1991; Armonies 1992; Commito et al. 1995). Transport has been correlated with wind velocity and sediment flux, suggesting that passive dispersal may be a widespread phenomenon (Miller and Sternberg 1988; Emerson and Grant 1991; Armonies 1992). The purpose of this note is to examine the role that wind-driven water

currents play in controlling bedload and water column transport of juvenile and adult macrofauna.

Our investigation was conducted at a site in the mid-intertidal zone on a sandflat adjacent to Wiroa Island in Manukau Harbour (37°02'S, 174°41'E). The area has been described in detail elsewhere (e.g. Thrush et al. 1989, 1992; Pridmore et al. 1990). Cylindrical devices similar to those of Emerson (1991) and Emerson and Grant (1991) with an outer sleeve and an inner trap were used to collect sediment and animals moving in the bedload and water column. Traps consisted of 50-cm lengths of PVC pipe with an inside diameter of 4.0 cm, resulting in an aspect ratio of 12.5:1. Bedload trap tops were flush with the sediment surface. Water column traps were identical in design except that the tops projected 15 cm above the sediment surface.

On 13 March 1992 a permanent grid was established for the deployment of traps. It consisted of four rows parallel to shore, with rows separated by 4 m. Because the site is so flat, there was a <10-min difference in duration of water cover between the highest and lowest rows over one tidal cycle. Ten sleeves per row were installed 4 m apart, for a total of 40 sleeves. Traps were deployed on 17 and 25 March, 9 April, and 12 and 13 May 1992. During the daytime at low tide on each sampling date, 20 bedload and 20 water column traps were placed in an alternating pattern. Traps were filled with seawater, left in place overnight, and sampled at low tide the next day. The contents were immediately removed and fixed in buffered 5% Formalin with Rose Bengal stain. Each sample was sieved on 63- and 500- $\mu$ m mesh, and all individuals of species that reach macrofaunal size as adults were removed, preserved in 70% isopropanol, and later identified. The dry weight of sediment in each trap was measured, and grain-size analyses were performed whenever sufficient sediment was collected in traps.

Relative water velocity integrated over each trap deployment period was estimated with the gypsum dissolution technique. The blocks in this study, modified from Yund et al. (1991), were oven-dried, 2.0-cm-thick slices cut from cylinders of cast plaster 7.0 cm in diameter. Each block was attached to its own metal tripod inserted into the sediment. Two tripod heights were used: 15 cm above bottom (the same height as the water column traps) and 5 cm above bottom (to estimate flow close to the bedload traps but avoiding abrasion from sediment moving along the sediment-water interface in the bedload). On each trap deployment date, 10 water column blocks and 10 bedload blocks were deployed in an alternating pattern 7 m apart from each other between the rows of traps. The blocks were retrieved at the same time as the traps and oven-dried to constant weight. The loss in weight represented relative water velocity during the deployment period.

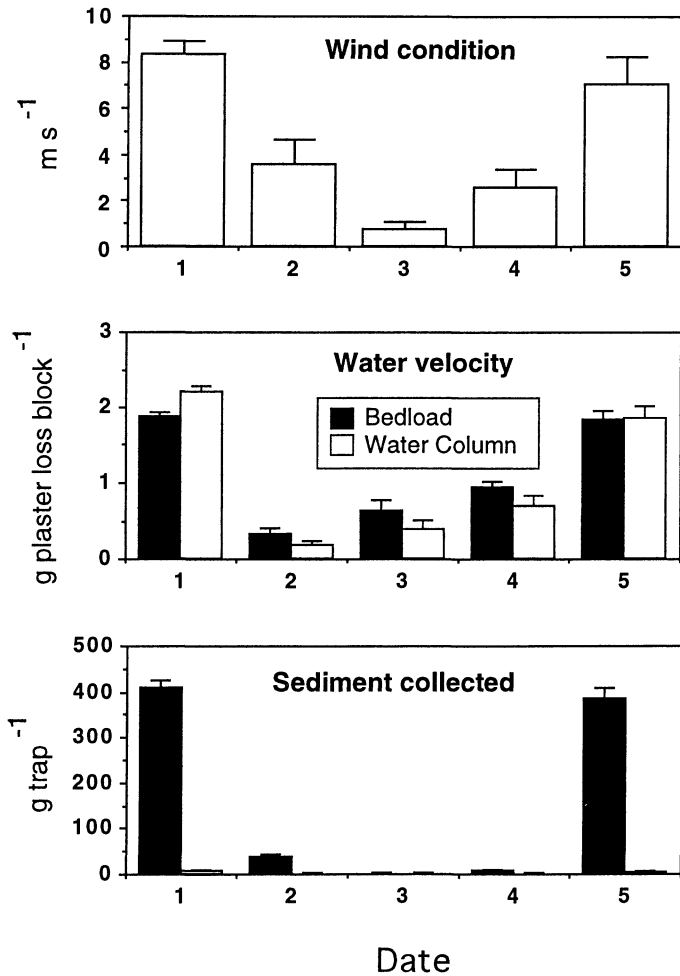


Fig. 1. Physical variables (mean  $\pm$  1 SE) on each date: 1—17 March; 2—25 March; 3—9 April; 4—12 May; 5—13 May.

Wind velocity values were determined from New Zealand Meteorological Service data for Auckland International Airport, which is directly adjacent to the study site. Mean wind condition on each deployment date was calculated for the time periods when water was covering the study grid. Hourly wind velocity means were multiplied by a fetch factor equal to the fetch length (which depended on wind direction) divided by the maximum possible fetch length of 15 km for this location in the harbor.

Only four variables (total number of individuals, number of species, and Shannon-Weiner  $H'$  and  $J'$ ) met the assumptions of ANOVA, and they were tested with the  $t$ -test or with ANOVA followed by the Student-Newman-Keuls multiple comparison procedure (Zar 1984). All other variables were analyzed in a nonparametric fashion, either with the Mann-Whitney test or with the Kruskal-Wallis test followed by Tukey's rank-sum multiple comparison procedure (Zar 1984). In all cases, the significance level was  $P \leq 0.05$ . There were significant differences in

mean wind condition, water velocity, and sediment flux among the five sample dates (Fig. 1). Significant differences in water velocity between heights were apparent only on the first and second sampling occasions, and no consistent differences were discovered (Fig. 1). On every date, bedload traps collected significantly more sediment than did those in the water column (Fig. 1). Sufficient sediment for grain-size analysis was collected in four sets of bedload traps (17 and 25 March; 12 and 13 May) and in one set of water column traps (17 March), yielding contents that were 98.9–99.9% sand with mean sizes of 2.59–2.85 ( $\phi$ ).

Significant differences in animal dispersal associated with wind condition were found among dates in both the bedload and the water column (Fig. 2). As many as  $665.10 \pm 49.16$  (SE) animals per trap were collected in the bedload; the bivalve *Macomona liliana* accounted for almost half of that total. On all dates except 9 April (lowest wind condition), significantly fewer animals were collected in the water column than in the bedload. The largest number collected in the water column was  $36.55 \pm 2.67$  animals per trap, almost two-thirds of which were *M. liliana*. On every date, bivalves were the most abundant taxonomic group in both types of trap. Of the eight common taxa, defined as having at least two individuals per trap in at least two treatments (dates and trap types), there were five bivalve species and one species each of a polychaete, gastropod, and amphipod.

Species richness also varied significantly among dates, with up to  $13.75 \pm 0.51$  species per bedload trap and  $6.60 \pm 0.32$  species per water column trap being collected (Fig. 2). Although species richness was significantly lower in water column traps than in bedload traps on most dates, the equitability component ( $J'$ ) of diversity was generally higher in water column traps (Fig. 2). Species richness rose but  $J'$  dropped on the windiest days because of the large numbers of *M. liliana* collected in traps under those conditions. As a result of this inverse relationship between species richness and  $J'$ , there were no consistent differences in  $H'$  among dates or between trap types (Fig. 2).

On a between-day temporal scale there were enormous differences in sediment flux and the dispersal rates of postlarval benthic organisms caused by relatively small differences in wind velocity. For example, although wind velocity varied 12-fold over the sample dates, sediment flux and animal dispersal varied 285-fold and 95-fold in the bedload.

More sediment and animals were collected in bedload traps than in water column traps. These results are consistent with those of Smith and Brumsickle (1989) who observed greatly reduced rates of postlarval dispersal into sediment plugs raised 5 cm above the bottom compared to plugs flush with the bottom. Most of the postlarval organisms dispersing in Manukau Harbour were small bivalves and gastropods, suggesting that some shelled

Fig. 2. Biological variables (mean  $\pm$  1 SE) on each date: 1—17 March; 2—25 March; 3—9 April; 4—12 May; 5—13 May.

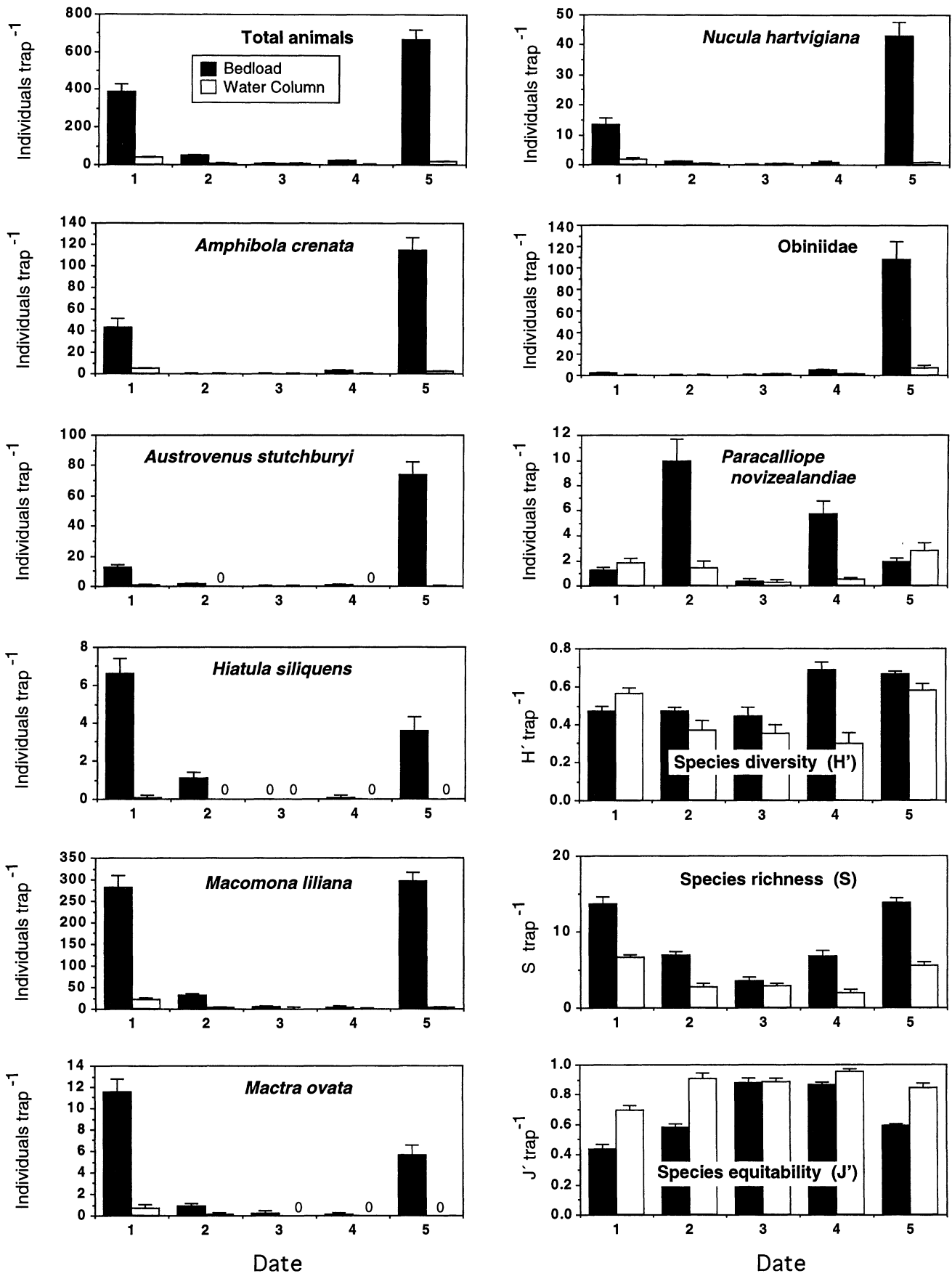


Table 1. Parameters of significant ( $P \leq 0.05$ ) regressions for mean values of physical and biological variables (wind condition,  $m\ s^{-1}$ ; water velocity,  $g\ plaster\ loss\ block^{-1}$ ; sediment collected,  $g\ trap^{-1}$ ; animals collected,  $ind.\ trap^{-1}$ ) on each date ( $N = 5$ ). Values are for bedload (b) and water column (w) positions.

y	x	Position	y-intercept	Slope	r <sup>2</sup>
Water velocity	Wind condition	w	-0.11	0.14	0.77
Sediment collected		b	-117.01	33.32	0.88
		w	-0.79	0.38	0.73
Animals collected					
<i>Hiatula siliquens</i>		b	-2.77	0.54	0.91
<i>Macomona liliana</i>		b	-80.10	23.68	0.85
<i>Mactra ovata</i>		b	-2.83	0.76	0.80
		w	-0.17	0.05	0.92
Species richness, <i>S</i>		b	2.52	0.74	0.95
		w	1.28	0.31	0.78
Species diversity, <i>H'</i>		w	-0.27	-0.02	0.77
Equitability, <i>J'</i>		b	-0.92	0.03	0.73
Sediment collected	Water velocity	b	-149.80	283.00	0.83
		w	-0.34	2.65	0.84
Animals collected					
Total		b	9.99	1.27	0.81
		w	3.46	0.06	0.68
<i>M. liliana</i>		b	-105.60	202.66	0.82
<i>M. ovata</i>		b	-0.08	0.31	0.86
Species richness, <i>S</i>		b	2.21	5.96	0.75
		w	3.91	4.72	0.83
Animals collected	Sediment collected				
Total		b	9.40	1.30	0.81
		w	-0.13	5.40	0.97
<i>Amphibola crenata</i>		w	-0.34	0.72	0.94
<i>M. liliana</i>		b	1.85	0.72	0.99
		w	2.50	1.20	0.78
<i>M. ovata</i>		b	-0.02	0.11	0.84
<i>Nucula hartvigiana</i>		w	0	0.22	0.91
Species richness, <i>S</i>		b	5.36	0.02	0.91
		w	1.28	0.31	0.85
Species diversity, <i>H'</i>		w	-0.32	-0.04	0.63
Equitability, <i>J'</i>		w	-0.95	0.04	0.86

molluscs may have transport characteristics similar to those of mineral particles when subjected to hydrodynamic forces (Muschenheim 1987). However, two species of shelled molluscs (*M. liliana* and the snail *Amphibola crenata*) were found in greater numbers in the water column traps than would have been expected if this were the case. Small *M. liliana* can initiate transport by moving up to the sediment surface and producing drift threads (Cummings et al. 1993). Some small gastropods increase their ability to float by producing mucus threads and rafting (Martel and Chia 1991; Martel and Diefenbach 1993), and *A. crenata* often floats high in the water column (R. D. Pridmore pers. obs.).

All regressions were model 1 (Zar 1984), and coefficients of determination were conservative because they were adjusted for degrees of freedom. Regressions were performed on mean values from each date for wind condition, water velocity, sediment flux, and number of animals collected in traps. In both the bedload and water

column, regressions revealed significant ( $P \leq 0.05$ ) positive, linear relationships between wind condition and water velocity, water velocity and sediment flux, and wind velocity and sediment flux (Table 1).

For bedload traps (Table 1), wind condition predicted *J'*, *S*, and the abundances of the dominant benthic organism, *M. liliana*, and another common bivalve, *Mactra ovata*. Water velocity and sediment flux each predicted the latter three variables plus the total number of individuals of all species.

For the water column traps (Table 1), wind condition predicted *S*, *H'*, and the abundance of *M. ovata*. Water velocity predicted *S* and the total number of individuals. Sediment flux predicted *S*, total number of individuals, *J'*, and the abundances of *M. liliana*, *A. crenata*, and the bivalve *Nucula hartvigiana*.

A number of species did not show linear responses to predictor variables. Spearman rank correlations were used to investigate whether any of these species responded



Table 2. Macrofaunal abundances in the ambient sediment on two dates during the study. Means ( $\pm$ SD) and percentage of the total number of individuals found in the 55 cores are given for the common species (i.e. those comprising  $>2\%$  of the total population) and those commonly collected by the traps during the study. The results of tests on changes between the two times for the species commonly collected in the traps are given as  $P$  values.

	26 March		14 May		$P$
	Abundance	%	Abundance	%	
Total No. of individuals	93.1 $\pm$ 17.2	—	94.5 $\pm$ 16.6	—	—
Total No. of species	15.6 $\pm$ 2.1	—	16.6 $\pm$ 2.5	—	—
<i>Macomona liliana</i>	36.3 $\pm$ 11.7	39.0	33.1 $\pm$ 7.5	34.9	0.78
<i>Aonides oxycephala</i>	10.6 $\pm$ 7.0	11.4	9.4 $\pm$ 6.5	10.0	0.45
<i>Nucula hartvigiana</i>	9.0 $\pm$ 3.3	9.6	12.3 $\pm$ 5.2	13.0	0.0001
<i>Maetra ovata</i>	6.4 $\pm$ 3.0	6.8	2.6 $\pm$ 2.1	2.7	0.0001
<i>Austrovenus stutchburyi</i>	5.7 $\pm$ 2.7	6.1	7.8 $\pm$ 3.0	8.3	0.0001
<i>Hiatula siliquens</i>	4.6 $\pm$ 2.5	5.0	7.5 $\pm$ 3.3	8.0	0.0001
<i>Orbinia papillosa</i>	4.5 $\pm$ 3.3	4.8	5.4 $\pm$ 2.8	5.7	0.51
<i>Magelona ?dakina</i>	2.4 $\pm$ 2.3	2.6	2.6 $\pm$ 2.3	2.8	0.73
<i>Amphibola crenata</i>	0.09 $\pm$ 0.35	0.1	0	0	0.31
<i>Paracallioppe novizealandiae</i>	0.04 $\pm$ 0.19	0.19	0.56 $\pm$ 0.81	0.6	0.002

monotonically, though not in a linear fashion, to physical variables. For bedload traps, significant ( $P \leq 0.05$ ) Spearman rank correlation coefficients of at least 0.9 were observed between wind condition and the bivalves *Austrovenus stutchburyi* and *N. hartvigiana* and the amphipod *Paracallioppe novizealandiae*; water velocity and *A. crenata*; and sediment flux and the bivalves *Hiatula siliquens* and *N. hartvigiana*. For water column traps, they were observed between wind condition and *A. crenata*, *M. liliana*, *N. hartvigiana*, and *P. novizealandiae*.

Previous studies in the intertidal zone have found significant but weak, positive relationships between wind velocity and sediment flux ( $r^2 = 0.26$ , False Bay, Washington: Miller and Sternberg 1988; Miller 1989) and between wind velocity and animal transport ( $r^2 = 0.06$ – $0.30$  for four drifting mollusc species, Oddewatt, Wadden Sea, Germany: Armonies 1992). Weak, positive coefficients of correlation have been observed between bedload sediment transport and dispersal of two bivalves, *Mya arenaria* ( $r = 0.33$  and  $0.51$  at sheltered and exposed intertidal sites, Eastern Passage, Nova Scotia: Emerson and Grant 1991) and *Gemma gemma* ( $r = 0.47$  and  $0.76$  in two sediment trap arrays, Tom's Cove, Virginia: Commito et al. 1995). Our results from Manukau Harbour demonstrated much stronger relationships among all the variables of wind velocity, water velocity, sediment flux, and dispersal of benthic species.

Data on ambient benthic organisms were collected on 26 March and 14 May 1992. On each occasion, 55 core samples (13-cm diam, 15-cm deep) were taken within the trap grid. Cores were positioned 4 m apart in five rows such that four cores were taken in a square around each trap. Samples were sieved on 500- $\mu$ m mesh and processed as described above. Bivalves were measured with an ocular micrometer or vernier calipers and placed into size categories ( $\leq 2.5$ , 2.5–5.0, 5.0–10.0, and  $> 10.0$  mm). Data from the four adjacent cores that formed a square around each trap were combined to produce a mean ambient

value for that trap. Ambient densities were remarkably consistent on the two sample dates, despite intervening periods of strong winds, high water velocities, and high rates of sediment flux (Table 2). However, examination of the bivalves *A. stutchburyi*, *H. siliquens*, *M. liliana*, *M. ovata*, and *N. hartvigiana* in the smallest size-class (0.5–2.5 mm, the size range most common in traps) and the amphipod *P. novizealandiae* revealed significant differences in the ambient sediment between the two dates for all species except *M. liliana*.

Stepwise linear regression analyses (SAS Inst. 1990) were conducted with data from individual traps (25 March and 13 May) and ambient cores (26 March and 14 May). The number of animals collected in traps and retained on 500- $\mu$ m mesh was regressed against sediment collected in traps, number of animals collected in alongshore and downshore traps, total number of animals in adjacent ambient cores, and number of 0.5–2.5-mm-long animals in adjacent ambient cores. The probability level used to enter and stay in the model was set at 0.15 (the default used by SAS 1990). Results revealed that sediment flux and abundance in other traps could often predict the number of individuals of many species in traps. However, in only one instance (*N. hartvigiana* in bedload traps on 14 May) was abundance in the adjacent ambient sediment a good predictor of the number of individuals collected in traps.

In systems such as this one with sufficient bedload and water column transport, postlarval movement provides a mechanism for immediate dispersal and patch recolonization. Small-scale disturbances can be smoothed out and long-term effects reduced so that only averaged reductions in density over scales of postlarval transport are apparent. For example, Commito et al. (1995) used bedload traps in conjunction with natural and simulated crab pits at a sandy, high-energy, intertidal site and showed that densities of the bivalve *G. gemma* in pits returned to control values within 1 d. The importance of this type

of averaging effect depends on local conditions. Our study revealed much greater rates of transport for most species on days with high wind and water velocities.

The results presented here demonstrate that in soft-bottom systems, especially high-energy environments like Manukau Harbour, postlarval dispersal can be important for many infaunal species and may play a significant role in controlling community dynamics. Our results emphasize the importance of passive, physically controlled processes as well as those that involve a behavioral component. The lack of correlation between local density in the ambient sediment and numbers of animals captured in traps may be due in part to differences in transport characteristics among species. Another possibility is that animals might travel long distances relative to the size of the study site. Postlarval transport over these distances may be an important reason why individual, small-scale disturbances in soft-bottom systems often fail to produce the long-term effects apparent in many rocky shore studies.

*J. A. Commito*<sup>1</sup>

Environmental Studies Program and  
Department of Biology  
Gettysburg College  
Gettysburg, Pennsylvania 17325

*S. F. Thrush*  
*R. D. Pridmore*  
*J. E. Hewitt*  
*V. J. Cummings*

Natl. Inst. of Water and Atmospheric Res.  
POB 11115  
Hamilton, New Zealand

## References

- ARMONIES, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Mar. Ecol. Prog. Ser.* **83**: 197–206.
- COMMITO, J. A., C. A. CURRIER, L. R. KANE, K. A. REINSEL, AND I. M. ULM. 1995. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. *Ecol. Monogr.* **65**: 1–20.
- CUMMINGS, V. J., R. D. PRIDMORE, S. F. THRUSH, AND J. E. HEWITT. 1993. Emergence and floating behaviours of post-settlement juveniles of *Macomona liliana* (Bivalvia: Tellinacea). *Mar. Behav. Physiol.* **24**: 25–32.
- EMERSON, C. W. 1991. A method for the measurement of bedload sediment transport and passive faunal transport on intertidal sandflats. *Estuaries* **14**: 361–371.
- , AND J. GRANT. 1991. The control of softshell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnol. Oceanogr.* **36**: 1288–1300.
- GONZÁLEZ-ANDUJAR, J.-L., AND J. N. PERRY. 1993. The effect of dispersal between chaotic and non-chaotic populations within a metapopulation. *Oikos* **66**: 555–557.
- HASTINGS, A. 1993. Complex interactions between dispersal and dynamics: Lessons from coupled logistic equations. *Ecology* **74**: 1362–1372.
- KUKERT, H., AND C. R. SMITH. 1992. Disturbance, colonization and succession in a deep-sea sediment community: Artificial-mound experiments. *Deep-Sea Res.* **39**: 1349–1371.
- MARTEL, A., AND F. S. CHIA. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *J. Exp. Mar. Biol. Ecol.* **150**: 131–147.
- , AND T. DIEFENBACH. 1993. Effects of body size, water currents and microhabitat on mucous-thread drifting in post-metamorphic gastropods, *Lacuna* spp. *Mar. Ecol. Prog. Ser.* **99**: 215–220.
- MILLER, D. C. 1989. Abrasion effects in sandy sediments. *Mar. Ecol. Prog. Ser.* **55**: 73–82.
- , AND R. W. STERNBERG. 1988. Field measurements of the fluid and sediment-dynamic environment of a benthic deposit feeder. *J. Mar. Res.* **46**: 771–796.
- MUSCHENHEIM, D. K. 1987. The dynamics of near-bed seston flux and suspension-feeding benthos. *J. Mar. Res.* **45**: 473–496.
- PALMER, M. A. 1988. Dispersal of marine meiofauna: A review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Prog. Ser.* **48**: 81–91.
- PRIDMORE, R. D., S. F. THRUSH, J. E. HEWITT, AND D. S. ROPER. 1990. Macrobenthic community composition of six intertidal sandflats in Manukau Harbour, New Zealand. *N.Z. J. Mar. Freshwater Res.* **24**: 81–96.
- , AND OTHERS. 1991. Effect of the organochlorine pesticide technical chlordane on the population structure of suspension and deposit feeding bivalves. *Mar. Ecol. Prog. Ser.* **76**: 261–271.
- SAS INSTITUTE, INC. 1990. SAS/STAT user's guide. Version 6. V. 2.
- SMITH, C. R., AND S. J. BRUMSICKLE. 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. *Limnol. Oceanogr.* **34**: 1263–1277.
- THRUSH, S. F., J. E. HEWITT, AND R. D. PRIDMORE. 1989. Patterns in the spatial arrangement of polychaetes and bivalves in intertidal sandflats. *Mar. Biol.* **102**: 529–535.
- , R. D. PRIDMORE, J. E. HEWITT, AND V. J. CUMMINGS. 1991. Impact of ray feeding disturbances on sandflat macrobenthos: Do communities dominated by polychaetes or shellfish respond differently? *Mar. Ecol. Prog. Ser.* **69**: 245–252.
- , ———, ———, AND ———. 1992. Adult infauna as facilitators of colonization on intertidal sandflats. *J. Exp. Mar. Biol. Ecol.* **159**: 253–265.
- VARON, R., AND D. THISTLE. 1988. Response of a harpacticoid copepod to a small-scale natural disturbance. *J. Exp. Mar. Biol. Ecol.* **118**: 245–256.
- YUND, P. O., S. D. GAINES, AND M. D. BERTNESS. 1991. Cylindrical tube traps for larval sampling. *Limnol. Oceanogr.* **36**: 1167–1177.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall.

<sup>1</sup> To whom correspondence should be sent.

## Acknowledgments

Field and laboratory assistance was provided by Richard Ford, Susan Hasler, and Karl Mischewski. Will Ambrose, Brian Beal, Jon Grant, and Walt Nelson made comments on an earlier version of the manuscript.

Research funding was provided by grants to J.A.C. from the Beneficial-Hodson Trust, Whitaker Foundation, and New Zealand National Institute of Water and Atmospheric Research.

Submitted: 25 July 1994  
Accepted: 17 July 1995  
Amended: 26 September 1995