

Distribution of barnacle larvae in Mahurangi Harbour, North Auckland

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Keywords barnacles; *Balanus variegatus*; *Elminius modestus*; nauplii; estuarine plankton; larval retention; Mahurangi Harbour; distribution; description; oyster

Abstract The naupliar stages of *Balanus variegatus* Darwin are described from laboratory-reared and field-collected specimens. In Mahurangi Harbour (36°30'S, 174°44'E), adults of *B. variegatus* occur in the upper reaches, *Elminius modestus* occurs throughout the harbour, and other coastal species of barnacles occur at the harbour entrance and outside. The plankton was sampled at 13 stations along the length of the harbour during the summer of early 1981 with a 65 µm mesh net. The larvae of *B. variegatus* were found in samples on 14 March (high and low tide) and 4 April (low tide). On these occasions, all stages of all barnacle larvae, and other zooplankton, were enumerated. Maximum numbers of the larvae of *B. variegatus* and *E. modestus* occurred in the middle harbour, with apparent accumulation of late stage nauplii and cyprids of the more numerous *E. modestus*. Maximum numbers of the nauplii of the coastal species *Balanus trigonus*, *Chamaesipho columna*, *Epopella plicata*, and *Chamaesipho brunnea* occurred at the harbour entrance, their pattern of distribution was similar to those of coastal cladocerans *Penilia avirostris* and *Evadne tergestina*. The only plankter with a restricted up harbour distribution was the estuarine copepod *Sulcanus conflictus*. The maxima of occurrence of larvae of *B. variegatus* down harbour from the position of the adult population is interpreted as a result of current flows and tidal oscillations, retaining the larvae within the harbour system. Such larval retention may explain why Mahurangi Harbour is a good place for oyster settlement.

INTRODUCTION

The Mahurangi Harbour is recognised as a good place for consistent settlement of oyster larvae (Dinamani & Lenz 1977), and oyster settlement farms have been established there to provide settled oysters for farms in other harbours and estuaries where spat settlement is less predictable. The better spatfall may be attributable to more favourable larval development conditions, but there is no evidence that planktonic conditions are any different from other northern New Zealand harbours. Alternatively it may be that the larvae are somehow retained or aggregated by the topography and hydrology of the harbour system. Plankton evidence for such larval retention is sparse, and the problem seems intractable because of difficulties of tracking pelagic larvae, or determining their origins.

This paper describes plankton samples taken at 13 stations in Mahurangi Harbour (Fig. 1), and describes how larvae are distributed within the system. Instead of oyster larvae, barnacle larvae have been used as indicators because of the ease with which the larvae can be aged (to moult stage) and because the adults of the various barnacle species are differently distributed within and outside the harbour (Fig. 1). One species in particular, *Balanus variegatus* Darwin (see below for discussion on taxonomy), is a convenient spatial marker because the adults are confined to the upper parts of the harbour where they occur on mangrove trunks and occasional low tidal hard substrata. Other species, like *Chamaesipho columna* sensu Darwin, *Epopella plicata* (Gray), and *Balanus trigonus* Darwin, are not characteristic of the harbour but occur abundantly at the harbour entrance and outside. The commonest barnacle throughout the harbour is *Elminius modestus* Darwin, occurring abundantly on stems and pneumatophores of mangroves along the banks of the middle and upper harbour and also across the oyster reefs of the lower harbour.

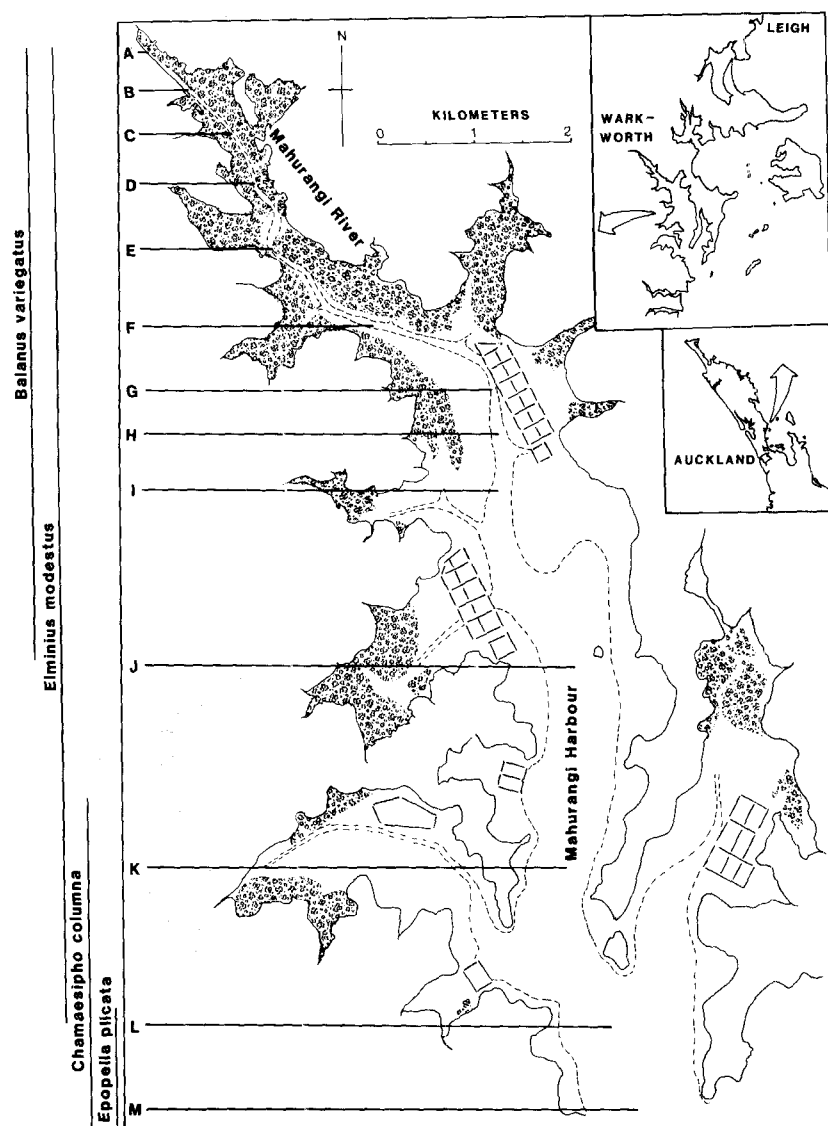


Fig. 1 Mahurangi Harbour showing positions of plankton sampling stations (A-M), low tide channels (dashed lines), mangroves (stippled), and oyster farms (boxes). Intertidal distribution of adult barnacles along the length of the harbour is shown on the left.

Larvae of some northern New Zealand barnacles have been described by Barker (1976), but because the larvae of *B. variegatus* from New Zealand have not been described they had to be identified for this study. To confirm the suspected *B. variegatus* identity of larvae from Mahurangi Harbour, larvae were reared from adults collected from the Harbour.

Karande (1974) described larvae from India as *B. variegatus* but it is likely that these Indian populations are *Balanus cirratus* Darwin. The type locality of *B. variegatus* is Sydney, Australia (Harding 1962), and Australian specimens are the same as New Zealand ones (Foster, unpub. obs.). Henry

and McLaughlin (1975) identified New Zealand specimens as the northern Pacific *Balanus kondakovi* Tarasov and Zevina, and synonymised *B. cirratus* with *B. variegatus*. Until the taxonomy of this group of barnacles is clarified, a stand is taken here that temperate Australasian populations are *B. variegatus**.

*Since this paper went to press, Lewis (1985) has confirmed that the Australian and New Zealand species is *Balanus variegatus* Darwin.

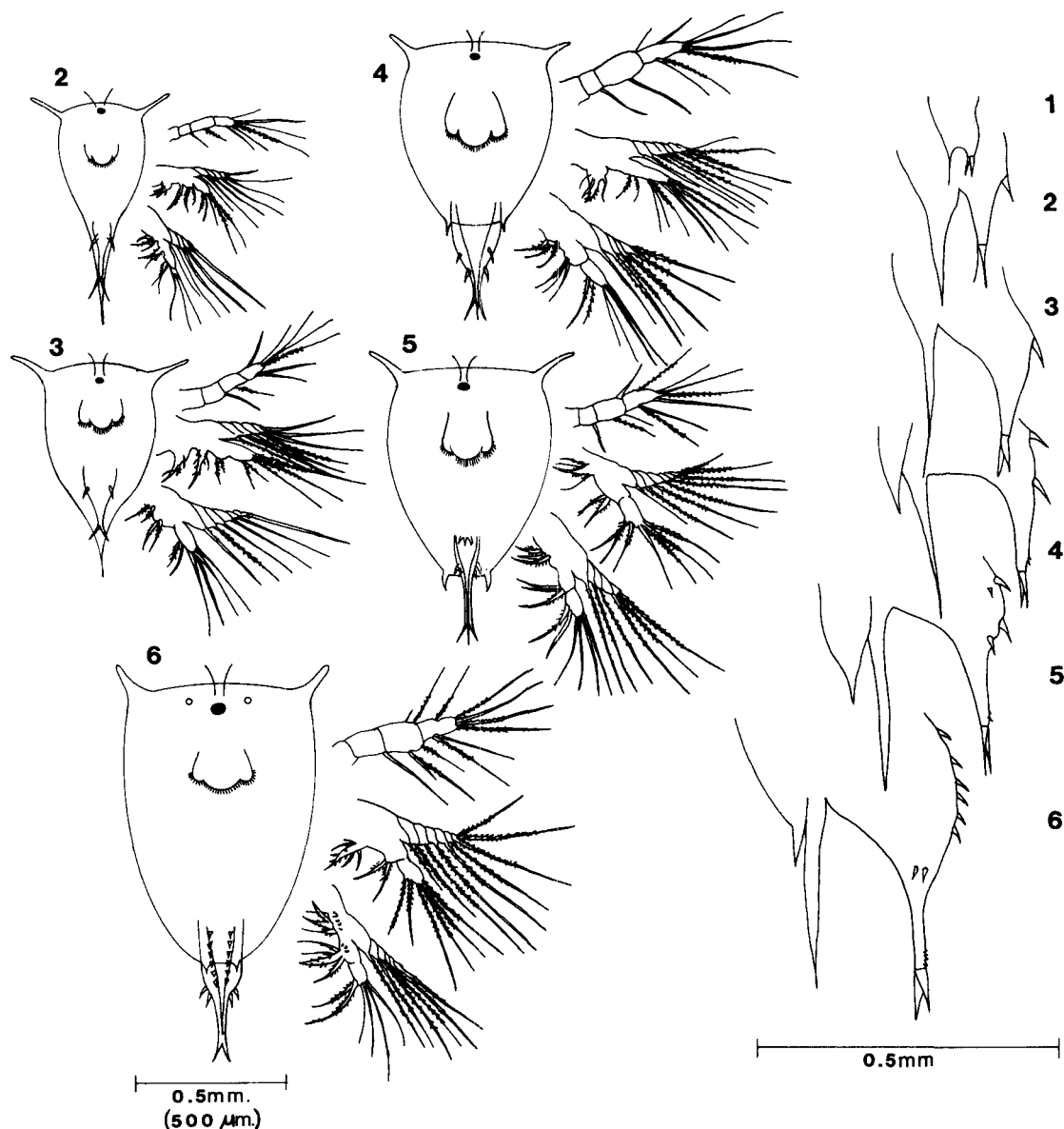


Fig. 2 *Balanus variegatus*: body (ventral view), appendages (antennule, antenna, and mandible), and lateral view of posterior part of body of naupliar stages.

Mahurangi Harbour (36°30'S, 174°44'E) is a drowned river valley on the eastern coast of the North Auckland Peninsula, 117 km north of Auckland city. The harbour is a shallow water estuary 16 km long, receiving the Mahurangi River at its northern end as the major freshwater input and opening seawards through a single, deep water

(18 m) mouth. The hydrology has been investigated by Harrison et al. (1974), who calculate a total high spring tide volume of $89 \times 10^6 \text{ m}^3$, and a low spring tide volume of $40 \times 10^6 \text{ m}^3$. There is a relatively low residence time (0.9 day by the method given in Heath 1976). In the upper harbour almost all the water leaves during the ebb tide. In the lower

harbour, there is a directional flow of water along the main channels flowing landward on the flood tide, but stratified on the ebb tide with a landward flowing bottom layer of water and a seaward drifting top layer. Dye and float tests made by Harrison et al. (1974) indicated that a body of water leaving an area of the lower harbour at high tide returned to approximately the same area with the next flood tide.

MATERIALS AND METHODS

In the summer of early 1980, samples of plankton were non-routinely collected from Mahurangi Harbour to search for likely *B. variegatus* larvae. Nauplii differing from published descriptions of other balanomorph nauplii of the region (Barker 1976) were found in samples collected from February to April. To confirm the suspected identity of these larvae, adult *B. variegatus* were collected at this time, and mature ovigerous lamellae hatched and reared on a diet of phytoplankton. The phytoplankton were collected from Waitemata Harbour with a 60 µm mesh net after refiltering through 75 µm mesh to remove zooplankton and large phytoplankton. The algae were mainly chain diatoms, including *Skeletonema*. Stages 1 to 6 nauplii were reared, and these were identical to the above-mentioned nauplii in the plankton samples, confirming their identity as *B. variegatus*.

In the summer of early 1981, the plankton was routinely (about every 2 weeks) sampled from a dinghy at 13 mid channel sampling stations (A-M) established along the length of the Harbour (Fig. 1). At each station, 3 vertical hauls of plankton were obtained with a weighted conical monyl net of 75 µm mesh, 1 m long and with a 30 cm mouth diameter. The net fished while being hand-hauled from near the bottom to the surface. The volume of water filtered was calculated from the length of rope let out and net diameter. Each sampling run took 3 h to complete, starting at Station A 1.5 h before high or low tide extreme and then proceeding down harbour. The samples were preserved in 4% formalin in sea water, and later qualitatively examined in the laboratory for nauplii of *B. variegatus*.

For quantitative assessment of only the plankton samples containing *B. variegatus* larvae, the dominant plankton species and the stage of barnacle larvae were enumerated from replicated one-tenth subsamples from each sample, using a Bogorov counting tray. Counts were converted to numbers per cubic metre as occurring in the harbour.

RESULTS

Identification of nauplii of *Balanus variegatus* Darwin

The nauplii of *B. variegatus* are illustrated in Fig. 2. They can be distinguished from larvae of other barnacles by carapace shape. *Chamaesipho* nauplii were recognised by the shape of the labrum and carapace. *B. trigonus* and *E. plicata* (Gray) have large nauplii with characteristic carapace shapes, fronto-lateral horns, and posterior carapace spines. The nauplii of *B. variegatus* particularly differ from the nauplii of *B. trigonus* (the only cogenitor in the locality) by their less rounded anterior carapace margins. Nauplii of *B. variegatus* and *E. modestus* are the most similar. The former can be distinguished by their large size (stage for stage), by the shorter central lobe of the tri-lobed labrum, the position of the lateral spines on the abdominal process (positioned anterior to the bifurcation rather than behind it as in *E. modestus*), and their larger fronto-lateral horns and posterior carapace spines, the latter being further apart and slightly curved.

Distribution of barnacle nauplii in the plankton

Of the samples enumerated and described herein, larvae of only 6 barnacle species were captured — *E. modestus*, *B. variegatus*, *C. columna*, *B. trigonus*, *E. plicata*, and *Chamaesipho brunnea* Moore in order of decreasing abundance. Only on 2 sampling occasions were the larvae of *B. variegatus* present — 14 March and 4 April 1981. On the former day, the 13 stations were occupied at both high and low tide, and on the latter only at low tide. The distribution of all nauplii of *E. modestus* on both the high and low tide sampling occasions on 14 March is shown in Fig. 3. The numbers of *B. variegatus* larvae are shown similarly in Fig. 4. *E. modestus* larvae were generally an order of magnitude more abundant than those of *B. variegatus*, with peak density at Station I at high tide, displaced down estuary to Station K at low tide. The nauplii of *B. variegatus* exhibited some bimodality of occurrence, peaking at Stations F and I at high tide, displaced down stream to H and J at low tide.

The distribution of the various larval stages, at each station, and for the 3 sampling occasions, is shown in Fig. 5 for *E. modestus* and Fig. 6 for *B. variegatus*. For *E. modestus* there were fewer larvae on the second sampling date, but the higher mid harbour peak reoccurred. The cyprid larvae (stage 7) at each station (except down harbour on high tide 14 March) were as abundant as early stage 2 nauplii, and mostly more abundant than late stage nauplii so that a bimodal pattern was apparent at the up harbour stations where they occurred. *B. variegatus* cyprids were not collected, and late stage

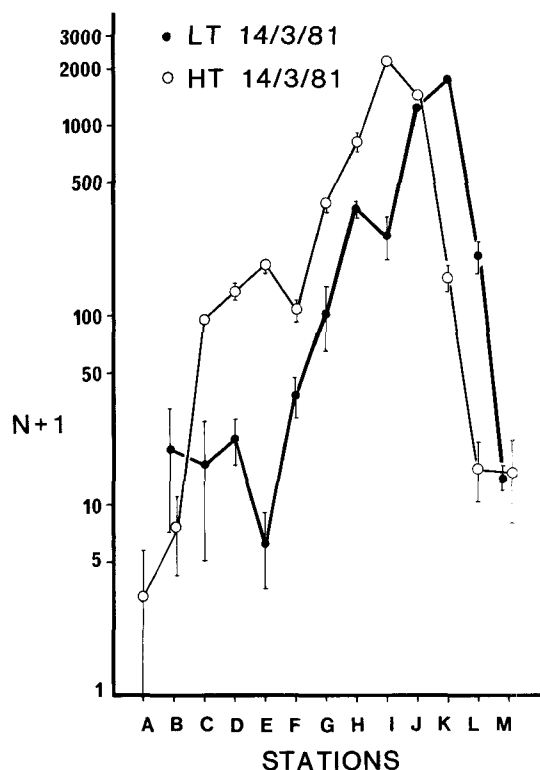


Fig. 3 Mean densities (m^{-3}) of nauplii of *E. modestus* in plankton samples collected over low tide (LT) and high tide (HT) on 14 March 1981. Vertical lines indicate standard error of the mean.

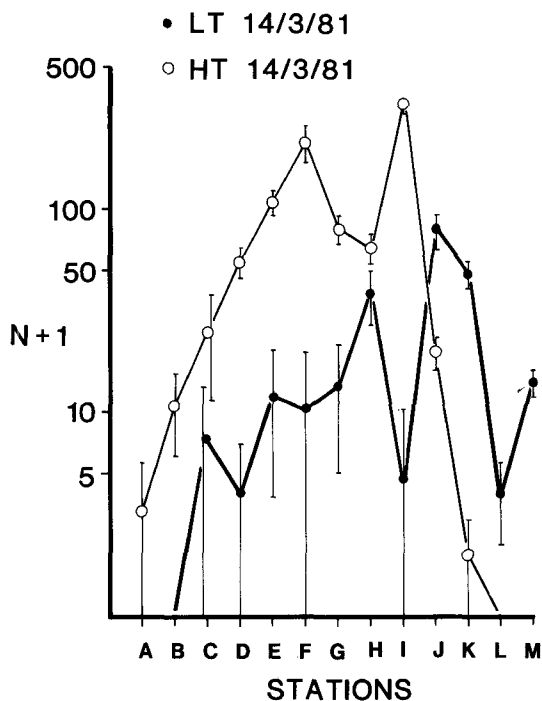


Fig. 4 Mean densities (m^{-3}) of nauplii of *B. variegatus* in plankton samples collected over low tide (LT) and high tide (HT) on 14 March 1981. Vertical lines indicate standard error of the mean.

nauplii were collected only at the mid harbour stations on 14 March, there contributing to the peaks shown in Fig. 4. These stations were down stream from the distribution of adults of this species (Fig. 1).

In contrast to the mid harbour accumulation of larvae of *E. modestus* and *B. variegatus*, the larvae of *C. columna* (Fig. 7) and *B. trigonus* (Fig. 8) were more common down harbour, with early nauplii more abundant than late stage nauplii. Nauplii of *E. plicata* were caught only at Stations I-K on all 3 occasions, and of *C. brunnea* at Stations J and K on 14 March only.

The numbers of some other zooplankton species collected at high tide on 14 March are shown in Fig. 9. These species have been selected to illustrate the following patterns:

(1) up harbour dominance of the copepod *Sulcanus conflictus*, the only species to show this pattern;

- (2) down harbour dominance of marine species like the cladocerans *Penilia avirostris* and *Evadne tergestina*;
- (3) a more widespread distribution within the harbour of the neritic copepods *Oithona similis* and *Paracalanus indicus*;
- (4) a mid harbour peak similar to the distribution of larvae of the barnacles *B. variegatus* and *E. modestus*, but for the larvae of the oyster *Crassostrea gigas*.

A fuller account of the zooplankton will be presented separately.

Correlation coefficients calculated from square root transformed numbers of each species among stations on 14 March showed strong, but not complete, correlation of the occurrence of larvae of *E. modestus* and *B. variegatus*. The coastal cladocerans *P. avirostris* and *E. tergestina* were strongly correlated with each other (and with coastal copepods such as *Temora turbinata* and *Corycaeus*

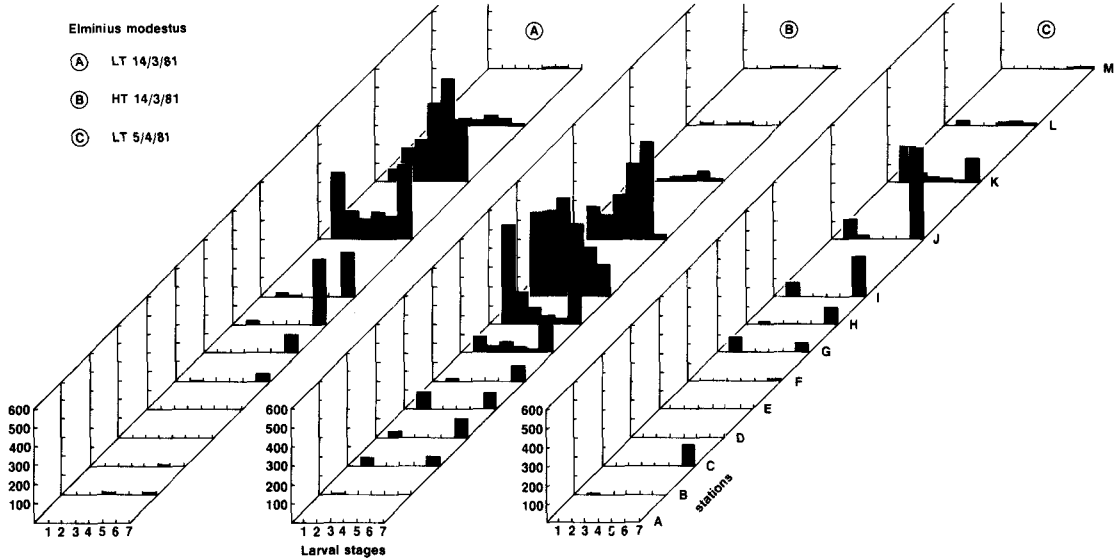


Fig. 5 A down harbour 'view' of the distribution of nauplii 1-6 and cyprids (7) of *E. modestus* in Mahurangi Harbour on 3 separate occasions. Stations shown in Fig. 1. Vertical scale: no. m⁻³.

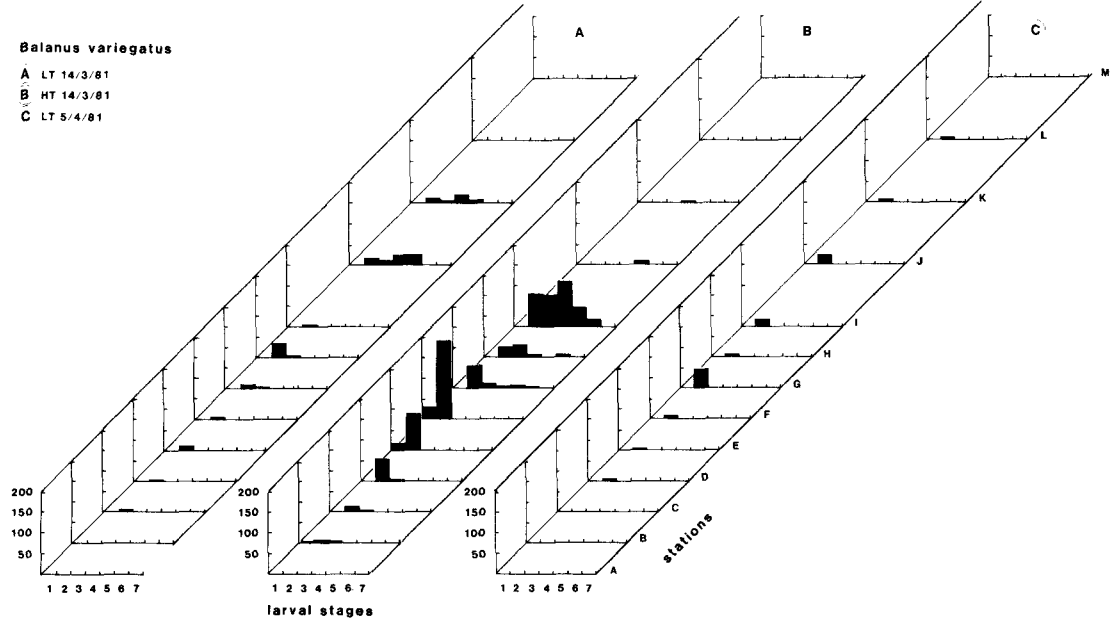


Fig. 6 A down harbour 'view' of the distribution of nauplii 1-6 of *B. variegatus* in Mahurangi Harbour on 3 separate occasions. Stations as shown in Fig. 1. Vertical scale: no. m⁻³.

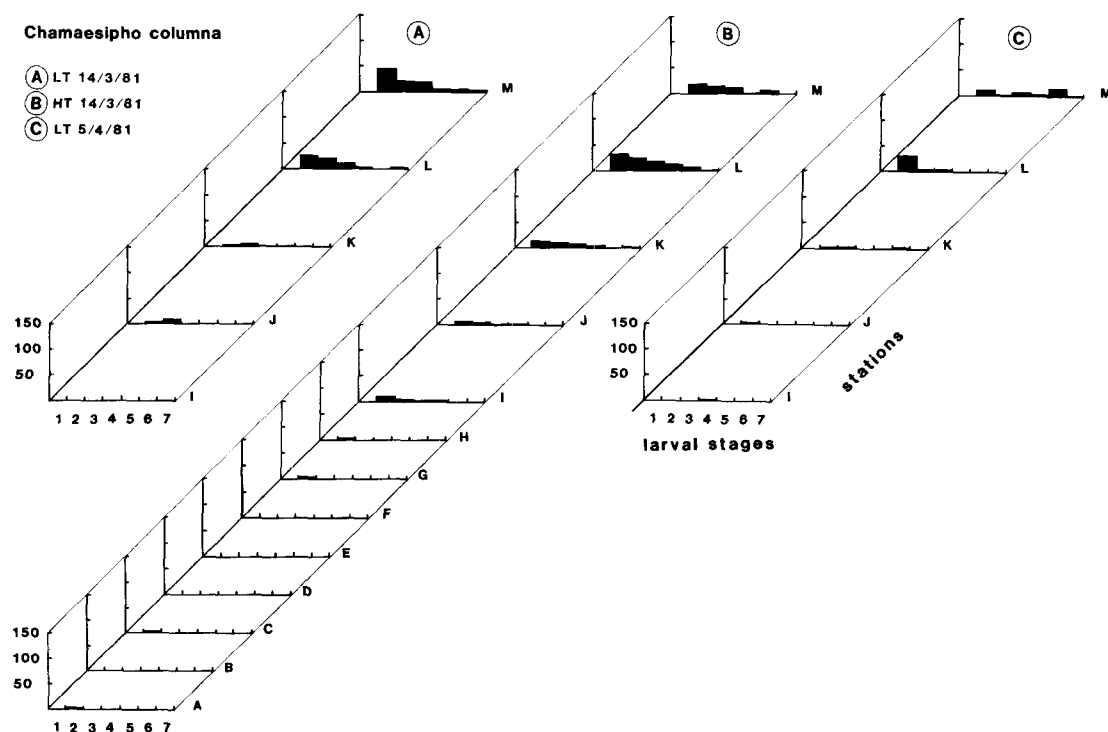


Fig. 7 A down harbour 'view' of the distribution of nauplii 1-6 and cyprids (7) of *C. columna* in Mahurangi Harbour on 3 separate occasions. Stations as shown in Fig. 1. Vertical scale: no. m⁻³.

aucklandicus). *S. conflictus* was negatively correlated with all the above and particularly the coastal species. The bimodality of distribution of *O. similis* and *P. indicus* resulted in non-significant correlation with the barnacle larvae.

DISCUSSION

The settlement phase in the life history of sessile marine invertebrates, like barnacles and oysters, has been intensively studied in laboratory and field contexts, but the planktonic phase is difficult to study quantitatively in situ. Barnes (1956), De Wolf (1973), and Grosberg (1982) have attempted to unravel some of the events that bring individual larvae into contact with suitable habitats, but the details of the planktonic phase still seem intractable. While in the plankton, larvae are subject to interacting and complex physical and biological processes so that they become dispersed and greatly reduced in numbers. The outcome of the pelagic phase may seem to be chaotic, or at least uninterpretable, but the resulting distribution of the larvae at the pre-settlement stage is apparently often aggregated rather than random, judging from fre-

quent high levels of recruits to adult populations (e.g., Osman 1977; Sutherland & Karlson 1977; Yoshioka 1982). Planktonic larvae have been shown to be dispersed and reaggregated by various hydrodynamic processes (Bousfield 1955; De Wolf 1973), and the distribution of barnacle larvae described in this paper support an aggregation effect in the Mahurangi Harbour system.

The pattern of distribution of the larvae of *B. variegatus* and *E. modestus* suggest a residual estuarine population and, for *B. variegatus* in particular, it is reasonable to assume that the larvae were indigenous to the harbour system. Given that the development time of barnacle larvae from hatching to cyprid is 6 days (minimum time achieved for *E. modestus* by Barker 1976), then it would seem that retention of some parcels of water in the harbour exceed the calculated one day residence time for the harbour as a whole.

The distribution patterns of *C. columna* and *B. trigonus* could represent tidal inflow of larvae from outside, showing both dilution towards up harbour and through the developmental stages. But *B. variegatus* larvae are concentrated down harbour away from the adults, with, on 14 March 1981, some evidence of accumulation of late stage nauplii at

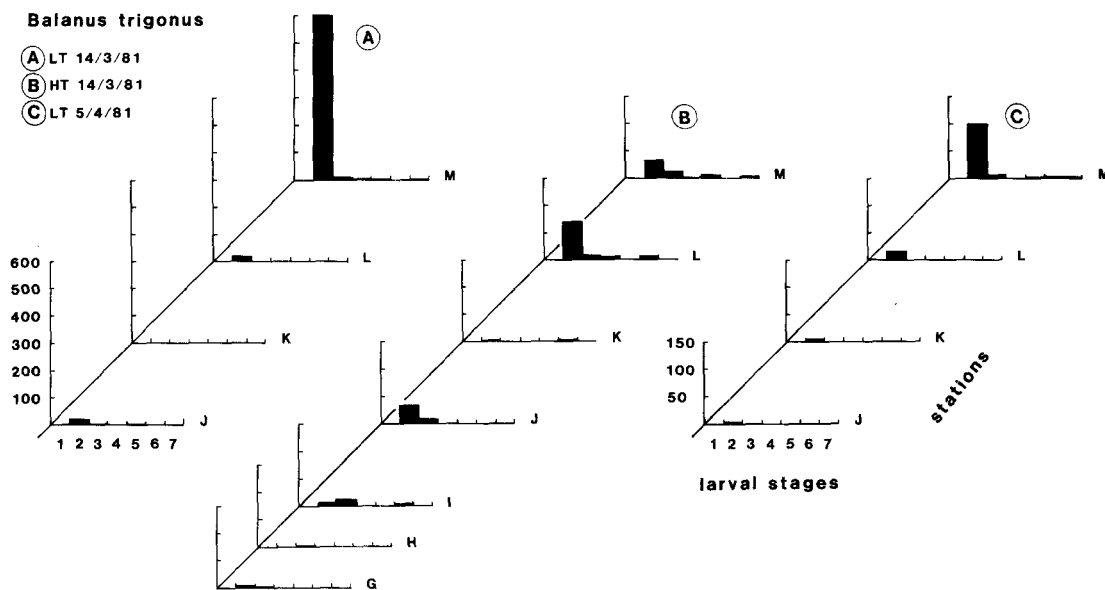


Fig. 8 A down harbour 'view' of the distribution of nauplii 1-6 and cyprids (7) of *B. trigonus* in Mahurangi Harbour on 3 separate occasions. Stations as shown in Fig. 1. Vertical scale: no. m^{-3} .

mid harbour stations, presumably after being displaced downstream by a combination of ebb tides and surface currents. This accumulation of larvae, may shift back and forth with the tide, but maintains some cohesion within the harbour system. The pattern is more clearly demonstrated by *E. modestus*, with more abundant larvae including cyprids, but the adults of this species are spread throughout the length of the harbour. Absence of cyprids of *B. variegatus* may have been because they were not present at that time. However, it is apparent that considerable variability occurs between time-sequence replicated hauls when mean densities are less than about $20 m^{-3}$, possibly a result of the small net mouth area and the small scale patchiness of the larvae in the plankton.

Extrapolation from patterns of occurrence to explanations involving plankton movements are largely speculative. Many accounts (see Riley 1967; Perkins 1974) invoke vertical movements of the plankters, influenced by light, gravity, current, or salinity gradients, thereby causing the plankters to enter differently flowing water layers. Sometimes special changes in orientation are ascribed to late stage larvae to bring about their 'return' to parent sites upstream (Bousfield 1955; Bayly 1965; Riley 1967). Indeed, some mechanism other than chance seems to be needed to enable recruitment to up harbour populations against the general outflow of water from estuarine systems. As well as the reac-

tions of the larvae themselves to the various physical gradients that must exist in estuarine systems, layered water flows and tidal oscillations could help to favour retention and aggregation of planktonic animals within an estuary.

An explanation of the distribution of barnacle larvae in the Mahurangi could be that tidal oscillations aggregate the photopositive nauplii in mid harbour. Photonegative cyprids could use the bottom salt wedge of flood tides to redisperse to up harbour adult habitats, or be dispersed across the tidal flats to mid harbour sites including settlement sticks of oyster farms. The distribution of oyster farms (Fig. 1) and oyster larvae (Fig. 9) is suggestive of similar influences operating on residual populations of oyster larvae. A mid harbour larval entrainment mechanism may explain why the Mahurangi Harbour is a good place for natural oyster spatfall, and also why oyster farm racks and sticks there become fouled with barnacle pests.

There are two other studies that describe the occurrence of barnacle larvae in estuarine systems in New Zealand. Roper et al. (1983) found, in the Avon-Heathcote Estuary, maximum numbers of nauplii ($212 m^{-3}$) and cyprids ($960 m^{-3}$) at the estuary entrance, and these and neritic copepods (e.g., *Oithona similis* and *Paracalanus indicus*) decreased in abundance progressively away from the sea. There was no evidence of accumulation in this apparently well flushed estuary.

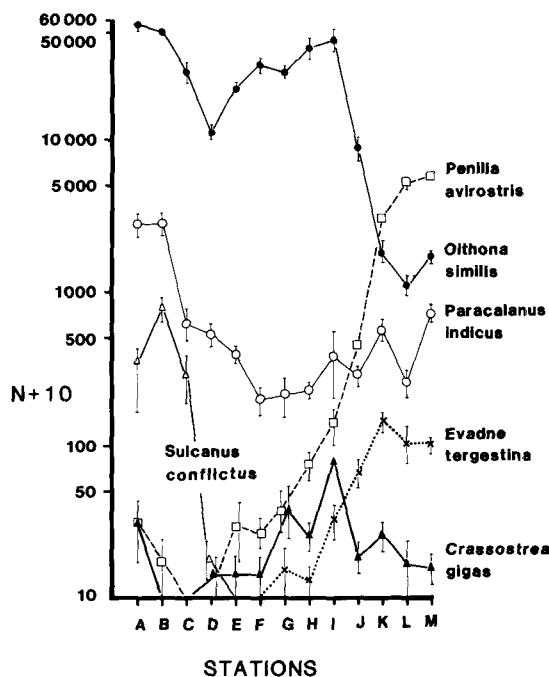


Fig. 9 Mean densities (m^{-3}) of selected plankters in Mahurangi Harbour collected at high tide on 14 March 1981. Vertical lines indicate standard error of the mean.

In Dusky Sound, Jillett and Mitchell (1973) also found maximum numbers of barnacle nauplii (332 m^{-3}) at the Sound entrance, contrasting to an accumulation of *P. indicus* and *Acartia* sp. at the head of the Sound. Jillett and Mitchell (1973) explain this latter accumulation as entrainment of plankton from inflowing subsurface full salinity waters which merge with outflowing surface low salinity waters which the marine plankton actively avoid.

It is clear the distribution of zooplankton in harbours, estuaries, or fiords cannot be discussed generally, and different hydrologies act to disperse, retain, or entrain larvae or plankters originating from either end of the system, or introduced from within it as larvae. For the Mahurangi Harbour, peak densities of barnacle nauplii of about 2000 m^{-3} are an order of magnitude higher than recorded for southern enclosed waters (Jillett & Mitchell 1973; Roper et al. 1983). So too are the densities of small copepods such as *O. similis* (3800 m^{-3} and 460 m^{-3} by the above authors, respectively), but different sized meshes that were used (132 and $200 \mu\text{m}$ compared with $65 \mu\text{m}$ in this study) could explain these differences.

ACKNOWLEDGMENTS

This work is part of a MSc thesis by one of us (ATM) at the Zoology Department, University of Auckland. We thank Messrs M. J. Chamberlain and P. D. Martin for field assistance, and the Leigh Marine Laboratory for use of a boat.

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