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To cite this article: R. G. Cole , P. J. Hull & T. R. Healy (2000) Assemblage structure, spatial patterns, recruitment, and post-settlement mortality of subtidal bivalve molluscs in a large harbour in north-eastern New Zealand, New Zealand Journal of Marine and Freshwater Research, 34:2, 317-329, DOI: [10.1080/00288330.2000.9516935](https://doi.org/10.1080/00288330.2000.9516935)

To link to this article: <https://doi.org/10.1080/00288330.2000.9516935>



Published online: 29 Mar 2010.



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## Assemblage structure, spatial patterns, recruitment, and post-settlement mortality of subtidal bivalve molluscs in a large harbour in north-eastern New Zealand

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**Abstract** Infaunal bivalve molluscs on the flood tidal delta of Tauranga Harbour, north-eastern New Zealand, were surveyed twice over a 6-month period, with the aim of assessing shellfish resources, assessing the magnitudes of temporal and spatial variability in abundances, and identifying potentially important processes. The surveys identified a total of 31 bivalve taxa from 27 sites. Species richness per site ranged between 0 and 9, and varied greatly in space and time, as did two other measures of diversity. Extremely high densities of bivalves ( $>20\,000\text{ m}^{-2}$ ) were encountered at several sites. Densities of several abundant species varied greatly in time, as a result of recruitment pulses. The abundances of the three species that dominated the fauna (*Paphies australis*, *Tawera spissa*, and *Ruditapes largillierti*) had characteristic spatial scales on the order of 200 m. Comparisons of size frequency distributions for individual sites suggested that mortality or emigration in the first year of benthic life was high. Substantial populations of bivalves occur on Centre Bank, and the most abundant of these are greatly influenced by events early in their lives.

**Keywords** clams; infauna; population dynamics; spatial autocorrelation analysis

### INTRODUCTION

Identifying spatial patterns in the species richness and densities of marine benthic organisms is fundamental to their management. At the simplest level, management requires information regarding where populations are, and mollusc fisheries provide good examples of spatial arrangement of habitats or refuges being important (e.g., Arsenault & Himmelman 1998). Patterns can be identified by relating sampling programs to natural scales of variation (Andrew & Mapstone 1987; Livingston 1987). The investigation of spatial patterns in soft-bottom communities is inherently difficult because of the difficulty of structuring sampling programmes for concealed organisms, whose habitat is frequently visually homogeneous (Thrush 1991).

Estuarine environments frequently are sites of intensive human activity, including maintenance dredging to maintain navigation channels, port activities, and stormwater discharges (e.g., Healy et al. 1996). They are also often the location of diverse and dense populations of macrobenthic organisms, some of which may feature prominently in commercial or recreational harvests. That confluence of human activities and ecological richness makes it important that the population dynamics of those organisms are understood.

This study investigated assemblage characteristics and population dynamics of bivalve molluscs in two surveys of the flood tidal delta of a large New Zealand tidal inlet system. We report here on surveys of bivalve diversity, spatial distribution, abundance, and population size structure across Centre Bank, Tauranga Harbour. The aims were to provide users of the harbour with an assessment of shellfish resources, to obtain preliminary information on the broad-scale temporal and spatial variability in abundances, and to identify potentially important processes affecting the sizes and densities of these

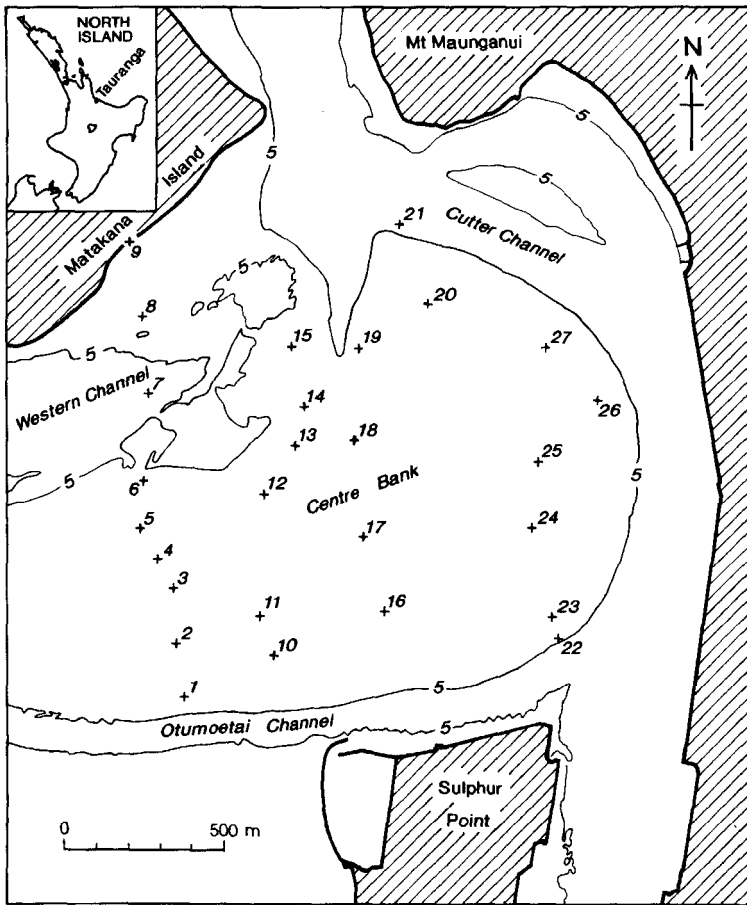


Fig. 1 Map of study area of New Zealand, showing sampling sites.

populations, in the light of which management decisions might be made.

## METHODS

### Study site

Tauranga Harbour ( $176^{\circ}09'E$   $37^{\circ}39'S$ ) (Fig. 1) is a natural tidal estuary which occupies an area of c. 200 km<sup>2</sup>. Centre Bank, the flood tidal delta of the southern, Tauranga, arm of the harbour (Fig. 1), is an area of very active sediment movement (Mathew et al. 1995).

### Sampling

The first broad-scale survey was undertaken over a week in December 1994 (summer), and it was repeated c. 6 months later in May 1995 (autumn-winter). Twenty-seven sites on four transects spaced c. 500 m apart, were sampled (Fig. 1). The samples

were nominally systematically distributed to maximise coverage; systematic surveys are most efficient for this (Dalenius et al. 1961). During the first survey, site positions were determined by compass fixes on navigation markers. Three bearings were recorded at each site, from which latitude and longitude were determined from navigational charts. GPS (Navtrac 4000) co-ordinates were used for site relocation during the second survey.

Samples were collected by SCUBA diving (water depths of 0.5–6 m below mean low water spring). A metal hand sampler (0.1 m<sup>2</sup>) was used to collect sediment to a depth of 10 cm. Sampler size was chosen to comply with an earlier study. Three randomly positioned replicate samples were collected within a 25 m<sup>2</sup> grid at each site. Samples were subsequently sieved (1 mm mesh) and fixed in 5% formalin in sea water. All bivalves were identified to the lowest possible taxonomic level (nomenclature follows Spencer & Willan 1995;

common names follow Morton & Miller 1968), counted and shell length measured ( $\pm 1$  mm).

### Data analysis

Plots of diversity and density of taxa (pooled over replicates at each site) across the survey area were constructed. Following Magurran (1988), diversity was assessed using species richness (number of species), and two well-known indices of diversity: the inverse Berger-Parker ( $N/N_{\max}$ ) and Margalef's  $((S-1)/\ln N)$  indices (where  $N$  = total number of individuals of all species,  $N_{\max}$  = number of individuals of the most abundant species,  $S$  = number of species recorded). These indices assess the distribution of individuals among species.

Spatial patterns were investigated using correlograms of Moran's  $I$ , calculated (with replicate samples remaining separate from each other) using SAAP (Legendre 1993). Moran's  $I$  is a coefficient of spatial autocorrelation which identifies spatial scales of self-similarity of distributions (e.g., Sokal & Oden 1978).

Densities of bivalves were monitored 3 times over a 2.5-year period from December 1991 to December 1993 at four subtidal sites, and pipi (*Paphies australis*) was found to be the most abundant species. As it is also harvested recreationally, and is of significance to Maori, its abundance was analysed further. Site 9, near the shore of Matakana Island had high densities of pipi and these data are analysed for

**Table 1** Bivalve taxa recorded in the two surveys of Centre Bank, Tauranga Harbour, New Zealand. Maximum densities are per site, not per sampling unit (3, 0.1 m<sup>2</sup> samples). Size is shell length.

| Taxon                            | Survey 1           |            |              |                 | Survey 2           |              |            |                 |
|----------------------------------|--------------------|------------|--------------|-----------------|--------------------|--------------|------------|-----------------|
|                                  | No. of individuals | % of total | Max. density | Size range (mm) | No. of individuals | Max. density | % of total | Size range (mm) |
| <i>Paphies australis</i>         | 670                | 18.2       | 283          | 2–82            | 4369               | 66.9         | 3330       | 3–80            |
| <i>Ruditapes largillierti</i>    | 813                | 22.1       | 423          | 2–80            | 453                | 6.9          | 197        | 1–59            |
| <i>Tawera spissa</i>             | 1195               | 32.5       | 349          | 1–28            | 791                | 12.1         | 442        | 1–33            |
| <i>Gari stangeri</i>             | 170                | 4.6        | 54           | 5–66            | 279                | 4.3          | 107        | 2–65            |
| <i>Macomona liliana</i>          | 178                | 4.8        | 67           | 3–53            | 81                 | 1.2          | 23         | 3–51            |
| <i>Soletellina siliquens</i>     | 263                | 7.2        | 80           | 2–26            | 166                | 2.5          | 63         | 2–32            |
| <i>Nucula nitidula</i>           | 52                 | 1.4        | 19           | 2–9             | 199                | 3.0          | 97         | 2–9             |
| <i>Nucula hartvigiana</i>        | 155                | 4.2        | 22           | 2–9             | 79                 | 1.2          | 24         | 2–9             |
| <i>Divaricella huttoniana</i>    | 60                 | 1.6        | 18           | 1–16            | 35                 | 0.5          | 6          | 2–9             |
| <i>Perna canaliculus</i>         | 41                 | 1.1        | 27           | 2–80            | 0                  | 0            | 0          | 0               |
| <i>Myadora striata</i>           | 10                 | 0.3        | 9            | 5–39            | 47                 | 0.7          | 18         | 4–50            |
| <i>Scalpomactra scalpellum</i>   | 4                  | 0.1        | 3            | 3–4             | 1                  | 0.02         | 1          | 4–7             |
| <i>Gari lineolata</i>            | 0                  | 0          | 0            | –               | 2                  | 0.03         | 2          | 47–48           |
| <i>Soletellina nitida</i>        | 6                  | 0.2        | 5            | 5–9             | 17                 | 0.3          | 5          | 4–16            |
| <i>Dosinia subrosea</i>          | 2                  | 0.05       | 1            | 11–50           | 3                  | 0.05         | 1          | 35–46           |
| <i>Gomphina maorum</i>           | 2                  | 0.05       | 2            | 15–16           | 0                  | 0            | 0          | –               |
| <i>Paphies subtriangulatum</i>   | 9                  | 0.2        | 3            | 2–6             | 0                  | 0            | 0          | –               |
| <i>Modiolus areolatus</i>        | 9                  | 0.2        | 5            | 3–5             | 0                  | 0            | 0          | –               |
| <i>Arthritica bifurca</i>        | 15                 | 0.4        | 4            | 3–4             | 0                  | 0            | 0          | –               |
| <i>Notocallista multistriata</i> | 1                  | 0.03       | 1            | 13              | 0                  | 0            | 0          | –               |
| <i>Zenatia acinaces</i>          | 3                  | 0.08       | 1            | 8–12            | 0                  | 0            | 0          | –               |
| <i>Hiatella arctica</i>          | 2                  | 0.05       | 2            | 2–3             | 0                  | 0            | 0          | –               |
| <i>Diplodonta striatula</i>      | 0                  | 0          | 0            | 0               | 2                  | 0.03         | 2          | 1–2             |
| <i>Felaniella zelandica</i>      | 1                  | 0.03       | 1            | 17              | 0                  | 0            | 0          | –               |
| <i>Dosinia lambata</i>           | 0                  | 0          | 0            | 0               | 1                  | 0.02         | 1          | 1–3             |
| <i>Tellina ?gaimardi</i>         | 0                  | 0          | 0            | 0               | 3                  | 0.05         | 1          | –               |
| Sp. 1                            | 4                  | 0.1        | 4            | 2–4             | 0                  | 0            | 0          | –               |
| Sp. 2                            | 4                  | 0.1        | 4            | 1–3             | 0                  | 0            | 0          | –               |
| Sp. 3                            | 1                  | 0.03       | 1            | 3               | 2                  | 0.03         | 2          | 2               |
| Sp. 4                            | 0                  | 0          | 0            | 0               | 1                  | 0.02         | 1          | 4               |
| Sp. 5                            | 0                  | 0          | 0            | 0               | 1                  | 0.02         | 1          | 3               |
| Totals                           | 3673               |            |              |                 | 6532               |              |            |                 |

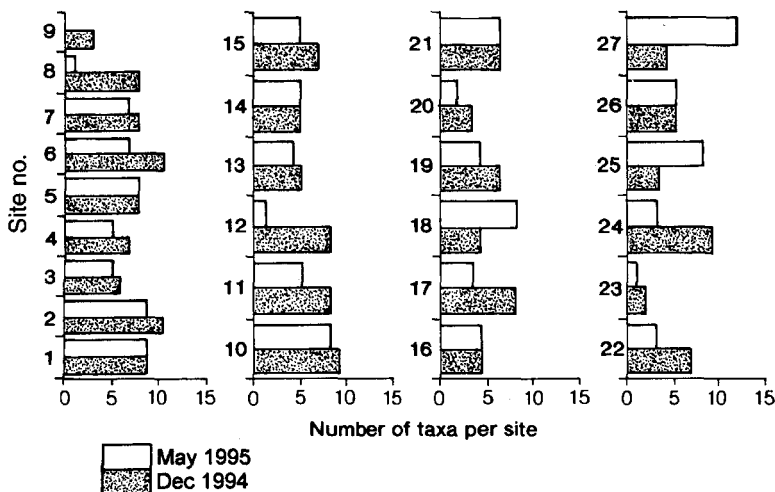


Fig. 2 Species richness of bivalve molluscs in Survey 1 (December 1994) and Survey 2 (May 1995). Values are pooled across 3 replicate samples at each site.

temporal patterns. Pigi were counted and measured in 10 replicate samples taken at that site in 1991 and 1992, and five samples in 1993. The software package ELEFAN (ICLARM, Philippines: see Rosenberg & Beddington 1988) which uses the Bhattacharya (1967) method to distinguish cohorts in size frequency data, was used to obtain mean lengths and standard deviations of cohorts. Two additional 0.1 m<sup>2</sup> samples in an area of high pigi density (Site 19) were taken in June 1995 to further document population size structure. These samples were stained with Rose Bengal to facilitate finding small pigi, but were not sieved to avoid disruption of paired shells still linked by ligament ("cluckers" —Orensanz 1986). Shell lengths of all intact individuals and cluckers were measured.

## RESULTS

### Assemblage composition

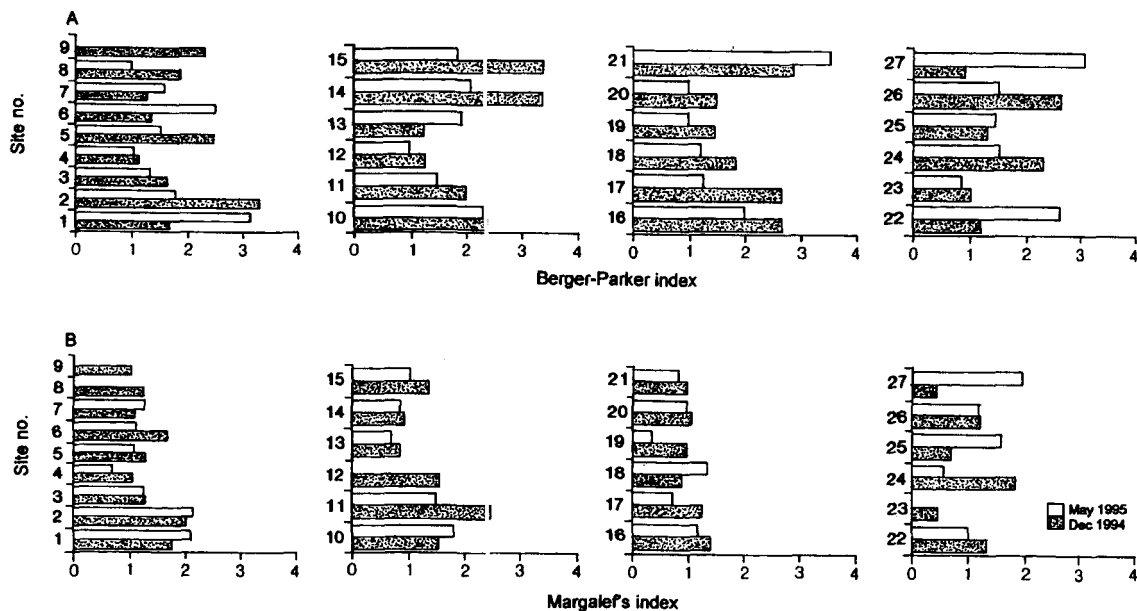
A total of 25 bivalve taxa was identified to species level in the 80 samples (one sample was lost) taken in Survey 1 (Table 1). The five most common taxa accounted for almost 85% of the 3673 individual animals recorded. The most common was the morning star shell (*Tawera spissa*) (33% of individuals), then the venus clam (*Ruditapes largillierti*) (22%), pigi (*Paphies australis*) (18%), the wafer shell (*Soletellina siliquens*) (7%), and the wedge shell (*Macomona liliana*) (5%). In Survey 2 the five most common taxa accounted for 93% of the 6532 individuals from 20 taxa recorded. The most common

taxon was *P. australis* (67% of individuals), then *T. spissa* (12%), *R. largillierti* (7%), the sunset shell (*Gari stangeri*) (4%), and the nutshell (*Nucula nitidula*) (3%).

In Survey 1 the most speciose sites were 2 and 6 at the estuarine end of Centre Bank, which had 11 species present (Fig. 2). The lowest number of taxa (2) was recorded from Site 23, near Sulphur Point. At all remaining sites between 3 and 9 taxa were recorded. The number of taxa recorded was the same or lower in Survey 2 than in Survey 1 for all sites except three in the central eastern part of the bank (Sites 18, 25, and 27). In 1995 Site 27 recorded the highest number of taxa, 12. In May, there were no bivalves at Site 9, close to the shore of Matakana Island. Several sites spread over most of Centre Bank recorded a single taxon (e.g., 8, 12, 20, and 23). Between 2 and 9 taxa were recorded at the remaining sites.

Temporal variation dominated trends in the Berger Parker dominance index (Fig. 3A). The Berger-Parker index was lower in Survey 2 than in Survey 1 at 18 of 27 sites (Fig. 3A). Consistently high dominance only occurred at Site 21, in the north-western part of the bank. An area of low dominance ran from the southern part of the grid (Sites 3 and 4), through Site 12, to Sites 18, 19, 20 in the central part of the bank.

Margalef's species diversity index similarly showed high temporal variability (Fig. 3B). Values at some sites were very low, but there was no geographic pattern to this (Fig. 3B). Sites on the south-eastern side of the sampling area had high values of the index.



**Fig. 3** A, Berger Parker dominance indices for the 27 sites sampled in Survey 1 (December 1994) and Survey 2 (May 1995). Values are pooled across 3 replicate 0.1 m<sup>2</sup> samples for each site. B, Margalef's diversity indices for the 27 sites sampled in Survey 1 (December 1994) and Survey 2 (May 1995). Values are pooled across 3 replicate 0.1 m<sup>2</sup> samples.

**Table 2** Results of variance component analyses (Proc Varcomp, SAS: SAS Institute Inc. 1989) for the log<sub>10</sub> (x+1)-transformed abundances of the 10 most abundant bivalves in December 1994 and May 1995 surveys of Centre Bank, Tauranga Harbour, New Zealand. Variance components (SE) are given for site and replicate. Sampling sites in Fig. 1. SEs on variance components were calculated by restricted maximum likelihood.

| Species                       | Dec 1994    |             | May 1995    |             |
|-------------------------------|-------------|-------------|-------------|-------------|
|                               | Site        | Replicate   | Site        | Replicate   |
| <i>Paphies australis</i>      | 0.31 (0.09) | 0.05 (0.01) | 0.60 (0.17) | 0.04 (0.01) |
| <i>Ruditapes largillierti</i> | 0.34 (0.10) | 0.03 (0.01) | 0.25 (0.07) | 0.03 (0.01) |
| <i>Tawera spissa</i>          | 0.32 (0.10) | 0.13 (0.02) | 0.29 (0.09) | 0.05 (0.01) |
| <i>Gari stangeri</i>          | 0.13 (0.04) | 0.03 (0.01) | 0.22 (0.06) | 0.02 (0.00) |
| <i>Macomona liliana</i>       | 0.14 (0.04) | 0.02 (0.00) | 0.06 (0.02) | 0.02 (0.00) |
| <i>Soletellina siliquens</i>  | 0.11 (0.04) | 0.07 (0.01) | 0.12 (0.04) | 0.03 (0.01) |
| <i>Nucula nitidula</i>        | 0.05 (0.01) | 0.02 (0.00) | 0.17 (0.05) | 0.02 (0.00) |
| <i>Nucula hartvigiana</i>     | 0.09 (0.03) | 0.03 (0.01) | 0.06 (0.02) | 0.03 (0.01) |
| <i>Divaricella huttoniana</i> | 0.01 (0.01) | 0.05 (0.01) | 0.00 (0.00) | 0.01 (0.00) |
| <i>Myadora striata</i>        | 0.02 (0.01) | 0.03 (0.01) | 0.03 (0.01) | 0.02 (0.00) |

**Spatial patterns**

For the 10 most abundant taxa, among-site variability was generally greater than within-site variability (Table 2). There was a general trend of greater among-site variation with increasing abundance.

Density of *Paphies australis* varied greatly among sites in both Survey 1 and Survey 2 (Fig. 4A). *P. australis* occurred in only one survey at several sites, and was absent in both surveys at several others (5, 13, 17, and 24). Seven sites across Centre Bank (four of those at the south-eastern end) recorded

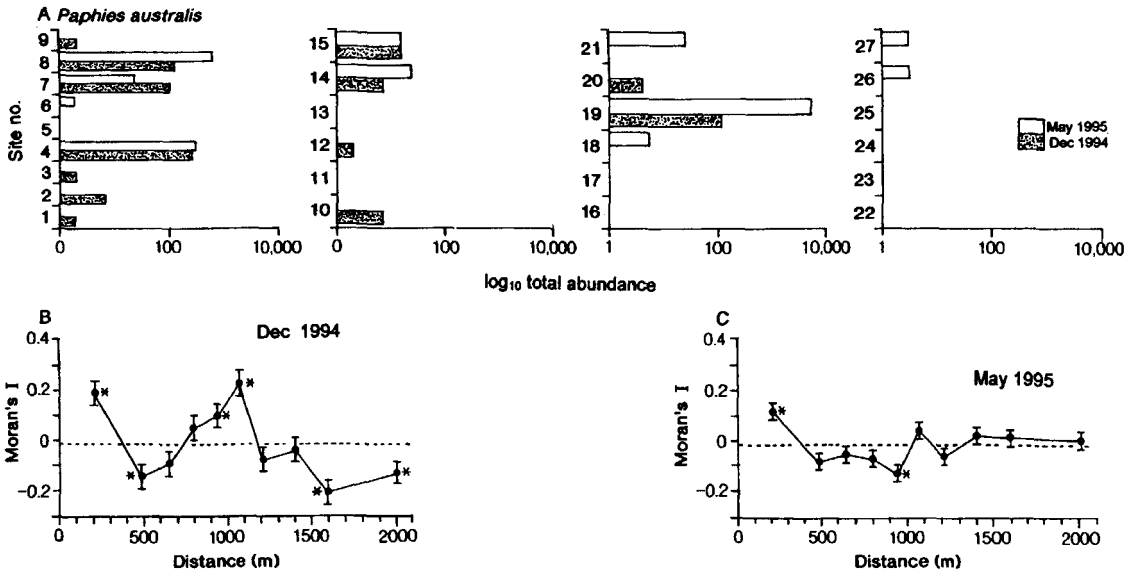


Fig. 4 A, Abundance patterns of *Paphies australis* in Survey 1 (December 1994) and Survey 2 (May 1995). Values are pooled across 3 replicate 0.1 m<sup>2</sup> samples. B, C, Correlograms of Moran's I for the abundance of *P. australis* in: B, Survey 1 (December 1994); and C, Survey 2 (May 1995).

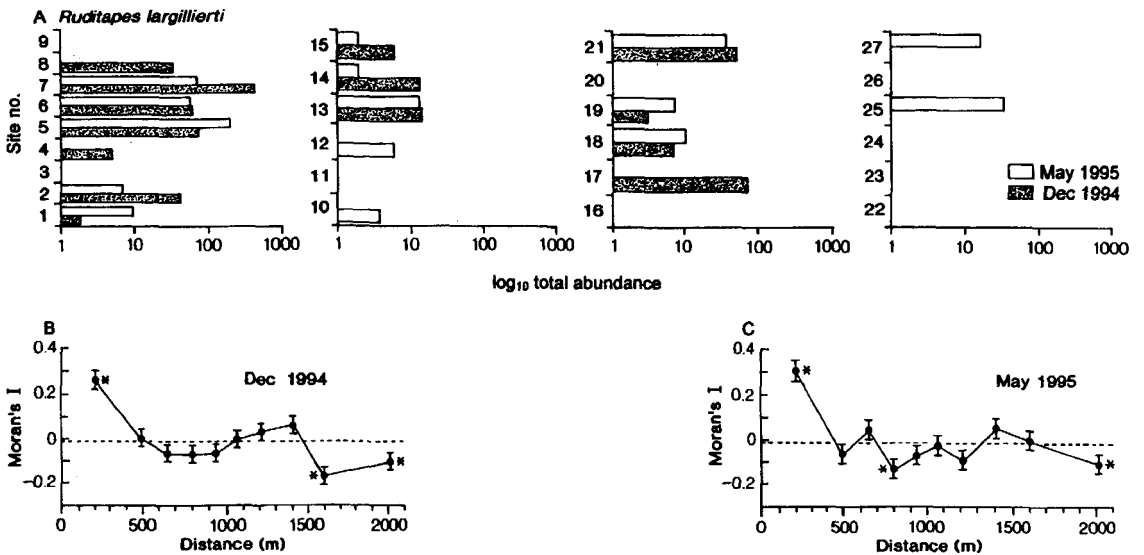
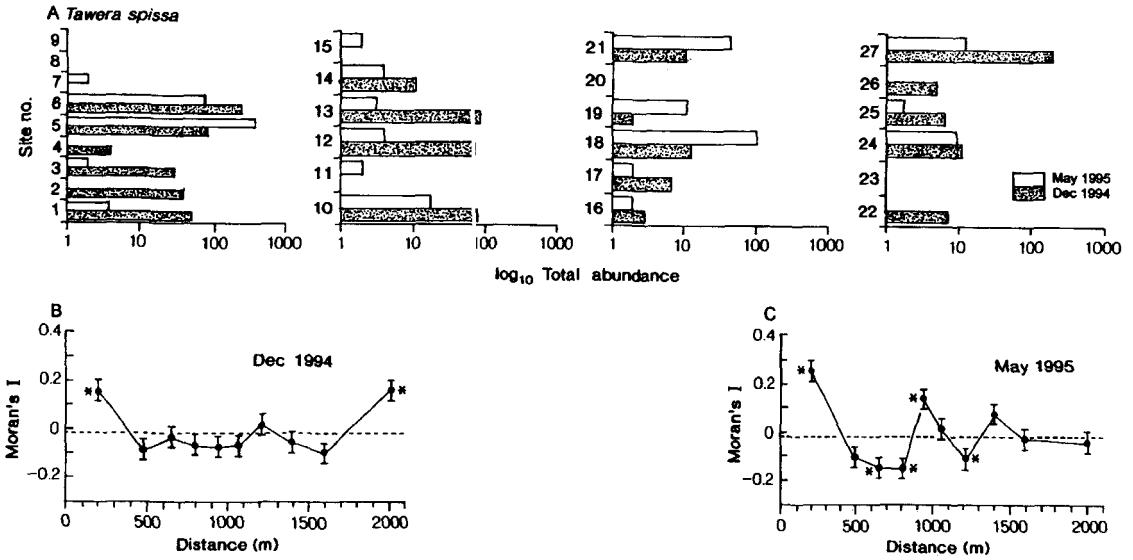


Fig. 5 A, Abundance patterns of *Ruditapes largillierti* in Survey 1 (December 1994) and Survey 2 (May 1995). Values are pooled across 3 replicate 0.1 m<sup>2</sup> samples. B, C, Correlograms of Moran's I for the abundance of *R. largillierti* in: B, Survey 1 (December 1994); and C, Survey 2 (May 1995).



**Fig. 6** A, Abundance patterns of *Tawera spissa* in December 1994 and May 1995 surveys. Values are pooled across 3 replicate 0.1 m<sup>2</sup> samples. B, C, Correlograms of Moran's I for the abundance of *T. spissa* in: B, Survey 1 (December 1994); and C, Survey 2 (May 1995).

*P. australis* in Survey 1 and not Survey 2. *P. australis* appeared in Survey 2 at Sites 6, 18, 21, 26, and 27 having been absent there in Survey 1. At sites where *P. australis* was recorded in both surveys, densities were relatively similar in both surveys, with the exception of Site 19, where abundance changed dramatically from a total of 93 individuals in Survey 1 to 3330 in Survey 2. Correlograms of Moran's I for the density of *P. australis* in Survey 1 suggested positive autocorrelation at distances of up to 200 m (Fig. 4B). Significant negative autocorrelation occurred at c. 500 m, with values becoming significantly positive again at c. 1 km. In contrast, Moran's I values in Survey 2 did not deviate far from the values expected under the null hypothesis, being significantly positive at 200 m and significantly negative at c. 1 km (Fig. 4C).

*Ruditapes largillierti* showed two distinct areas of high density, one across Sites 5, 6, 7, and 8, the other across Sites 13, 14, and 15 (Fig. 5A). Sites 8 and 17 changed conspicuously, recording a high density in Survey 1, then zero density in Survey 2. Similarly, individuals were recorded at Sites 4, 10, and 12 in Survey 1, but were absent there in Survey 2. *R. largillierti* was not present in Survey 1 at Sites 25 or 27, but appeared in moderate numbers there in

Survey 2. Sites 18, 19, and 20 recorded consistent densities in Survey 1 and 2. The overall shape of the correlogram for *R. largillierti* did not change from Survey 1 to Survey 2 (Fig. 5B,C). Correlograms of Moran's I for *R. largillierti* were significantly positive at a distance of 200 m for both surveys. Negative autocorrelation occurred at distances of 1600 and 2000 m in Survey 1 but not in Survey 2.

*Tawera spissa* was evenly distributed across the entire bank, with individuals being present at most sites in both surveys and it was absent from only four sites (8, 9, 20, and 23) (Fig. 6A). Densities of *T. spissa* varied among sites and between the two surveys. At only four of the 14 sites (5, 18, 19, and 21) at which *T. spissa* occurred did Survey 2 densities increase over densities recorded in Survey 1. In Survey 1 densities of *T. spissa* were found to be significantly positively autocorrelated at two extreme distances, 200 and 2000 m (Fig. 6B). Distances between these two extremes were non-significantly negatively autocorrelated. The shape of the correlogram for *T. spissa* in Survey 2 was quite different, with densities being significantly positively autocorrelated at a short distance of 200 m then again at c. 1 km, with intervening negative autocorrelation at distances of 450–800 m (Fig. 6C).



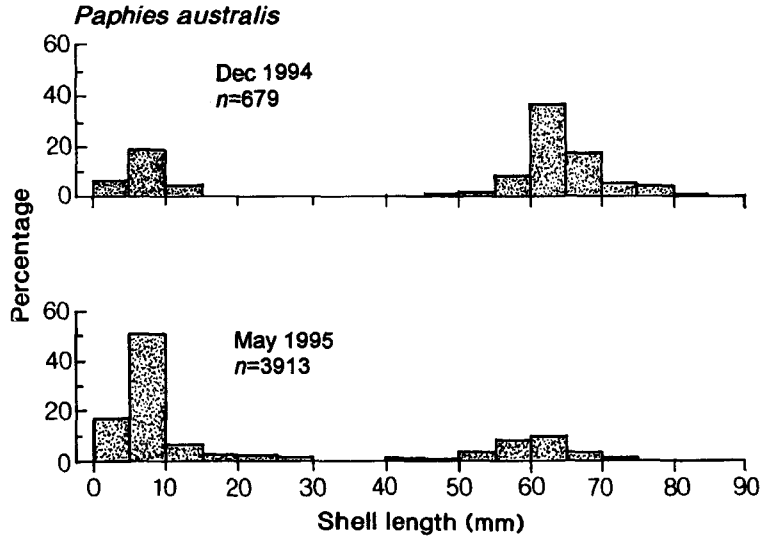


Fig. 7 Size frequency distribution for *Paphies australis* in Survey 1 (December 1994) and Survey 2 (May 1995), pooled across all sites.

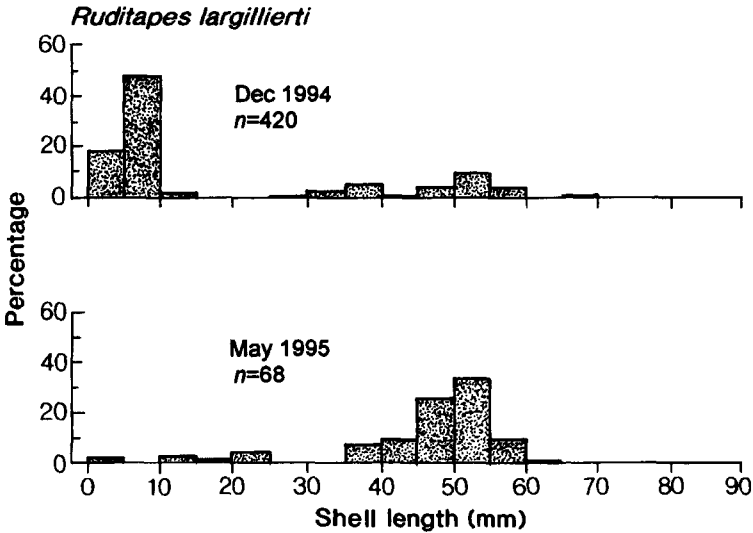


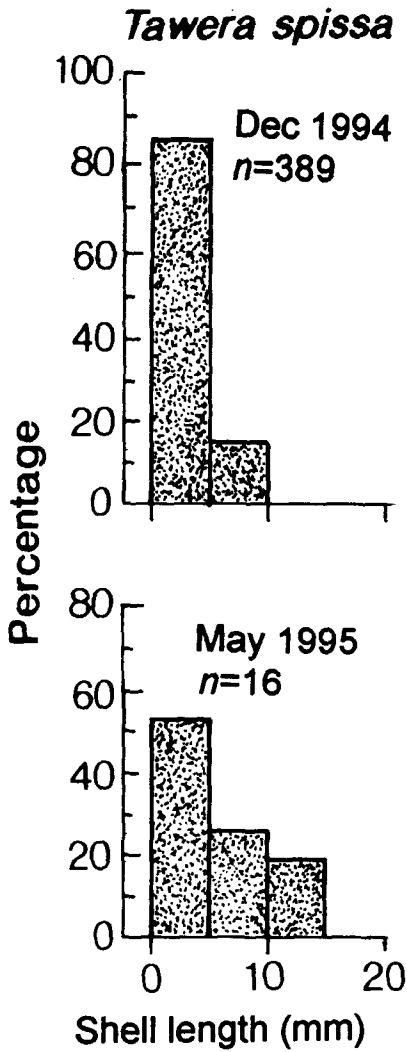
Fig. 8 Size frequency distributions for *Ruditapes largillierti* at Site 7 in Survey 1 (December 1994) and Survey 2 (May 1995).

### Population size structures

As bivalve assemblages across Centre Bank were dominated by *Paphies australis*, *Ruditapes largillierti*, and *Tawera spissa*, their population size structures were investigated further. In Survey 1 *P. australis* had an obviously bimodal size structure; there was a distinct juvenile cohort centered around 5–10 mm, and a larger adult cohort in the 55–65 mm range (Fig. 7). Recruitment changed the size structure of the population of *P. australis* across the sampling area dramatically from Survey 1 to Survey 2, with the percentage of individuals in the 5–10 mm size class increasing markedly (Fig. 7). The increase

in the 5–10 mm size class was mainly because of a heavy recruitment at Site 19 where roughly 30 times ( $n=2899$ ) more pipi were recorded in Survey 2 than in Survey 1, with most (68%) being 5–10 mm. The 12% of the total comprising adult *P. australis* (55–65 mm) in Survey 2 was a marked decrease from 53% in Survey 1.

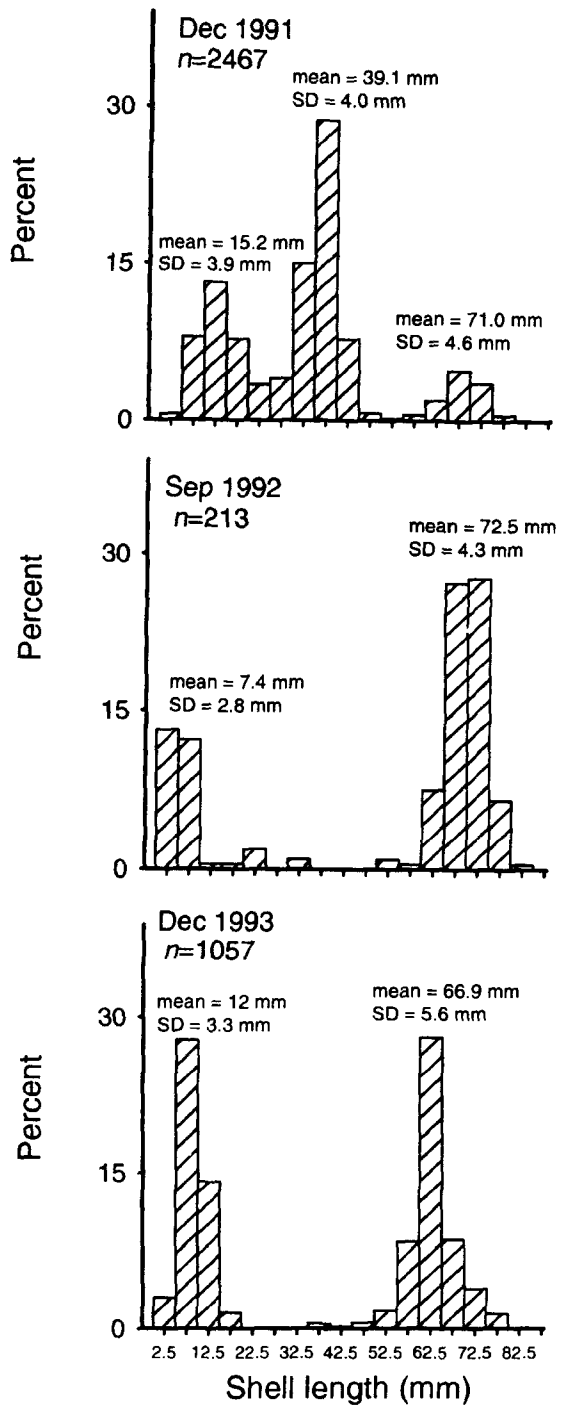
There were bimodal size frequency distributions for *Ruditapes largillierti* in both surveys. In Survey 1 the population was dominated by juveniles (1–15 mm) and an adult cohort (45–60 mm). Approximately half the juveniles recorded in Survey 1 occurred at Site 7 (Fig. 8). The juvenile cohort of



**Fig. 9** Size frequency distributions for *Tawera spissa* at Site 27 in Survey 1 (December 1994) and Survey 2 (May 1995).

*R. largillierti* was much less abundant in the second survey.

*Tawera spissa* showed a unimodal structure in Survey 1 (Fig. 9). There was a dominant cohort of very small animals (0–5 mm), with the remaining size classes combined accounting for less than 33% of individuals. Approximately one-third of all *T. spissa* recorded across Centre Bank in Survey 1 were found at Site 27. The length-frequency histogram for the *T. spissa* population in Survey 2 at that site indicates that the abundance of the cohort of small juveniles seen in Survey 1 decreased (Fig. 9).



**Fig. 10** Population size structure of *Paphies australis* at Site 9 during December 1991–December 1993. Means and standard deviations of shell lengths are given for each cohort (as derived by ELEFAN analysis). ( $n$  = number measured.)

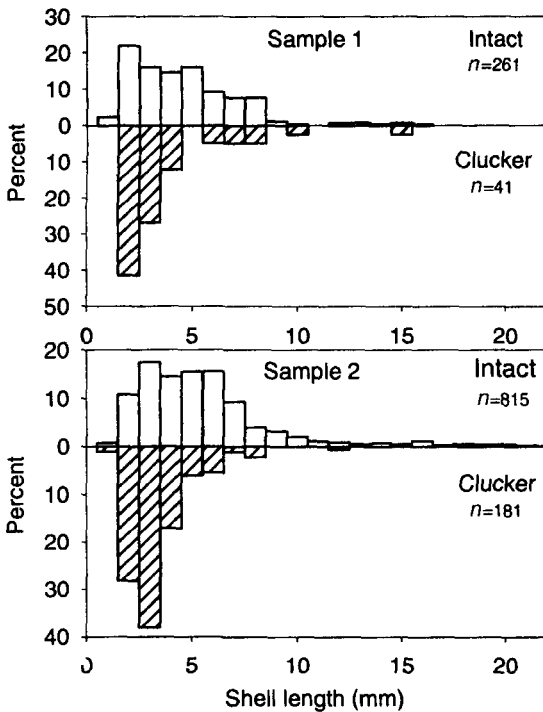


Fig. 11 Size frequency distributions for live (upper bars) and "clucker" (lower bars) *Paphies australis* in two samples (upper and lower panels) at Site 19 in June 1995.

Mean density of pipi at Site 9 fluctuated greatly over time from 248 (SE = 27) in 1991, it decreased to 24 (SE = 3), and then increased to 212 (SE = 22) in 1993. The population size structure suggested that an intermediate cohort vanished from the site during that time, whereas small and large cohorts remained present throughout (Fig. 10). The two additional samples from Site 19 had high abundances of both cluckers and live pipi (Fig. 11). The modal sizes of cluckers were slightly smaller than live animals in both samples.

## DISCUSSION

Bivalve assemblages were diverse and locally dense on Centre Bank. There was conspicuous spatial variation in their abundances, with the most abundant species having variability at spatial scales of the order of 200 m. Much of the temporal variation in densities of abundant species resulted from recruitment events. Recruitment for some species was extremely localised, and population size

structures suggested heavy post-settlement mortality and/or dispersal.

Great variability in populations of bivalves as a result of events early in life are well-known (e.g., Coe 1953). The increase in the total number of individuals recorded in Survey 2 is because of the recruitment of juvenile pipi at Site 19. Creese (unpubl. data) found high inter-annual variability in recruitment of pipi at Whangateau Harbour (36°19'S 174°46'E). The declines in cohorts of small individuals of the abundant species are similar to those described for intertidal populations of *Macomona liliana* (Roper et al. 1992), and could be explained by mortality and/or dispersal. Gosselin & Qian (1997) reviewed several studies of bivalves and found that the greatest survivorship over the first 60 days of juvenile life was 50%. Post-settlement migration (e.g., Hooker 1995a) confounds the simplest way of assessing mortality (cohort monitoring), and our clucker data suggest that mortality occurring at the time of dispersal may be high.

Post-larval juveniles of many bivalves are capable of active drifting (e.g., Cummings et al. 1993; Cummings et al. 1995; Hooker 1995a; Olivier et al. 1996), and we observed pipi doing so in Tauranga Harbour. Various cues for drifting, such as contaminants (Pridmore et al. 1991), local densities (Hooker 1995a; Commito et al. 1995a,b), lunar cues (Armonies 1992), as well as changes in water currents and temperature (Sorlin 1988) have been proposed or experimentally demonstrated, but simple developmental events are equally valid explanations. Hooker (1995a) also found that drifting by pipi was highly episodic and suggested that it occurred mainly at night. We suggest that the cohort dynamics of pipi at the site monitored between 1991 and 1993 reflect successive recruitments and subsequent losses via mucus drifting and mortality. Hooker (1995b) found pipi reached 30 mm shell length after 1 year, so growth from the ~10 mm cohort to the 60 mm+ cohort in one year is unlikely, but size-specific predation could also have caused the loss of cohorts. Growth to 30 mm shell length in the first year also suggests that successive cohorts recruited to Site 9. The variations in the mean shell length of the largest cohort are within 2 standard deviations of the mean, and probably a result of sampling error.

Vertebrate predators of bivalves such as eagle rays and wading birds influence distributions of intertidal bivalves in Manukau Harbour (Thrush et al. 1994). Wading birds seldom have access to bivalve populations of a subtidal area such as Centre Bank. Fishes, crabs, whelks, and starfish are more

likely predators in the subtidal parts of Tauranga Harbour. Ray pits occur on Centre Bank (P. J. Hull pers. obs.), but at much lower densities than in Manukau Harbour (Thrush et al. 1994; Hines et al. 1997), and we doubt that they play an important role. Putt's (1996) study of three invertebrate predators of bivalves present across Centre Bank, (the sea stars *Coscinasterias calamaria* and *Patiriella regularis* and the whelk *Cominella adspersa*) suggested that abundances of these predators are generally not high, and that the low movement rates of those predators in patches of an abundant resource were a result of satiation. We have no information regarding other possible predators. The presence of cluckers in the samples of juveniles is consistent with predation by non-crushing predators, but other agents (e.g., starvation, disease, physical stress) would also produce cluckers.

We found little evidence of distinctive "communities" (= assemblages) characteristic of particular parts of the flood tide delta. Whereas some abundant species are limited to harbour environments (e.g., *Paphies australis*), others are abundant offshore also (e.g., *Tawera spissa*, *Gari stangeri*) (Kamenev et al. 1993; Cole, Healy, & Foster unpubl. data). We predict that if distinct assemblages were to exist they would likely segregate along lines of species with similar dispersal abilities and timing of dispersal events. The most conspicuous events at the assemblage level (alterations to dominance and evenness) were driven by individual species.

Spatial autocorrelation revealed that densities of the three most abundant bivalves were similar at distances up to about 200 m in both surveys. Thrush's (1991) review suggested homogeneous abundances of soft sediment organisms at scales ranging from 0.01 to 100 m. It is difficult to compare spatial patterns identified in this study with others as there have been few similar subtidal studies. (As different sampling designs are sensitive to different scales of pattern, comparisons must be informal.) In a small-scale grid study, Hooker (1995b) found similarity of pipi densities at 5 and 10 m scales, with variable patchiness at distances of up to 50 m. His study site was a much smaller harbour whose channels are not dredged. Harbour channels are probably the main habitat of adult pipi (Hooker 1995b), and Hull's (1996) grid study revealed similar results to that of Hooker's (1995b). Thrush et al. (1989) estimated scales of distribution of 5–30 m for several intertidal bivalves in the Manukau Harbour. Hewitt et al. (1996) identified smaller scale (5 m – 3 m) patchiness in abundances of two intertidal

bivalves using similar techniques; the present study did not address those scales.

## ACKNOWLEDGMENTS

Thanks to Port of Tauranga Ltd (especially G. Thompson, N. Sinclair, and P. Barrow) for financial and logistic support; W. Blom and H. Grenfell for organising the early monitoring; F. Putt, N. Dobbie, S. Purdue, S. Stephens, R. Butler, and D. Foster for field assistance; C. Grant and M. Wilkie for the ELEFAN analysis; and K. R. Grange, S. J. Handley, D. Keuskamp, D. J. Morrissey, M. A. Morrison, and M. D. Taylor for comments on the manuscript.

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