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Post-settlement movement by intertidal benthic macroinvertebrates: Do common New Zealand species drift in the water column?

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Abstract To determine whether post-settlement juveniles of New Zealand soft-sediment macrofauna drift in the water column, samples were collected, day and night, above an intertidal sandflat in Manukau Harbour, New Zealand. Forty benthic taxa were collected in the net samples. Most taxa were Polychaeta (18 taxa), Bivalvia (9 taxa), or Amphipoda (4 taxa). All bivalves and gastropods collected were post-settlement juveniles, 3 mm or less in size. Most of the polychaetes captured were either metamorphosing planktonic larvae or young benthic stages. In contrast, most of the captured arthropods were adults. Generally, benthic species found in the water column were also common in the benthos. Definite patterns in migratory activity were exhibited by some taxa over each 24 h sampling period. Taxa collected in the water column varied with sampling date, time of day, state of the tide, and depth of sampling. Only one of the benthic species collected in the net samples showed some ability to partition itself vertically within the water column. The large number and variety of soft-bottom macrofauna collected emphasises the potential importance of post-settlement dispersal in the survival of post-larval organisms.

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INTRODUCTION

Dispersal is an important component of population and community ecology, affecting population demography and enabling organisms to respond to habitat patches of different quality (Hastings 1990; Possingham & Roughgarden 1990). The survival of a species over time or in a given geographical area often depends upon its ability to disperse (e.g., Jablonski 1986; Scheltema 1989).

Many species of marine macrobenthic invertebrates produce planktonic larvae which serve as their primary agent of dispersal. Such larvae are important because they provide an opportunity for wide geographic distribution. However, as planktonic larvae do not always settle or survive in areas best suited for adult growth (e.g., Beukema & de Vlas 1989) other means of dispersal are likely to be important. Several recent studies of intertidal soft-sediment macrofauna (Beukema & de Vlas 1989; O'Foighil 1989; Martel & Chia 1991; Armonies 1992; Martel & Diffenbach 1993) have indicated that drifting by post-settlement juveniles or small adults is an important dispersal mechanism for many marine bivalves and gastropods both with and without planktonic larval stages. Such drifting may occur after a prolonged benthic existence and may allow individuals to settle, at a later time and with greater size, in areas unsuitable for small, recently-metamorphosed larvae. Post-settlement drifting in many bivalve and several gastropod species appears to be aided by the production of microscopically thin mucous threads which increase the individuals' hydrodynamic drag and enable them to be lifted from the sediment surface and transported in the water column (Sigurdsson et al. 1976; Cummings et al. 1993). Some species (e.g., the gastropods *Littorina saxatilis* and *Hydrobia ulvae*) drift by means of rafting on fragments of plants or detritus (Highsmith

1985; Johannesson 1988; O'Foighil 1989) or by floating at the water surface (Little & Nix 1976; Levinton 1979). In other cases, the behaviour of infauna render themselves more susceptible to physical resuspension and distribution by currents (e.g., see Tamaki 1987).

The ability of post-settlement stages to enter the water column and redisperse has important implications for colonisation of new or disturbed areas (e.g., Bonsdorff 1980; Bell & Devlin 1983; Levin 1984; Thrush et al. 1992a) and allows species to maintain existing populations and escape adverse local conditions (Highsmith 1985; Martel 1988; Frid 1989; Pridmore et al. 1991).

Although the literature indicates the prevalence of post-settlement movement, to date only a few New Zealand soft-sediment macroinvertebrates are known to employ post-settlement drifting as a means of dispersal (Pridmore et al. 1991; Cummings et al. 1993). To determine whether many New Zealand species utilise post-settlement drifting we conducted a preliminary study which involved sampling the water column, day and night, above an intertidal sandflat. The aim of this study was primarily to document evidence of post-settlement movement by these species and gain some insight into their drifting behaviour. It was not to elucidate patterns in the presence of animals in the water column or to identify mechanisms which account for the observed patterns, as this can only be done via much more extensive sampling programmes.

SITE DESCRIPTION

The study was conducted on a semi-exposed intertidal sandflat located east of Wiroa Island (37°01'S, 174°49'E) in Manukau Harbour, adjacent to Auckland, New Zealand. Light to moderate westerly and south-westerly winds (5–10 m s^{-1}) commonly blow over the beach and help to rework near-surface sediments to a depth of 1–3 cm. During strong winds (> 15 m s^{-1}) near-surface sediments are disturbed to a depth of 5 cm. Near-surface sediment on the beach is generally moderately sorted and comprises principally medium to fine sand (Pridmore et al. 1990). There are no large biogenic structures (e.g., no crab burrows and faecal mounds) on the sandflat, although pits (c. 20 cm deep, 30 cm diameter) created by feeding eagle rays (*Myliobatis tenuicaudatus*) are moderately abundant (about 10 pits created in 9000 m^2 of sandflat after one tide) from November through March (Thrush et al. 1991). Macrofauna have been collected in the water column in previous studies conducted at this site (Pridmore et al. 1991).

Macroinvertebrates (> 500 µm) commonly found on this sandflat (median densities > 70 individuals m^{-2}) include the gastropod *Amphibola crenata*; the bivalves *Austrovenus stutchburyi*, *Hiatula siliquens*, *Macomona liliana*, and *Nucula hartvigiana*; the polychaetes *Aonides oxycephala*, *Magelona ?dakini*, and *Orbinia papillosa*; the echinoderm *Trochodota dendyi*; the crab *Halicarcinus whitei*; the amphipods *Paracalliope novizealandiae*, *Torridoharpinia hurleyi*, and *Waitangi brevirostris*; and the cumacean *Colurostylis lemurum* (Pridmore et al. 1990, 1992; Thrush et al. 1992a). Samples collected from a long-term monitoring site, immediately adjacent to our study site, during October and December of 1991, indicated that each of these species was prevalent during the course of this study (see Thrush et al. 1992b).

METHODS

Macroinvertebrates drifting in the water column were collected by pushing a net (20 cm diam., 180 µm mesh) through the water in a circle of 9.4 m circumference (Fig. 1), 6 times, sieving c. 1.8 m^3 of sea water. Three replicates were collected at all depths sampled on each date. As the aim of this study was to sample as much of the water column as possible to provide a reasonable indication of the number and variety of infauna present, the replicates at each depth were combined, and statistical analyses were not conducted.

Samples were collected at various stages over two tidal cycles on both 10–11 October and 22–23 December 1991. Samples were taken 15 cm above the sediment surface on each occasion and at either 63 cm or 118 cm above the sediment surface depending upon water depth (Fig. 1). On the first sampling date, all three depths were sampled, sieving a total of c. 86 m^3 of sea water. On the second sampling date, however, only two depths (i.e., 15 cm and 63 cm) could be sampled due to a lower tidal height, hence a total of c. 64 m^3 of sea water was sieved. Times of sampling and corresponding water depths are shown in Fig. 2 and 3. Current velocity profiles were obtained using a Whitney Inc. electromagnetic flow velocity metre (Model pvm–2a).

Immediately after collection, samples were fixed in a mixture of 5 % formalin and 0.1 % rose bengal in sea water. In the laboratory, macrofauna were

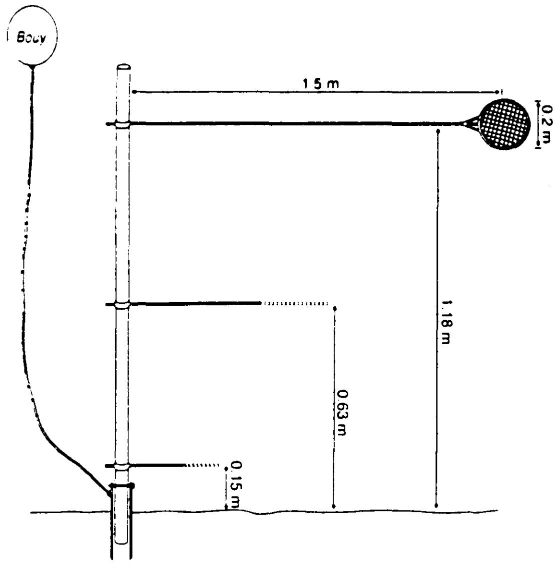


Fig. 1 Diagram of the net mechanism used to sample the water column, showing the heights above the bottom at which it was used.

sorted, identified to the lowest possible taxonomic level, counted, and preserved in 70 % isopropanol.

RESULTS

Light to moderate south-westerly winds (6–12 m s^{-1}) prevailed on both sampling dates, producing waves 10–30 cm in height. Measured water velocities generally declined with depth but did not follow a logarithmic profile. Hence, no attempt was made to estimate shear bed stress by the Prandtl-von Karman equation (see Wright et al. 1992). The maximum water current velocity recorded (mid-depth) on 10–11 October 1991 and 22–23 December 1991 was 37 and 42 cm s^{-1}, respectively. On both occasions, sediment ripples 1 cm high and 2–3 cm in wavelength were observed. The hydrodynamic conditions recorded during this study are typical of those observed at this site (Dolphin 1992).

Forty benthic taxa were collected in the net samples (Table 1). Most taxa were Polychaeta (18 taxa), Bivalvia (9 taxa), or Amphipoda (4 taxa). For 16 taxa, three or fewer individuals were obtained. About half of the taxa (54 %) were caught on only one of the two sampling dates. Of those taxa caught in moderate to high numbers (> 20 individuals) on both dates, 61 % were more abundant in the December sampling, despite a smaller volume of water being sampled.

All bivalves and gastropods collected in the net samples were post-settlement juveniles, 3 mm or less in size (longest shell axis), with thin or transparent shells. They were of the same stage and size as post-larvae collected previously in the benthos at this site (e.g., Thrush et al. 1992b; authors' unpubl. data). Most of the polychaetes captured (Aphroditiformia, Orbinidae, Spionidae) were either metamorphosing planktonic larvae or young benthic stages, hence we were unable to confidently identify many of the polychaetes to genus or species level. Fifteen adult polychaetes, however, were collected (1 *Aglaophamus macroura*, 2 *Aquilaspio aucklandica*, 1 *Eteone* near *aurantiaca*, 7 *Heteromastus filiformis*, 3 *Orbinia papillosa*, and 1 *Sphaerosyllis semiverricosa*). In contrast, most of the arthropods captured were adults. One notable exception was the crab *Halicarcinus whitei*, which was represented principally by juveniles 2 mm or less in size (carapace width). There were no differences in the size and stages of respective animals collected between sampling dates.

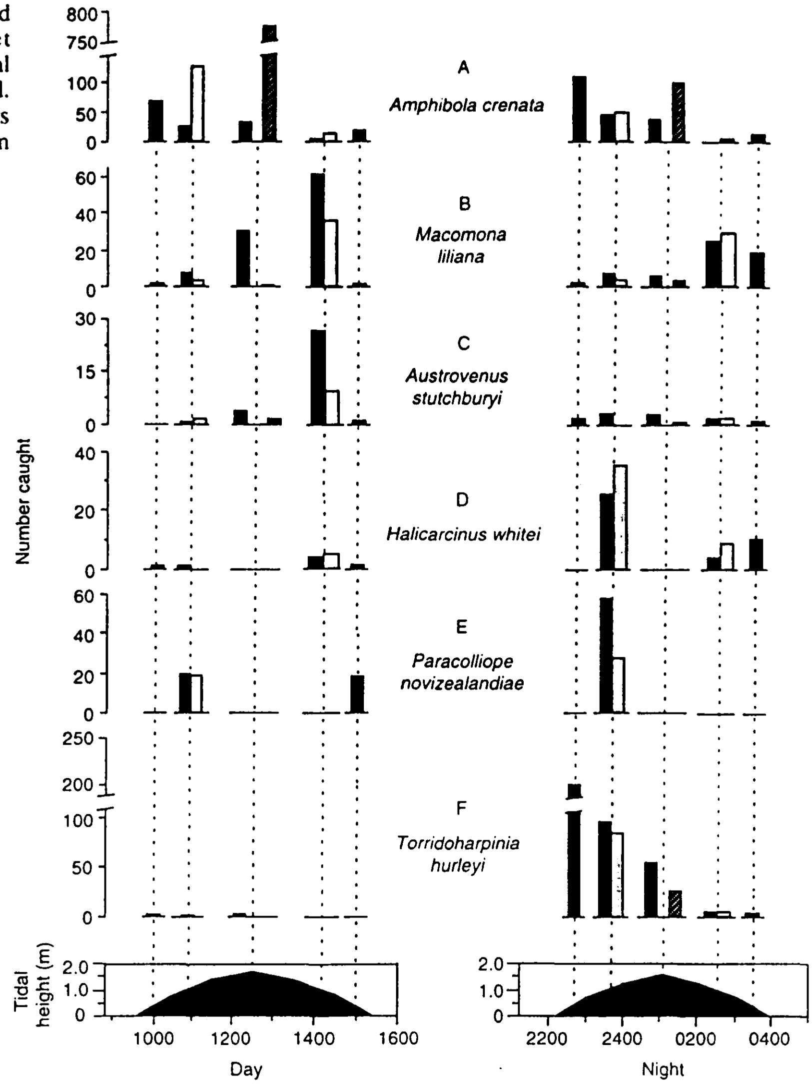
Definite patterns in migratory activity were exhibited by some taxa over each 24 h sampling period. Taxa collected in the water column varied with sampling date, time of day, state of the tide, and depth of sampling. Numbers of *Amphibola crenata* caught in the nets were highest during flood tides and slack water on each sampling date (Fig. 2A and 3A); numbers of *Macomona liliana* were highest on ebb tides (Fig. 2B and 3B). The bivalve *Austrovenus stutchburyi* was more abundant during the day-time (Fig. 2C and 3C). The crab *Halicarcinus whitei* was considerably more abundant at night, and during this time numbers were higher on the incoming tides (Fig. 2D and 3D). The amphipods *Paracalliope novizealandiae* (Fig. 2E and 3E) and *Torridoharpinia hurleyi* (Fig. 2F and 3F) also occurred more frequently at night on an incoming tide. Densities of the polychaetes Orbinidae (Fig. 3G) and Spionidae (Fig. 3H) were noticeably higher during the day.

Juveniles of the polychaete taxa Aphriditiformia (Table 1) and Orbinidae (Fig. 3G) and the bivalve Mytilidae (Table 1) were collected in large numbers on the second sampling date. None of these taxa was collected on the first sampling date. Numbers of juvenile Spionidae collected during the December sampling were 40 times higher than

Table 1 Benthic taxa caught in net hauls on 10–11 October and 22–23 December 1991. For each date, the number given is a total of all replicates at all depths sampled. Note that during the October sampling a larger volume of water was filtered owing to the greater tidal height (c. 86.4 m^3 in October cf. 64.8 m^3 in December). Numbers in parentheses for 10–11 October have been adjusted to 64.3 m^3, to enable direct comparison with December abundances. n.d. = not determined.

Taxa	10–11 Oct 91		22–23 Dec 91
ANNELIDA			
Oligochaeta n.d.	2	(1.5)	–
Polychaeta			
Aglaophamus macroura	1	(0.75)	3
Aonides oxycephala	1	(0.75)	–
Aphroditiformia n.d.	–		289
Aquilaspio aucklandica	2	(1.5)	–
Eteone near *aurantiaca*	1	(0.75)	–
Glyceridae n.d.	1	(0.75)	–
Heteromastus filiformis	24	(18)	3
Lepidodontinae n.d.	–		17
Magelona ?dakini	–		7
Malacoseros sp.	–		1
Maldanidae n.d.	1	(0.75)	–
Nereidae n.d.	1	(0.75)	1
Orbinidae n.d.	–		92
Orbinia papillosa	6	(4.5)	4
Phyllodoce sp.	1	(0.75)	–
Sphaerosyllis semiverricosa	1	(0.75)	–
Spionidae n.d.	24	(18)	911
Syllidae n.d.	3	(2.25)	–
ARTHROPODA			
Decapoda			
Halicarcinus whitei	87	(65.25)	92
Helice crassa	–		1
Isopoda			
Exosphaeroma ?falcatum	20	(15)	3
Cumacea			
Colurostylis lemurum	94	(70.5)	276
Amphipoda			
Methalimedon sp.	4	(3)	8
Paracalliope novizealandiae	143	(107.25)	222
Torridoharpinia hurleyi	484	(363)	630
Waitangi brevirostris	–		1
ECHINODERMATA			
Holothuroidia n.d.	2	(1.5)	–
Trochodota dendyi	2	(1.5)	–
MOLLUSCA			
Gastropoda			
Amphibola crenata	1421	(1065.75)	> 6500
Bivalvia			
Arthritica bifurca	5	(3.75)	20
Austrovenus stutchburyi	61	(45.75)	384
Mactra ovata	3	(2.25)	–
Mytilidae n.d.	–		43
Nucula hartvigiana	18	(13.5)	10
Paphies australis	–		2
Hiatula siliquens	22	(16.5)	9
Macomona liliana	242	(181.5)	91
Zenatia acinaces	12	(9)	–
NEMERTINEA n.d.	11	(8.25)	3

Fig. 2 Numbers of selected species collected in the net samples on 10–11 October. A total of c. 86 m^3 of water was sieved. Solid bars = 0.15 m, speckled bars = 0.63m, hatched bars = 1.18 m above the sediment surface.



those collected on the first sampling date (see Table 1). Juvenile *Amphibola crenata* and *Austrovenus stutchburyi* were also collected in considerably greater numbers (> 4.6 and 6.3 times greater, respectively) on the second sampling date (Table 1).

Only one of the benthic species caught in the net samples showed some ability to partition itself vertically within the water column. *Amphibola crenata* was frequently collected in higher numbers from the net nearest the water surface than at greater depths. Numbers of this gastropod were greatest at the highest point sampled in the water column on all but one sampling occasion (see results for 1100 h, 1230 h, and 0100 h on Fig. 2A and 2315 h, 0115 h and 1345 h on Fig. 3A).

Combining data of less abundant taxa by class, functional group (e.g., mobile vs sedentary polychaetes), or habitat depth did not help to elucidate further patterns.

DISCUSSION

The large number and variety of mainly juvenile benthic organisms collected in the water column during this study illustrate the importance of post-settlement dispersal for intertidal macrofauna. The

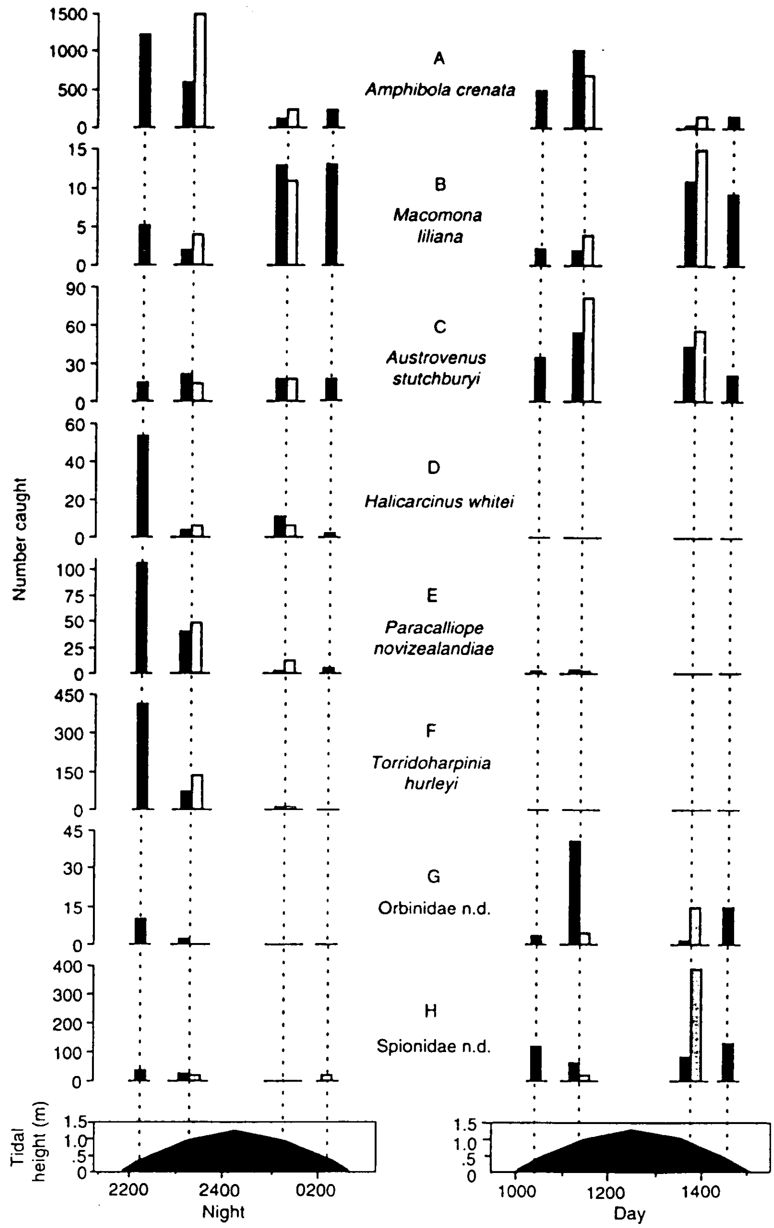


Fig. 3 Numbers of selected species collected in the net samples on 22–23 December. A total of c. 64 m^3 of water was sieved. Solid and speckled bars denote samples collected 0.15 m and 0.63 m above the sediment surface, respectively.

number collected varied with the time of day, tide, and sampling. Generally, benthic species found in high numbers in the net samples were also common in the benthos (the gastropod *Amphibola crenata*; the bivalves *Austrovenus stutchburyi* and *Macomona liliana*; the amphipods *Paracalliope novizealandiae*, and *Torridoharpinia hurleyi*; the cumacean *Colurostylis lemurum*; and the crab *Halicarcinus whitei*). Some common benthic species, however, were rarely captured (the echinoderm *Trochodota dendyi*; the amphipod *Waitangi brevirostris*; and the polychaete *Aonides oxycephala*) or were collected in small numbers only (the bivalves *Hiatula siliquens*, and *Nucula hartvigiana*; and the polychaetes *Magelona ?dakini* and *Orbinia papillosa*). No species which was rare or lowly abundant in the benthos (Thrush et al. 1992b) was found in moderate to high numbers

(> 20) in the net samples. Quantitative relationships between water column and benthic densities were not attempted as species abundance on the sandflat is highly variable (Thrush et al. 1989) and the distance over which organisms drift is not known.

Benthic macroinvertebrate species entering the water column are potentially dispersed over large distances. Macrofauna can therefore maximise their survival chances by moving to a different habitat if their initial settlement site is disturbed or no longer best suited to successful development and growth. Post-settlement processes appear to play a significant role in population regulation and community organisation in marine soft-sediments (Olafsson et al. 1994). A number of important areas in ecology are influenced by such processes; for example, drifting post-settlement juveniles and adults can recolonise disturbed areas, and may also potentially confound small-scale experiments by swamping localised treatment effects (see Frid 1989; Hall et al. 1990; Thrush et al. 1994). Post-settlement dispersal must also be taken into account when describing the spatial distribution/abundance patterns of soft-sediment macrofauna, as patterns observed on one occasion may alter markedly from one sampling date to the next (authors' unpubl. data). Greater understanding of the physical and behavioural mechanisms which initiate drift by post-settlement organisms will aid our understanding of its importance in population and community dynamics.

Some of the organisms collected in the water column during this study showed obvious differences in abundance between sampling dates, suggesting there may have been a seasonal component to their presence. Over half of the taxa were collected on only one of the sampling dates, and most of the organisms collected on both dates in moderate to high numbers were more abundant in December (Table 1, Fig. 2 and 3). In all instances this increase was attributable to the presence of a large number of juveniles, suggesting these patterns may be associated with recruitment. Martel & Chia (1991) have shown seasonal patterns in the abundance of bivalve and gastropod species in the water column which coincide with periods of recruitment.

For some species, the number of individuals collected in the water column varied depending upon the time of day. The arthropods *Paracalliope novizealandiae*, *Torridoharpinia hurlyei*, and *Halicarcinus whitei* were all prevalent at night on an incoming tide (Fig. 2 and 3). Many arthropods (in particular amphipods) and polychaetes documented in the literature move into the water column at night (see e.g., Dean 1978; Borowsky & Aitken-Ander 1991), a behaviour which is often attributed to predator avoidance. The juvenile polychaetes Spionidae n.d. and Orbinidae n.d. (Fig. 3) and the bivalve *Austrovenus stutchburyi* (Fig. 2C and 3C) were collected in larger numbers during the day. The day-time occurrence of species in the water column may indicate dispersal is of greater importance than predator avoidance (Alldredge & King 1985). Night-time drifting of macrofauna in order to avoid visual predators may be less important in Manukau Harbour compared with other waters, owing to its very poor water clarity (Vant & Budd 1993).

Tidal variations in abundance were also apparent for some of the species collected. The gastropod *Amphibola crenata* and the arthropods mentioned above consistently appeared in the water column on a flood tide, whereas the bivalve *Macomona liliana* was prevalent on ebb tides. By moving at a particular stage of the tidal cycle, an organism may maintain its preferred distribution (e.g., Hough & Naylor 1992), or migrate to another habitat (e.g., Xaio & Greenwood 1992). The presence of an intertidal species in the water column only on the flood tide may help minimise its movement by tidal currents downshore to deeper, subtidal areas. In this study, the flood tide movement of the above organisms is likely a behaviour to maintain their preferred distribution, and in the case of *Amphibola crenata*, enable dispersal to another habitat (see below).

One species collected during this study showed some vertical differentiation within the water column. *Amphibola crenata* was consistently collected high in the water column on all incoming tides (Fig. 2 and 3). Control over its vertical distribution within the water column is another mechanism by which an organism can take advantage of tidal currents and control its intertidal position (Warman et al. 1991; Hough & Naylor 1992; Xaio & Greenwood 1992). Juvenile *Amphibola crenata* present high in the water column on a flood tide would tend to be moved onshore by strong tidal currents, hence placing them in locations where the adults occur in the benthos.

This study has documented, for the first time in New Zealand, the presence of post-settlement juveniles (and adults) of several intertidal benthic macroinvertebrate species in the water column. We have suggested patterns in the presence of these species in the water column which are likely to be associated with recruitment and maintenance of preferred distribution patterns. To elucidate these patterns with certainty requires more extensive sampling campaigns. However, the ability of New Zealand species to move as post-settlement juveniles has important implications for recolonisation of new or disturbed areas and in the interpretation of field experiments and provides a potential mechanism whereby organisms can escape from adverse local conditions (Pridmore et al. 1991). Moreover, it is a further illustration that settlement is not the dominant process determining population and community pattern in marine soft-sediments.

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