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## Studies on twelve common bivalve larvae, with notes on bivalve spawning seasons in New Zealand

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**Abstract** Twelve common bivalve larvae occurring in the plankton from the Bay of Islands (35°15'S, 174°10'E), Wellington Harbour (41°16'S, 174°51'E), and off Raumati Beach (40°56'S, 174°58'E), New Zealand, during 1970–72 are described and, wherever possible, provisionally identified. The seasonal occurrences of these larvae in the plankton are also described. Information on the spawning cycles of some New Zealand adult bivalves is reviewed; although some species have a short (4 months or less) spawning season, for most it is much longer, possibly with 'trickle' spawning through several months of the year.

**Keywords** Bivalvia; larvae; plankton; zooplankton; Bay of Islands; Wellington Harbour; Raumati Beach; seasonal variations; spawning; spawning seasons; Pectinacea; Leptonacea; Veneracea; Macracea; Hiatellacea; Pholadacea; *Paphies australis*; *Chione (Austrovenus) stutchburyi*; morphology

### INTRODUCTION

With the growing interest in marine shellfish farming in New Zealand, an important requirement is that the common bivalve larvae in the plankton be distinguished. In the longer term, it will be helpful if the species are identified; this usually requires laboratory culture of the species.

Bivalve larvae from New Zealand so far described and identified have been members of the Mytilidae (Booth 1977; Siddall 1980; Tortell 1980), Pinnidae (Booth 1979a), Pectinidae (Bull 1977), Anomiidae (Booth 1979a), Ostreidae (Hollis 1963; Dinamani 1971, 1973, 1976; Booth 1979a; Chanley & Dinamani 1978, 1980), Erycinidae (Booth 1979b; Chanley & Chanley 1980), Veneridae (Stephenson & Chanley 1979), and Mesodesmatidae (Rapson

1952; Redfearn 1974, 1982). Observations on the seasonal occurrence of specific bivalve larvae in the plankton have been confined to members of the families Mytilidae, Pinnidae, Anomiidae, Erycinidae (Booth 1977, 1979a, 1979b), and Ostreidae (Dinamani 1971, 1973, 1974a, 1975, 1978, 1981a, 1981b; Booth 1979a; Anon 1980). Further information on the seasonal occurrence of mytilid larvae in the Marlborough Sounds is given in the Ministry of Agriculture and Fisheries Mussel Spatfall Bulletins (see Meredyth-Young 1981).

This is the final paper in a series (Booth 1977, 1979a, 1979b) describing some of the common bivalve larvae recovered from plankton samples taken in the Bay of Islands, Wellington Harbour, and off Raumati Beach (Booth 1972). Twelve commonly occurring and generally distinctive bivalve larval species are described, and in some instances provisionally identified to superfamily or specific level. As in the previous papers, the late-stage veligers (veliconchae) and pediveligers are mainly dealt with, these being the stages at which the species are most readily distinguished. They are compared with species of the same genus or family described from outside New Zealand. In addition, the seasonal occurrences of the larvae in the plankton are outlined. The literature on the spawning seasons of New Zealand bivalves is reviewed, and annual and geographic differences in spawning season of some species summarised.

### SAMPLING AREAS AND METHODS

Details of the plankton sampling programme, including the areas, times, and methods have already been described (Booth 1977). Three plankton stations were occupied in the Bay of Islands (35°15'S, 174°10'E) (April 1970–December 1971), 4 in Wellington Harbour (41°16'S, 174°51'E) (May 1970–February 1972), and 4 off Raumati Beach (40°56'S, 174°58'E) (June 1971–June 1972); the positions of these stations were given by Booth (1977, fig. 1 and 2). Details of the hydrology of the Bay of Islands and Wellington Harbour during the sampling period were given by Booth (1974, 1975). Plankton sampling was carried out at approximately monthly intervals, usually with a free-fall net of 120 µm mesh based on a design by Smith et al. (1968).

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**Table 1** Occurrences of 12 late-stage bivalve larvae, Bay of Islands, Wellington Harbour, and Raumati Beach, 1970-72. a, abundant, i.e.,  $\geq 100$  larvae per 1000 litres of seawater; c, common, i.e.,  $\geq 10$  but  $< 100$ ; f, frequent, i.e.,  $\geq 1$  but  $< 10$ ; o, occasional, i.e.,  $< 1$ ; n.o., never observed.

Species	Bay of Islands	Wellington Harbour	Raumati Beach
Pectinid 1	Jul/Aug-Oct (f) Dec-Jun/Jul (o)	May-Dec/Jan (f,c) Jan/Feb-April (o)	Mar (f) Jun, Jul (o,f)
Leptonacean 2	Oct-Feb (f) Mar-Sep (o)	Dec, Jan (f,c) Apr-Jun (f,c) Feb, Mar (o) Jul-Nov (o)	Feb (o)'
Venerid 1	Sep-Nov (c,a) Dec-Aug (f)	Dec-Feb (f,c) Apr-Jun (f,c) Jul-Sep (f or c)	n.o.
Mactrid 1	n.o.	n.o.	Mar, Apr (o,f) Dec-Feb (o)
Mesodesmatid 1	Aug-Feb/May (f,c) Mar/Jun-Jul (f)	Dec-Feb (c,a) Mar-Nov (f,c)	Feb, Mar (f) Sep, Dec (o)
Hiatellid 1	Most of year (o,f)	May, Jul-Sep (o,f) Dec (o)	Most of year (o,f)
Pholad 1	Jul-Nov (o,f)	Jun-Sep (o) Dec (o)	Dec, Jan, Mar (o) Jun, Jul (o)
Teredinid 1	Dec-Feb (f,c) Apr, May (f,c) Jun-Sep (o,f)	Mar, Apr (o,f) Jul-Nov (o,f)	Most of year (o,f)
Unidentified Larva 1	May (o,f)	n.o.	n.o.
Unidentified Larva 2	Sep, Oct (f,c) Feb-Mar/Apr (f)	Oct, Nov (o)	n.o.
Unidentified Larva 3	Jan-Feb/Mar (f) Jul-Nov (o,f)	Nov/Dec-Jan/Feb (f,c,a) Oct(f)	n.o.
Unidentified Larva 4	Jan-May (f) Aug-Dec (o)	Jan, Feb (f) Apr-Jul (f) Sep-Dec (o)	n.o.

The larvae are described using the terminology of Chanley & Andrews (1971) for most features, and Rees (1950) in particular for hinge characters. The lengths given for the pelagic late-stage larvae (which in this study refer to both late veliger and pediveliger stages) are the range of sizes for larvae most often observed in the plankton samples. Hinge-line length is the length of the provinculum or straight edge section of the hinge. Other details relating to the larval descriptions are noted in Booth (1977). A Cambridge 600 Stereoscan electron microscope was used to examine and illustrate particular larval features where possible.

Larvae were described as being abundant in the plankton if their numbers equalled or exceeded 100

per 1000 litres of seawater, common ( $\geq 10$  but  $< 100$ ), frequent ( $\geq 1$  but  $< 10$ ), or occasional ( $< 1$ ).

The condition of adult bivalves of many species has been demonstrated to decrease rapidly after spawning (Giese 1959), and hence the condition cycle in the adult populations in the study areas can give some indirect evidence about the identity of the larvae in the plankton. Therefore, coincident with the plankton sampling programme, the condition index of 2 commonly occurring bivalves, (*Chione (Austrovenus) stutchburyi* and *Paphies australis* in the Bay of Islands, and *C. (Austrovenus) stutchburyi* in Wellington Harbour) was investigated (Appendix 1). Species naming is based mainly on Powell (1979).

**Table 2** Relative abundance of the adults of some bivalve families at the Bay of Islands, Wellington Harbour, and Raumati Beach, 1970–72. The most abundant species present in each locality are listed (a, abundant; c, common; f, frequent; o, occasional; -, absent). Other species in the same family were either much less common or else absent in that locality. Sources of data: Beu & Climo (1971), Booth (1972), Climo (1972), Powell (1979), McKoy (1980a), Richardson et al. (1982), reports from local shell clubs.

	Bay of Islands	Wellington Harbour	Raumati Beach
<b>Pectinidae</b>			
<i>Pecten novaezelandiae</i>	f	o	o
<i>Chlamys zelandiae</i>	c	f	o
<i>C. gemmulata</i>	f	f	f
<i>C. dieffenbachi</i>	-	f	o
<i>C. zeelandona</i>	f	f	o
<b>Veneridae</b>			
<i>Dosinia (Asa) lambata</i>	f	c	o
<i>D. (Phacosoma) subrosea</i>	c	o	o
<i>D. (Austrodosinia) anus</i>	o	o	c
<i>D. (Kereia) greyi</i>	f	c	o
<i>Tawera spissa</i>	a	f	c
<i>Notopaphia elegans</i>	c	c	-
<i>Protothaca (Tuangia) crassicosta</i>	c	c	-
<i>Notirus reflexus</i>	c	c	-
<i>Venerupis (Paphirus) largillierti</i>	f	f	o
<i>Chione (Austrovenus) stutchburyi</i>	a	a	-
<i>Dosina zelandica zelandica</i>	f	f	o
<b>Macluridae</b>			
<i>Mactra discors</i>	f	f	c
<i>M. murchisoni</i>	-	f	c
<i>M. (Cyclomactra) ovata ovata</i>	f	f	o
<i>Scalpomactra scalpellum</i>	f	f	f
<i>Spisula (Crassula) aequilateralis</i>	o	o	c
<i>Zenatia acinaces</i>	f	f	f
<i>Resania lanceolata</i>	f	f	f
<b>Mesodesmatidae</b>			
<i>Paphies australis</i>	c	c	o
<i>P. subtriangulata</i>	o	o	a
<i>P. donacina</i>	-	o	c
<b>Hiatellidae</b>			
<i>Hiatella arctica</i>	c	f	o
<i>Panopea zelandica</i>	o	o	o
<b>Pholadidae</b>			
<i>Anchomasa similis</i>	f	o	o
<i>Pholadidea spathulata</i>	o	o	o
<b>Teredinidae</b>			
<i>Bankia australis</i>	c	-	f
<i>B. neztalia</i>	-	c	f
<i>Lyrodus pedicellatus</i>	o	o	f
<i>L. medilobatus</i>	f	-	-

## LARVAL DESCRIPTIONS AND SEASONAL OCCURRENCES IN THE PLANKTON

Provisional identification of each of the following larvae has been made, wherever possible, based on available material and after comparison with

published descriptions and other information. The reasons for the identifications are given at the end of each description. This section has therefore been arranged taxonomically, with the larval material being provisionally grouped into families or superfamilies.

## Superfamily Pectinacea

### PECTINID 1

Fig. 1, Tables 1 and 2

*Dimensions:* Late-stage larvae 200–230  $\mu\text{m}$  long, with average length to height ratio of 1:1.07 and ratio of length of larva to length of hinge line of 1:0.40.

*Shape* (Fig. 1): In the late-stage larva, the umbones are equal in size, and angular or only slightly knobby in shape. The anterior end is more pointed and longer than the posterior end, and the posterior shoulder is much steeper than the anterior shoulder. The ventral margin is pointed. These features give the larva an ovate, trigonal shape.

*Hinge:* In a larva 230  $\mu\text{m}$  long the hinge in both valves has 3–4 taxodont teeth at each end of the provinculum, separated by a narrow undifferentiated region.

*Other features:* Late-stage larvae appear dark grey in colour under white light. An approximately central eyespot develops in larvae over 210  $\mu\text{m}$  in length. There are fine concentric lines in both prodissoconch I and II shells seen under Nomarski differential interference contrast (DIC); no prominent radial lines; dark lines towards the outer edge of the prodissoconch II shell are obvious in larvae over 200  $\mu\text{m}$  in length. The prodissoconch I shell is not clearly delineated from the prodissoconch II shell, although it does tend to be more punctate in texture.

*Comparison with other species:* This larva closely resembles in shape and other features the larva of *Pecten* (*Chlamys*) *striatus*, provisionally identified by Jorgensen (1946) and Rees (1950). The hinge features closely resemble those of several indirectly identified, as well as laboratory-grown, pectinid larvae (Jorgensen 1946; Rees 1950; Chanley & Andrews 1971; Costello et al. 1973; Culliney 1974; Le Pennec 1974; Dix 1976).

*Distribution and seasonal abundance* (Table 1): This larva was observed at all 3 sampling localities, but was most abundant in the Bay of Islands and Wellington Harbour. In the Bay of Islands, the larva occurred in greatest numbers at stations with most estuarine influence (Confluence and Brampton Reef). It occurred frequently in late winter and spring and occasionally during summer and autumn. In Wellington Harbour, the larva occurred at all stations, frequently or commonly during spring 1970 and winter, spring, and early summer 1971. At Raumati Beach the larva occurred frequently during autumn and winter.

These observations suggest that the adults spawn throughout much of the year, with peaks at different seasons according to locality.

*Provisional identification:* This larva has several features in common with pectinid (superfamily Pectinacea) larvae. The pectinids occurring most commonly in the sampling locations are *Pecten novaezelandiae* and 4 *Chlamys* species (Table 2). The larva of *P. novaezelandiae* has been provisionally identified (Bull 1977), and so it is most likely that Pectinid 1 is 1 of the *Chlamys* species. The distribution of Pectinid 1 is consistent with the distribution of the adults of *C. zelandiae*. In addition, a dissoconch shell (Fig. 1), probably that of *C. zelandiae*, exhibits the Pectinid 1 prodissoconch II shell shape.

## Superfamily Leptonacea

### LEPTONACEAN 2

Fig. 2, Table 1

(Leptonacean 1 was described in Booth 1979b).

*Dimensions:* Late-stage larvae 300–380  $\mu\text{m}$  long, with average length to height ratio of 1:0.87 and ratio of length of larva to length of hinge line of 1:0.20. The absence from the plankton of readily identifiable larvae less than 290  $\mu\text{m}$  in length suggests hyperlarviparous development.

*Shape* (Fig. 2): In the late-stage larva the umbones are equal in size and knobby in shape; the anterior end is slightly longer and less pointed than the posterior end; the anterior shoulder is more rounded than the posterior shoulder; and the ventral margin is broadly rounded.

*Hinge* (Fig. 2): In a larva 360  $\mu\text{m}$  long, the hinge has no true provinculum, as defined by Rees (1950), although the straight edge does bear many small serrations.

*Other features:* The larva usually appears grey in colour. Concentric lines over prodissoconch I and II shells, and radial lines, particularly over prodissoconch II shell, can be seen clearly under Nomarski DIC (Fig. 2, middle). There is no visible eyespot.

*Comparison with other species:* The larva resembles in shape *Rochefortia planulata* and *Glycymeris glycymeris* provisionally identified by Sullivan (1948) and Rees (1950) respectively, and *Montacuta substriata* reared by Gage (1966).

*Distribution and seasonal abundance* (Table 1): In the Bay of Islands, the larva occurred throughout much of the year, particularly at the inner harbour stations (Confluence and Brampton Reef). Peak densities were during autumn 1970, summer 1970–71, and spring 1971.

In Wellington Harbour, the larva occurred throughout most of the year at all plankton stations, with peak densities during summer 1970–71 (and possibly 1971–72) and late autumn 1971 (and possibly 1970).

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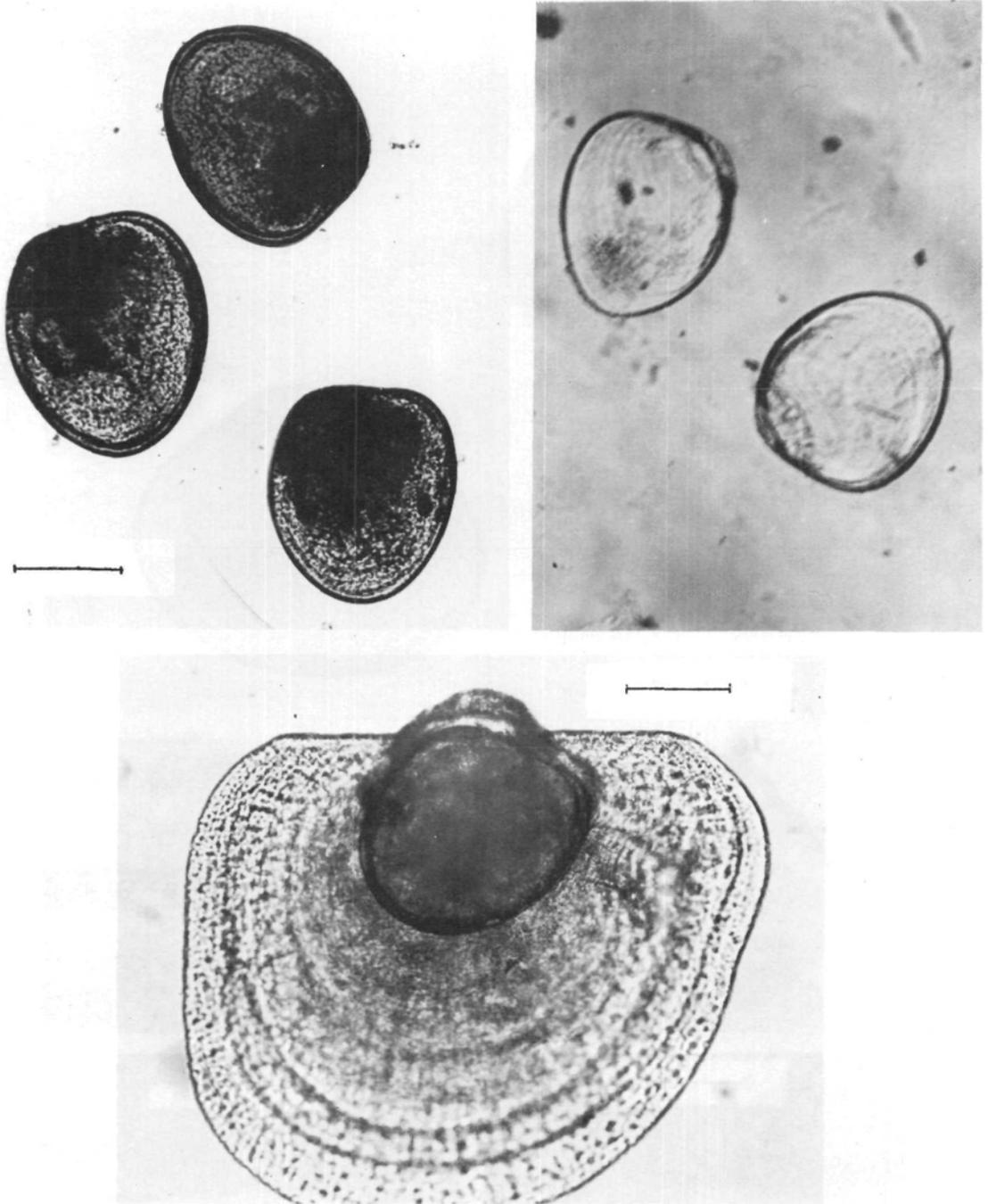


Fig. 1 Late stage larvae (upper left) and single valves (upper right) of Pectinid 1; early postlarva, probably *Chlamys zelandiae* (lower). Scale lines, 100  $\mu$ m.

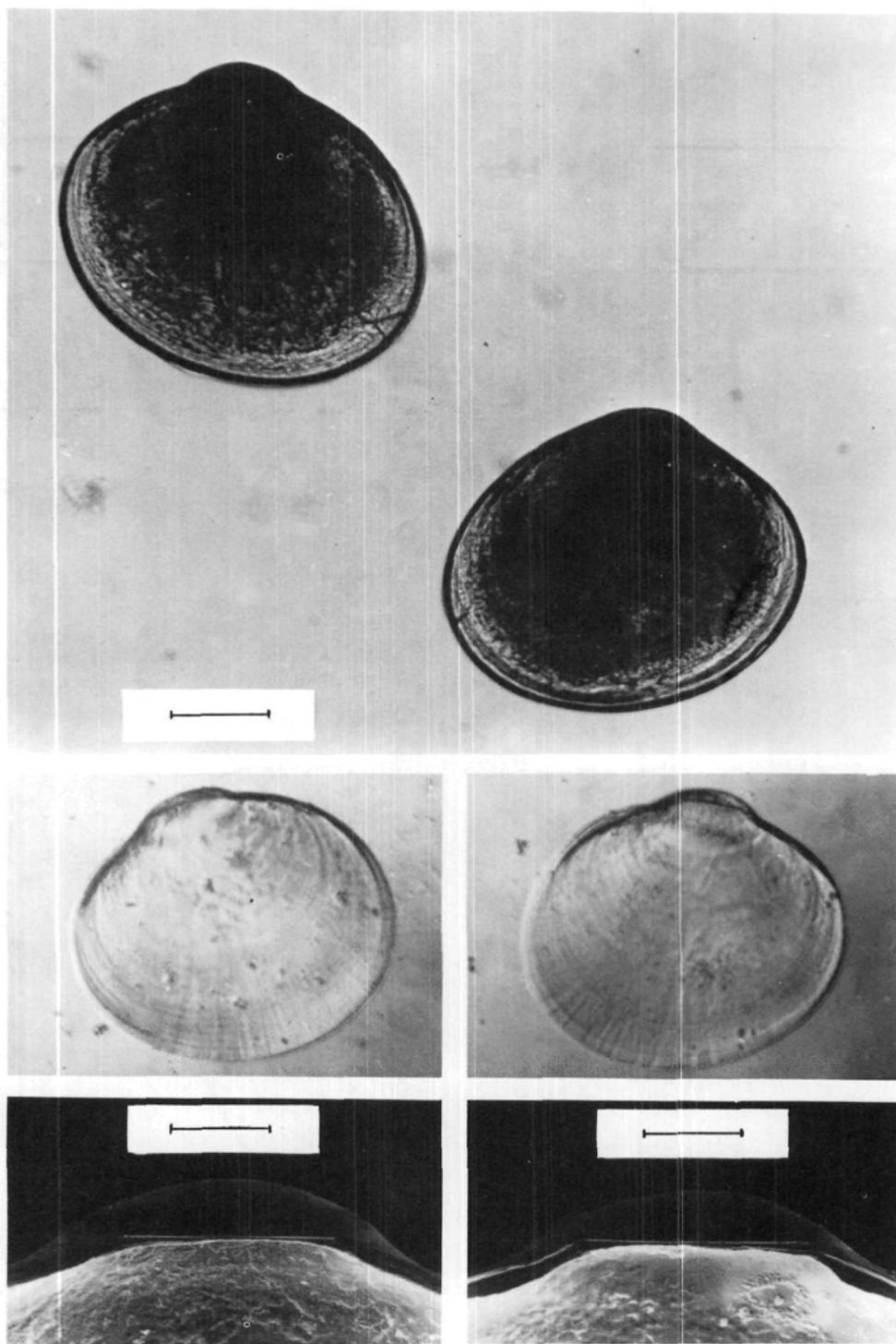


Fig. 2 Late stage larvae (upper) and single valves (middle) of Leptonacean 2; scale line, 100  $\mu\text{m}$ . Hinge of left valve (lower left) and right valve (lower right) of late stage larva (length 360  $\mu\text{m}$ ) of Leptonacean 2 (not both from the same larva); scale lines, 40  $\mu\text{m}$ .

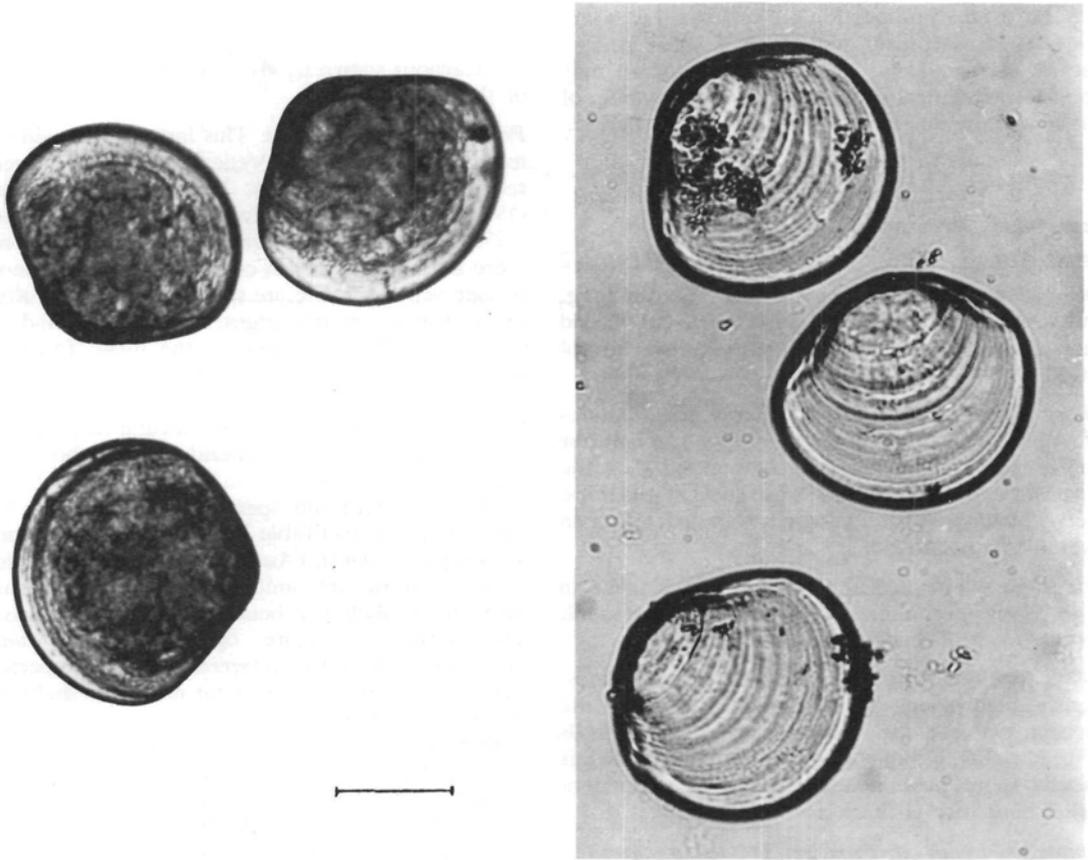


Fig. 3 Late stage larvae (left) and single valves (right) of Venerid 1; scale line, 100  $\mu\text{m}$ .

The larva occurred occasionally during summer off Raumati Beach.

**Provisional identification:** This larva resembles in shape members of family Glycymeridae, but lacks the small provincial teeth and 'pill-box' arrangement around the shell margin observed by Rees (1950) for this group.

This larva is identified with 1 of the 2 superfamilies, Lucinacea and Erycinacea (= Leptonacea), reported by Rees (1950) to lack a provincialum. The larva resembles in shape the erycinid *Rochefortia planulata* described by Sullivan (1948). Furthermore, the most common species of these 2 superfamilies found by Booth (1979b) at the sampling localities during 1970–72 and for which the late-stage larva has not yet been described is the allied erycinid species *Borniola reniformis*. However, Powell (1979) lists several other species in these superfamilies which are widespread throughout the North Island, including *Divaricella (Divalucina) huttoniana*, *Diplodonta (Zemysina)*

*globus*, *D. (Zemysina) striatula*, *Felaniella (Zemysia) zelandica*, *Melliteryx parva*, *Myllita (Zemyllita) stowei*, and *Myllitella vivens vivens*.

An adult *B. reniformis* collected in the Bay of Islands in February 1971 contained numerous D-shaped larvae 120  $\mu\text{m}$  in length (Booth 1979b). A further specimen collected near Auckland in October 1977 contained numerous larvae 100–110  $\mu\text{m}$  in length. In addition, Ponder (1967) reported occasional specimens containing large numbers of early stage larve, each having "a large velum and a well developed foot". Since the adult is small (7–11 mm in length—Powell 1979), hypolarviparous development is indicated. This should result in pelagic larvae at all stages of development beyond D-shaped, yet distinguishable stages of Leptonacean 2 less than 290  $\mu\text{m}$  in length were absent from the plankton. If Leptonacean 2 is *B. reniformis*, then a situation similar to that suggested for *Kellia cycladiformis* by Booth (1979b) is indicated, where alternative developmental strategies are possible. It could be that most larvae are released at a small

size, but a small proportion are incubated to a late stage of development and have a short pelagic period. Alternatively, considerable variation may occur intraspecifically regarding both the number of larvae and the duration of their incubation period.

### Superfamily Veneracea

#### VENERID 1

Fig. 3, Tables 1 and 2

**Dimensions:** Late-stage larvae 220–250  $\mu\text{m}$  long, with average length to height ratio of 1:0.92 and ratio of length of larva to length of hinge line of 1:0.31.

**Shape (Fig. 3):** In the late-stage larva, the umbones are equal in size and angular in shape. The anterior end is slightly longer and more pointed than the posterior end. Both shoulders are straight and slope steeply, and the ventral margin is rounded, giving an overall trigonal shape.

**Hinge:** In a larva 230  $\mu\text{m}$  long, the provinculum in both valves bears a series of approximately 20 small, similar teeth. The ligament is posterior.

**Other features:** Widely separated concentric lines, clearly seen under Nomarski DIC, obscure the division between the prodissoconch I and II shells (Fig. 3, right), although the prodissoconch I shell is usually more punctate. There are no prominent radial lines, nor is there a visible eyespot.

**Comparison with other species:** This larva resembles in shape and size several veneracean species, many of which have been described from laboratory culture. These include *Venerupis pullastra*, described by Quayle (1952), *Mercenaria mercenaria* and *Petricola pholadiformis*, by Loosanoff & Davis (1966), and *Venus striatula*, *V. fasciata*, *Venerupis aurea*, and *V. verrucosa*, by Le Pennec & Lucas (1970) and Le Pennec (1973). However, Venerid 1 bears less resemblance to *Chione cancellata*, described by LaBarbera & Chanley (1970), and *C. (Austrovenus) stutchburyi*, described by Stephenson & Chanley (1979).

**Distribution and seasonal abundance (Table 1):** This larva was observed only at the Bay of Islands and Wellington Harbour.

In the Bay of Islands, it occurred commonly, sometimes abundantly at all stations. Peak densities of the larva occurred during the spring of both years, when it was 1 of the most abundant species in the plankton.

In Wellington Harbour, the larva occurred frequently, sometimes commonly at all stations. Peak densities occurred during early spring 1970 (not repeated in spring 1971), summer 1970–71, and winter 1971.

These observations suggest that the species spawns mainly during spring, although in Wellington Harbour spawning also occurred at other times of the year.

**Provisional identification:** This larva is most similar to venerid (Superfamily Veneracea) larvae. Jorgensen (1946), Rees (1950), LaBarbera & Chanley (1970), Chanley & Andrews (1971), and Le Pennec (1973) have reviewed venerid larval descriptions; there are few features in common except that most pelagic venerid larvae are small, and the shell often bears distinct lateral ridges. Rees (1950) and Le Pennec (1973) have detailed the hinge forms of several venerid larvae, those described by Le Pennec being based on laboratory-grown species. Many have a series of small provincial teeth similar to those observed in Venerid 1, and the hinge ligament is posterior.

Eleven veneracean species occur often in the sampling localities (Table 2), all belonging to family Veneridae. *Chione (Austrovenus) stutchburyi* and *Tawera spissa* are among the most numerous bivalves on sheltered beaches, although *T. spissa* also occurs on more open shores. *Dosinia (Austrodosinia) anus* is a typical open coast species. The other venerid species occur mostly on sheltered and semi-sheltered shores.

The occurrence of Venerid 1 in the plankton correlated to some extent with the changes in the condition cycle of the only venerid species investigated, *Chione (Austrovenus) stutchburyi* (Appendix 1). However, since this study was completed the larva of *C. (Austrovenus) stutchburyi* has been described from laboratory culture (Stephenson & Chanley 1979), and the evidence now points to Venerid 1 being 1 of the other 10 venerid species. Since the larva was not observed at Raumati Beach, Venerid 1 is unlikely to be *Dosinia (Austrodosinia) anus*.

### Superfamily Mactracea

#### MACTRID 1

Fig. 4, Tables 1 and 2

**Dimensions:** Late-stage larvae 260–320  $\mu\text{m}$  long, with average length to height ratio of 1:0.97 and ratio of length of larva to length of hinge line of 1:0.23.

**Shape (Fig. 4):** In the late-stage larva, the umbones are equal in size and angular to knobby in shape. Both ends are of similar length, but the anterior end is more pointed. The posterior shoulder is higher than the anterior shoulder, the posterior end is almost flat, and the ventral margin is rounded.

**Other features:** Concentric lines are visible over the entire shell under Nomarski DIC, with no clear

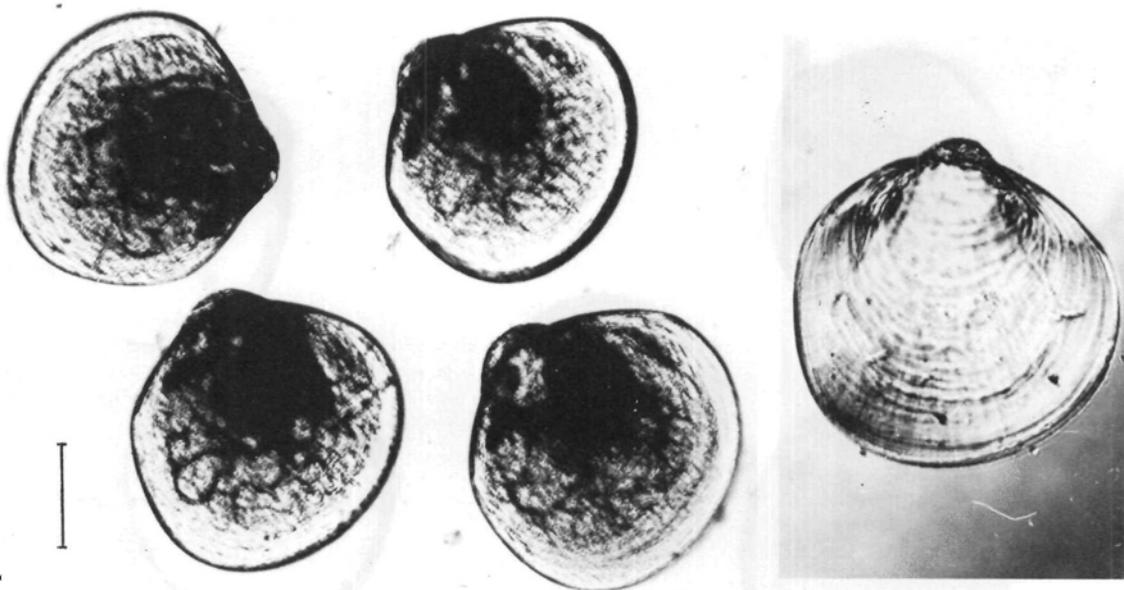


Fig. 4 Late stage larvae (left) and single valve (right) of Mactrid 1; scale line, 100  $\mu\text{m}$ .

distinction between prodissoconch I and II. There are no prominent radial lines, nor is there a visible eyespot.

**Comparison with other species:** This larva is very similar in shape to the mactrids *Spisula subtruncata*, provisionally identified by several workers including Jorgensen (1946) and Rees (1950) and later described from laboratory culture by Le Pennec (1980), *S. solidissima*, provisionally identified by Sullivan (1948) and later confirmed from laboratory culture by several workers including Chanley & Andrews (1971), *S. elliptica*, provisionally identified by Rees (1950), and *Mulinia lateralis*, described from laboratory culture by Loosanoff et al. (1966).

**Distribution and seasonal abundance** (Table 1): This larva was observed only off Raumatī Beach, where it was 1 of the most abundant bivalve larvae present in the plankton during the summer and autumn of 1971–72.

**Provisional identification:** The shape of this larva is similar to several mactrids (superfamily Mactracea), including *Spisula* spp.

The most abundant mactrid species occurring at Raumatī Beach, the only locality where this larva was observed, were *Spisula* (*Crassula*) *aequilateralis*, *Mactra discors*, *M. purchisoni*, *Scalpomactra scalpellum*, *Zenatia acinaces*, and *Resania lanceolata* (Table 2). Of these *S. (Crassula)*

*aequilateralis* was the mactrid species least abundant in the Bay of Islands and Wellington Harbour. Mactrid 1 is identified with this species.

#### MESODESMATID 1

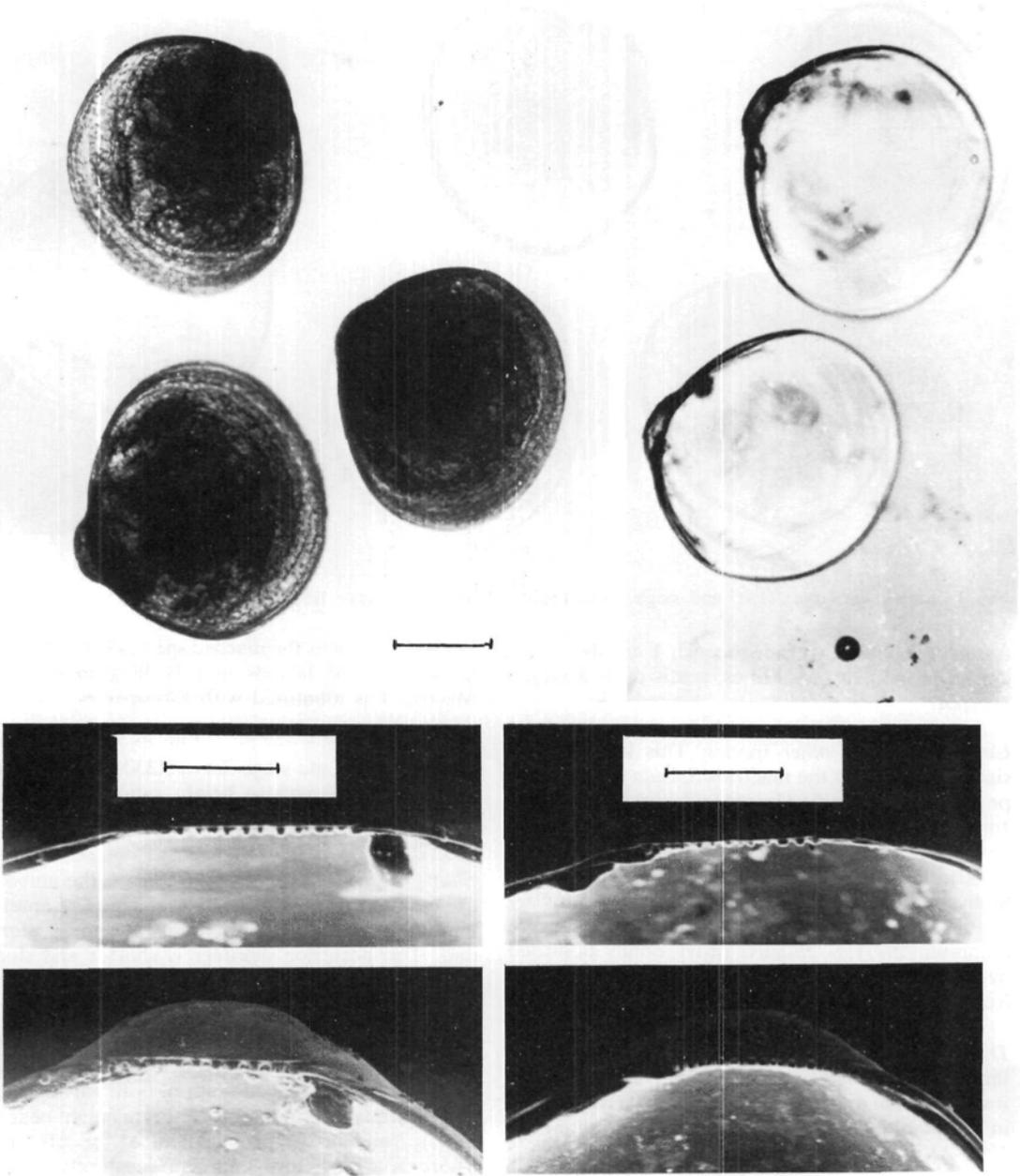
Fig. 5, Tables 1 and 2

**Dimensions:** Late-stage larvae 230–280  $\mu\text{m}$  long, with average length to height ratio of 1:0.95 and ratio of length of larva to length of hinge line of 1:0.24.

**Shape** (Fig. 5): In the late-stage larva, the umbones are equal in size and knobby in shape. The anterior end is longer and more pointed than the posterior end. The posterior shoulder is shorter and slopes more steeply than the anterior shoulder. The ventral margin is rounded.

**Hinge** (Fig. 5): In a larva 270  $\mu\text{m}$  long, the hinge consists of a thickened provinculum bearing about 12 small, evenly spaced teeth in both valves, and a large spatulate tooth about 25  $\mu\text{m}$  in height near the anterior end of the provinculum of the left valve. There is a long, low laminar ridge tooth, derived from the lateral hinge system, anterior to the provinculum of the right valve. The ligament attachment point lies towards the posterior end of the provinculum.

**Other features:** Widely separated concentric lines are visible under Nomarski DIC, particularly over the prodissoconch II shell, but there are no prominent radial lines. The larva usually has a slightly amber colour. There is no visible eyespot.



**Fig. 5** Late stage larvae (upper left) and single valves (upper right) of *Mesodesmatid 1*; scale line, 100  $\mu\text{m}$ . Hinge of left valve (middle and lower left) and right valve (middle and lower right) of late stage larvae (lengths 270–290  $\mu\text{m}$ ) of *Mesodesmatid 1* (not all from the same larva); scale lines, 40  $\mu\text{m}$ .

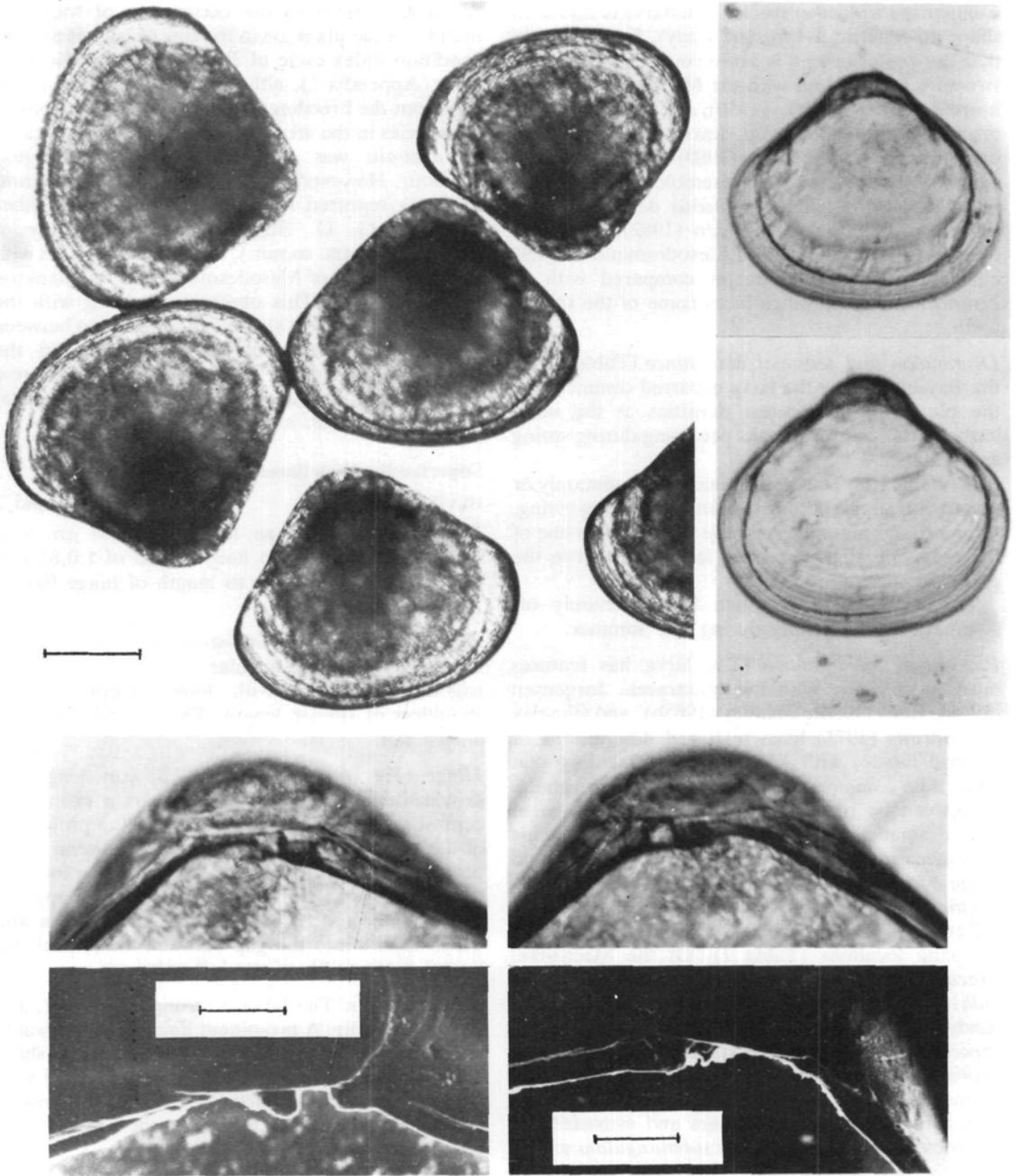


Fig. 6 Late stage larvae (upper-most left) and single valves (upper-most right) of *Hiattellid 1*; scale line, 100  $\mu\text{m}$ . Hinge of left valve (lower left) and right valve (lower right) of late stage larvae (lengths 310–330  $\mu\text{m}$ ) of *Hiattellid 1* (not all from the same larva); scale lines, 40  $\mu\text{m}$ .

*Comparison with other species:* This larva is similar in shape to Mactrid 1 (present study), but differs in that the posterior end is more rounded. The hinge structure is consistent with the Mactracean Type A hinge described by Rees (1950), and the hinge of the mactrid *Spisula subtruncata*, described from laboratory culture by Le Pennec (1980). Both the larval shape and hinge closely resemble those of the mesodesmatid *Paphies ventricosa* described from laboratory culture by Redfearn (1982). The most obvious differences are that Mesodesmatid 1 is less elongate at the same height compared with *P. ventricosa*, and the hinge lacks some of the special teeth.

*Distribution and seasonal abundance* (Table 1): In the Bay of Islands, the larva occurred commonly in the plankton, in greatest densities at the inner harbour stations with peaks occurring during spring and summer.

In Wellington Harbour, it occurred commonly or abundantly at all stations, particularly during spring, summer, and autumn. At these times, it was one of the most abundant late-stage larvae present in the plankton.

The larva occurred much less commonly off Raumati Beach, mainly during late summer.

*Provisional identification:* The larva has features most in common with the Mactracea. Jorgensen (1946), Rees (1950), Chanley (1965b), and Chanley & Andrews (1971) have reviewed descriptions of mactrid larvae, with Chanley (1965b) noting that there is no common taxonomic feature by which the group can be recognised. However, the hinge of Mesodesmatid 1 is consistent with that described for mactracean larvae by Rees (1950), and its shape and hinge structure are similar to those of *Paphies ventricosa* described by Redfearn (1982).

Ten mactracean species occur often in the sampling localities (Table 2). Of the Mactridae, *Mactra discors*, *M. murchisoni*, and *Spisula (Crasula) aequilateralis* occur most commonly on open sandy beaches, *Scalpomactra scalpellum*, *Resania lanceolata*, and *Zenatia acinaces* occur on both protected and open shores, and *Mactra (Cyclomactra) ovata ovata* is the only mactrid occurring commonly in enclosed harbours and estuaries. Of the Mesodesmatidae, *Paphies subtriangulata* and *P. donacina* are typically open shore bivalves, and *P. australis* is often a dominant bivalve on protected sand beaches and lower estuaries (Morton & Miller 1968; Booth 1972; Beu & de Rooij Schuiling 1982).

Mesodesmatid 1 occurred mainly at the Bay of Islands and Wellington Harbour, where *Mactra (Cyclomactra) ovata ovata*, *Scalpomactra scalpellum*, *Zenatia acinaces*, and *Paphies australis* are the most abundant mactraceans. It is therefore likely that the larva is 1 of these 4 species. There was no

correlation between the occurrence of Mesodesmatid 1 in the plankton in the Bay of Islands and the condition index cycle of *P. australis* from Kerikeri Inlet (Appendix 1), although these adults may not represent the breeding cycle of other populations of the species in the area. The condition index cycle of *P. australis* was not monitored in Wellington Harbour. However, dense settlement of *P. australis* spat was reported at Petone Beach in November 1970 (T. G. G. Biggs, Victoria University of Wellington, pers. comm.), this being consistent with the spring peak of Mesodesmatid 1 in the plankton about this time. This observation, along with the marked similarity in shape and hinge form between this larva and that of *P. ventricosa*, and the consistent distribution patterns between this larva and the adults of *P. australis*, point to Mesodesmatid 1 being that of *P. australis*.

### Superfamily Hiatellacea

#### HIATELLID 1

Fig. 6, Tables 1 and 2

*Dimensions:* Late-stage larvae 280–330  $\mu\text{m}$  long with average length to height ratio of 1:0.81 and ratio of length of larva to length of hinge line of 1:0.19.

*Shape* (Fig. 6): In the late-stage larva the umbones are equal in size and angular. The larva is deep and trigonal in shape, with long, steeply sloping shoulders of similar length. The ventral margin is almost flat.

*Hinge* (Fig. 6): In a larva 320  $\mu\text{m}$  long, the provinculum of the left valve bears a prominent central tooth, while there is a tooth-like projection of the lateral hinge system at the anterior end of the provinculum. In the right valve, there is a tooth at the anterior end of the provinculum which appears to be connected to the lateral hinge system and which inserts into the gap between the central and lateral hinge teeth of the left valve.

*Other features:* The larva is strong and heavy, and amber in colour. A prominent line is visible towards the outer edge of the prodissoconch II shell, although the line does not coincide precisely with the concentric lines which are clearly visible under Nomarski DIC. There are no prominent radial lines, nor is there a visible eyespot.

*Comparison with other species:* This larva is similar in shape to *Hiatella arctica*, grown in the laboratory and depicted in line drawings by Lebour (1938). It also resembles in shape and hinge structure *Saxicava* (= *Hiatella*) *arctica* (Superfamily Saxicavacea), provisionally identified by Jorgensen (1946) and Rees (1950).

*Distribution and seasonal abundance* (Table 1): This larva was observed at all sampling localities.

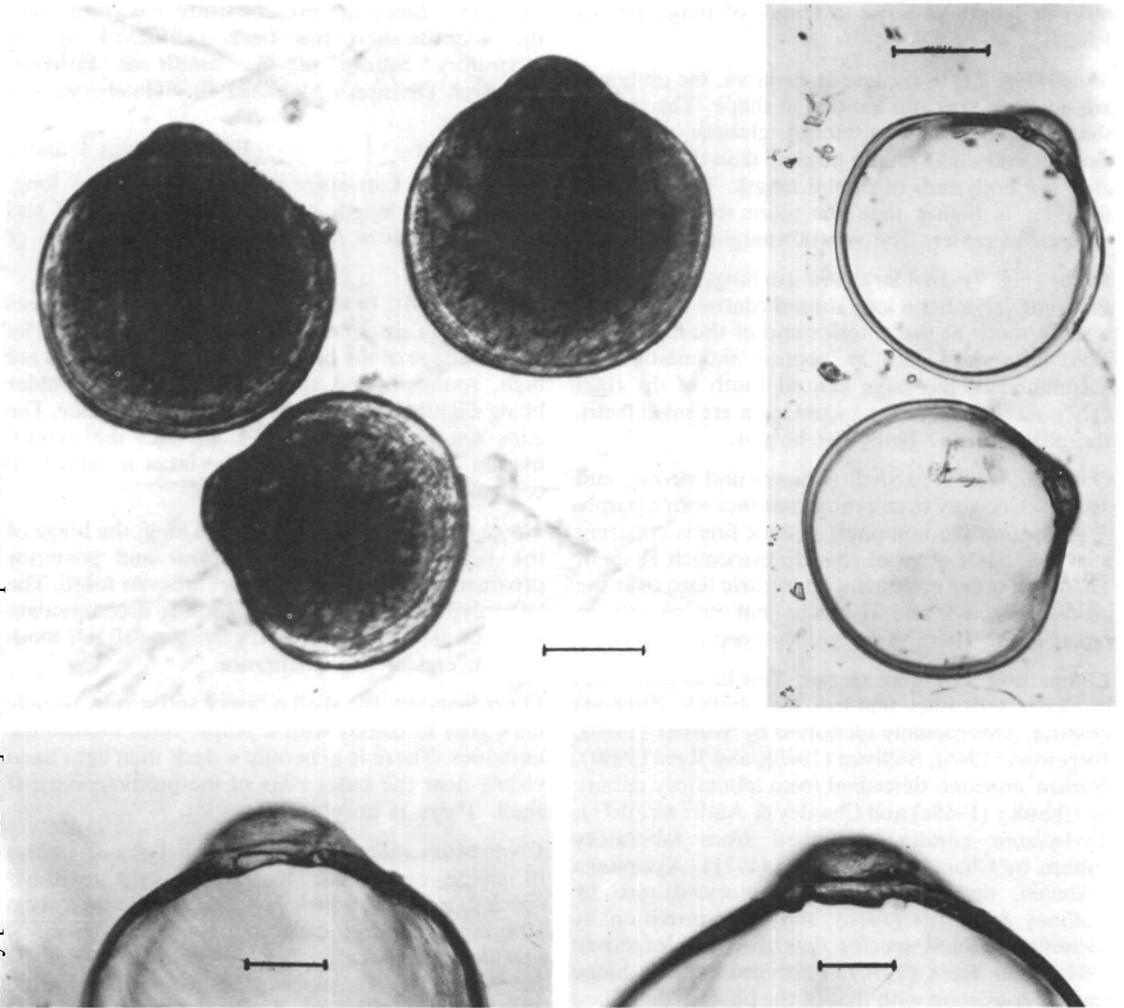


Fig. 7 Late stage larvae (upper left) and single valve (upper right) of Pholad 1; scale lines, 100  $\mu\text{m}$ . Hinge of left valve (lower left) and right valve (lower right) of late stage larva (length 290  $\mu\text{m}$ ) of Pholad 1; scale lines, 40  $\mu\text{m}$ .

In the Bay of Islands, it occurred most commonly at the outer harbour station, being taken occasionally or frequently throughout most of the year, and with peak densities occurring during winter and spring 1971.

This larva was 1 of the species most often observed in offshore samples taken near the Bay of Islands during 1972, and was abundant in samples taken 8 km south-east of Cape Brett on 12 January 1972.

In Wellington Harbour, the larva occurred occasionally, sometimes frequently, throughout the year, with peak densities occurring during winter and spring 1971.

At Raumati Beach, this larva occurred occasion-

ally or frequently throughout the year, except during autumn.

It appears that this species spawns throughout much of the year at all localities.

*Provisional identification:* This larva has several features in common with saxicavacean larvae, including its overall shape and general hinge structure. Hiatellid 1 is identified with the most common and widespread species, *H. arctica* (Table 2).

#### Superfamily Pholadacea

##### PHOLAD 1

Fig. 7, Tables 1 and 2

*Dimensions:* Late-stage larvae 260–300  $\mu\text{m}$  long, with average length to height ratio of 1:1.00 and

ratio of length of larva to length of hinge line of 1:0.28.

*Shape* (Fig. 7): In the late-stage larva, the umbones are equal in size and knobby in shape. The overall shape of the larva is almost globose, with the anterior end slightly more pointed than the posterior end, but both ends of similar length. The posterior shoulder is higher than the more steeply sloping anterior shoulder. The ventral margin is rounded.

*Hinge* (Fig. 7): In a larva 290  $\mu\text{m}$  long, the hinge of the right valve has a long, broad central tooth, with a small tooth at the anterior end of the hinge line. The left valve has a central indentation to accommodate the large central tooth of the right valve. At the end of the indentation are small teeth, the posterior one being the largest.

*Other features:* The shell is heavy and strong, and usually dark grey in colour, sometimes with a purple tinge around the umbones. A dark line is apparent near the outer edge of the prodissoconch II shell. There are other prominent concentric lines over the prodissoconch I and II shells, but no prominent radial lines. There is no visible eyespot.

*Comparison with other species:* This larva resembles in shape and other features the pholads *Zirphaea crispata*, provisionally identified by Werner (1939), Jorgensen (1946), Sullivan (1948), and Rees (1950), *Barnea truncata*, described from laboratory culture by Chanley (1965a) and Chanley & Andrews (1971), *Cyrtopleura costata*, described from laboratory culture by Chanley & Andrews (1971), *Xylophaga atlantica*, described from laboratory culture by Culliney & Turner (1976), and other provisionally identified pholad species described by Jorgensen (1946) and Rees (1950). Furthermore, the hinge form is consistent with that of the pholads described by Werner (1939), Jorgensen (1946), Rees (1950), Chanley (1965a, fig. 2), Chanley & Andrews (1971), and Culliney & Turner (1976).

*Distribution and seasonal abundance* (Table 1): In the Bay of Islands, this larva occurred most commonly at the inner harbour stations (Confluence and Brampton Reef) during late winter and spring 1970 and 1971.

The larva was occasionally observed during winter and summer in Wellington Harbour and off Raumati Beach.

*Provisional identification:* This larva has several features in common with pholad larvae described elsewhere, including its overall globose shape, short hinge line, and hinge structure.

Two pholad species, *Anchomasa similis* and *Pholadidea spathulata*, occur often in the sampling localities (Table 2). *Anchomasa similis* is the most abundant species, and is therefore identified with

this larva. Since the present study was completed, this identification has been confirmed by the laboratory culture of *A. similis* at Fisheries Research Division's Mahanga Bay Hatchery.

#### TEREDINID 1

Fig. 8, Tables 1 and 2

*Dimensions:* Late-stage larvae 200–250  $\mu\text{m}$  long, with average length to height ratio of 1:1.17 and ratio of length of larva to length of hinge line of 1:0.29.

*Shape* (Fig. 8): In the late-stage larva, the umbones are equal in size and slightly knobby in shape. The overall shape of the larva is ovate. The shoulders are high, rounded, and short, the posterior shoulder being slightly higher than the anterior shoulder. The ends are of nearly equal length and the ventral margin is sharply rounded. The larva is very deep compared to many other species.

*Hinge* (Fig. 8): In a larva 230  $\mu\text{m}$  long, the hinge of the right valve has large central and posterior provincial teeth, with a smaller anterior tooth. The left valve has a central indentation to accommodate the central tooth of the right valve, as well as 1 tooth at each end of the indentation.

*Other features:* The shell is heavy and strong, usually dark grey in colour with a purple tinge around the umbones. There is generally a dark then light band visible near the outer edge of the prodissoconch II shell. There is no visible eyespot.

*Comparison with other species:* This larva resembles in shape and other features several teredinid species, many of which have been described from laboratory culture, including *Teredo japonica*, *T. megotara*, *T. navalis*, *T. (Lyrodus) pedicellata*, *T. furcifera*, *Bankia setacea*, *B. indica*, *B. gouldi*, *Lyrodus pedicellatus*, *Teredora malleolus*, and *Nototeredo knoxi* (Miyazaki 1935; Jorgensen 1946; Sullivan 1948; Rees 1950; Isham & Tierney 1953; Quayle 1953; Nair 1956; Loosanoff & Davis 1963; Loosanoff et al. 1966; Turner & Johnson 1969; Scheltema 1971; Chanley & Andrews 1971; Turner & Boyle 1974; Culliney 1975). Furthermore, the hinge form is consistent with that of the teredinids described by Jorgensen (1946), Rees (1950), Quayle (1953), Nair (1956), Turner & Johnson (1969), Scheltema (1971), and Guérin (1973).

*Distribution and seasonal abundance* (Table 1): This larva was observed at all sampling localities.

In the Bay of Islands, it occurred throughout much of the year, most commonly during late autumn 1970, summer 1970–71, and winter and spring 1971.

In Wellington Harbour, and off Raumati Beach, this larva occurred occasionally or frequently throughout most of the sampling periods.

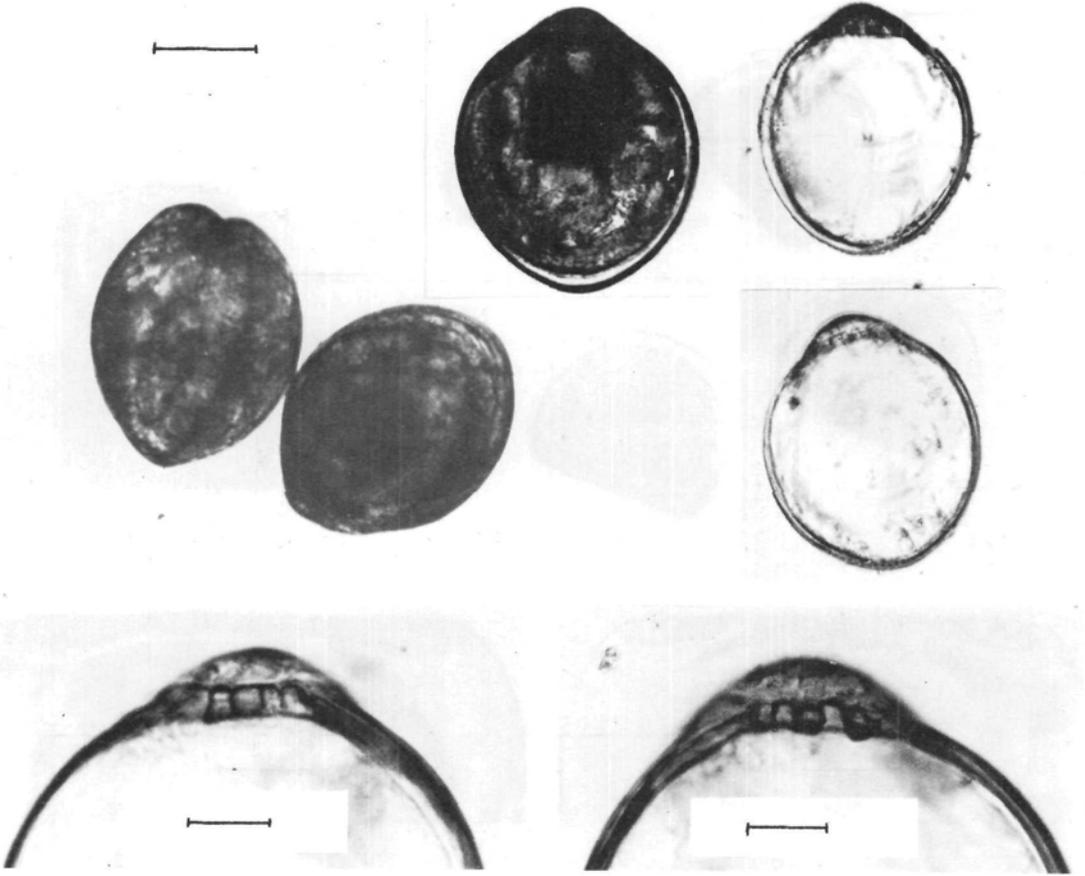


Fig. 8 Late stage larvae (upper left) and single valves (upper right) of Teredinid 1; scale line, 100  $\mu\text{m}$ . Hinge of left valve (lower left) and right valve (lower right) of late stage larva (length 230  $\mu\text{m}$ ) of Teredinid 1; scale lines, 40  $\mu\text{m}$ .

These observations suggest that this species spawns throughout much of the year at each locality.

**Provisional identification:** This larva has several features in common with teredinid larvae described elsewhere, including its ovate shape, short hinge line, and distinctive hinge structure.

Turner & McKoy (1979) and McKoy (1980a) give 5 teredinid species which occur often in 1 or more of the sampling localities (*Lyrodus medilobatus*, *L. pedicellatus*, *Nototeredo edax*, *Bankia australis*, and *B. neztalia*), and Teredinid 1 is identified with 1 of these species. However, the difficulty often experienced in separating teredinid larval species (e.g., see Culliney 1975) means that it is quite possible that during this study the New Zealand species have been partially or totally grouped.

#### Unidentified larvae

##### UNIDENTIFIED LARVA 1

Fig. 9, Table 1.

**Dimensions:** Late-stage larvae 200–220  $\mu\text{m}$  long, with average length to height ratio of 1:0.77 and

ratio of length of larva to length of hinge line of 1:0.82. Larvae less than 200  $\mu\text{m}$  long were never observed, suggesting hyperlarviparous development.

**Shape** (Fig. 9): The late-stage larva is truncate, with an almost symmetrical D-shaped form.

**Hinge** (Fig. 9): In a larva 220  $\mu\text{m}$  long, the hinge of both valves consists of 2–3 taxodont teeth at each end of the hinge line, with an undifferentiated central region.

**Other features:** The larva is strong and heavy, and dark grey in colour. A single line, which may correspond to the edge of the prodissoconch I shell, is prominent near the outer edge of the larva. Other concentric and radial lines are not prominent. The prodissoconch II shell appears to be poorly developed. There is an approximately central eyespot in larvae 210  $\mu\text{m}$  or more long, which could be present in smaller larvae as well.

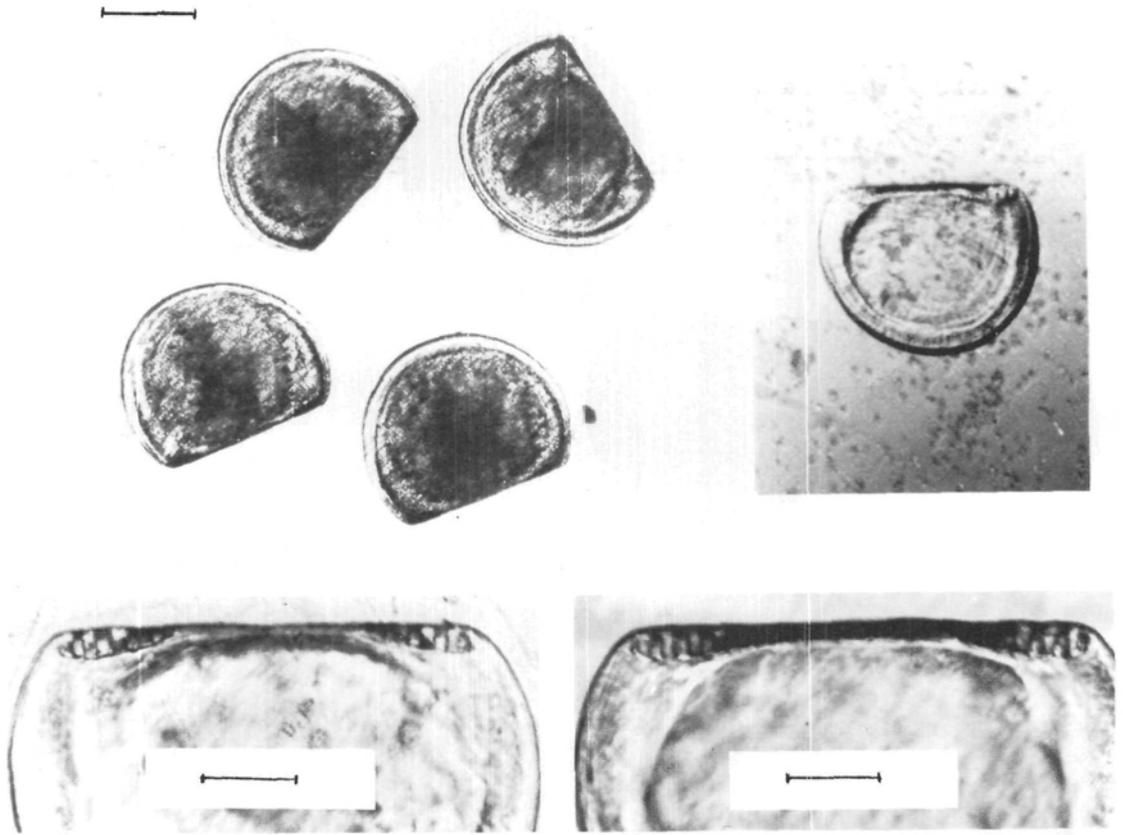


Fig. 9 Late stage larvae (upper left) and single valve (upper right) of Unidentified Larva 1; scale line, 100  $\mu\text{m}$ . Hinge of left valve (lower left) and right valve (lower right) of late stage larva (length 220  $\mu\text{m}$ ) of Unidentified Larva 1; scale line, 40  $\mu\text{m}$ .

*Comparison with other species:* This larva most resembles some mytilid, pectinid, and pandoracean larvae. It is similar in size, shape, hinge structure, and colour to the mytilid *Perumytilus purpuratus*, described from laboratory culture by Ramorino & Campos (1979). However, the taxodont hinge system of Unidentified Larva 1 differs from that of *P. purpuratus* and the New Zealand mytilids so far described (Booth 1977) in that the central region of the hinge is undifferentiated and lacks teeth.

Taxodont dentition (often with an undifferentiated central region) also occurs in superfamilies Arcacea (Chanley & Andrews 1971), Pectinacea, and Anomiacea (Jorgensen 1946; Rees 1950). No arcacean or anomiecean larvae similar in shape to Unidentified Larva 1 were found in the literature. However, the pectinid *Equichlamys bifrons* described by Dix (1976) is similar in size, shape, and hinge structure to this larva.

The pandoracean larvae most similar to Unidentified Larva 1 are *Pandora gouldiana*, provisionally

identified by Sullivan (1948), and *P. inaequalvis*, *Lyonsia hyalina*, and *Entodesma cuneata*, described from laboratory culture by Allen (1961), Chanley & Castagna (1966), and Campos & Ramorino (1981). However, the similarity extends only to the general shape and colour, and not to the hinge structure. Furthermore, Unidentified Larva 1 is more strictly D-shaped than these species.

Other larvae similar in shape to Unidentified Larva 1 are the much larger, non-pelagic larvae of the venerid *Gemma gemma*, provisionally identified by Sullivan (1948) and confirmed by Chanley & Andrews (1971), and the ostreids and erycinids *Tiostrea lutaria*, *T. chilensis*, *Lasaea rubra*, *L. rubra hinemoa*, and *L. maoria*, described from brooded or released larvae (Oldfield 1964; Booth 1979b; Chanley & Dinamani 1980). However, taxodont dentition is absent in these larvae.

*Distribution and seasonal abundance* (Table 1): This larva was observed only at the Bay of Islands on 1

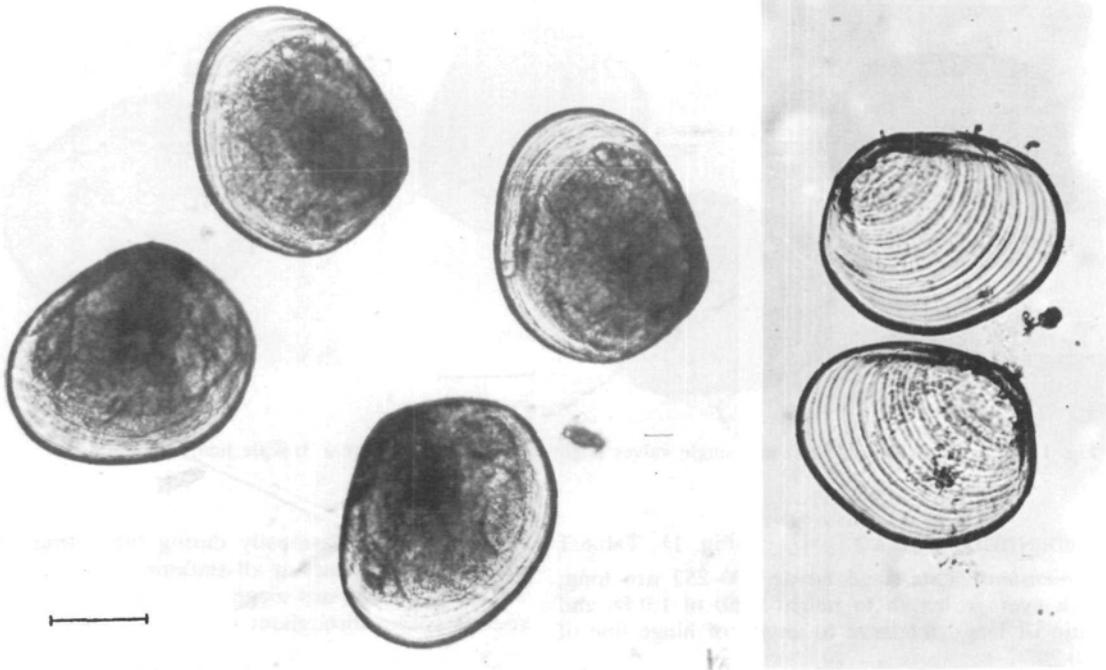


Fig. 10 Late stage larvae (left) and single valves (right) of Unidentified Larva 2; scale line, 100  $\mu\text{m}$ .

occasion (May 1970), when it occurred in large numbers from the surface to 4 m depth at the inner harbour stations (Confluence and Brampton Reef).

*Provisional identification:* The size, shape, colour, and hinge structure most strongly point to this larva belonging to superfamilies Mytilacea or Pectinacea. Powell (1979) listed 12 mytilacean (Family Mytilidae) species and 19 pectinacean (families Pectinidae and Dimyidae) species. However, Rees (1950) appeared to include family Limidae in superfamily Pectinacea, and Powell (1979) listed 8 New Zealand members of this family. Five mytilid and 2 pectinid larvae from New Zealand have been provisionally identified (Booth 1977; Bull 1977; present study). Unidentified Larva 1 may be 1 of the yet undescribed members of these families which occurs at least in the north of the country. The large prodissoconch I shell and poor development of the prodissoconch II shell, giving a D-shaped form to the late-stage larva, point to a species with hyperlarviparous development. The absence of larvae less than 200  $\mu\text{m}$  long in the plankton during the sampling period also supports this possibility.

#### UNIDENTIFIED LARVA 2

Fig. 10, Table 1

*Dimensions:* Late-stage larvae 230–260  $\mu\text{m}$  long, with average length to height ratio of 1:0.88, and

ratio of length of larva to length of hinge line of 1:0.25.

*Shape* (Fig. 10): In the late-stage larva, the umbones are equal in size and angular. The anterior end is much longer and more pointed than the posterior end. The posterior shoulder is much shorter and slopes more steeply than the anterior shoulder. The ventral margin is almost flat.

*Other features:* Prominent concentric lines cover both prodissoconch I and II shells, but there are no obvious radial lines. A prominent ridge line is visible near to and almost parallel with the anterior shoulder. There is no visible eyespot.

*Comparison with other species:* This larva resembles in shape some of the tellinid (superfamily Tellinacea) species provisionally identified by Rees (1950).

*Distribution and seasonal abundance* (Table 1): This larva was observed only in the Bay of Islands and Wellington Harbour.

In the Bay of Islands, it occurred commonly or frequently during the spring and autumn of both years.

The larva occurred occasionally during spring 1971 in Wellington Harbour.

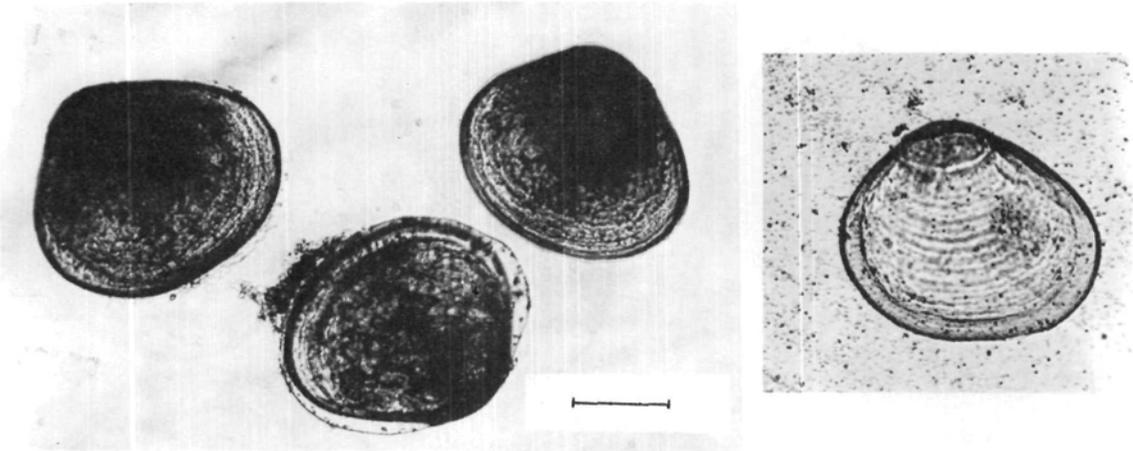


Fig. 11 Late stage larvae (left) and single valves (right) of Unidentified Larva 3; scale line, 100  $\mu\text{m}$ .

#### UNIDENTIFIED LARVA 3

Fig. 11, Table 1

*Dimensions:* Late-stage larvae 200–250  $\mu\text{m}$  long, with average length to height ratio of 1:0.86 and ratio of length of larva to length of hinge line of 1:0.20.

*Shape* (Fig. 11): In the late-stage larva, the umbones are equal in size and angular. The anterior end is longer and more pointed than the posterior end. The posterior shoulder is much shorter and slopes more steeply than the anterior shoulder. The ventral margin is almost flat.

*Other features:* Prominent concentric lines are obvious towards the outer edge of the prodissoconch II shell. Under Nomarski DIC, concentric lines can be observed over both prodissoconch shells, but the prodissoconch I shell is also punctate in texture; there are no obvious radial lines. There is no visible eyespot.

*Comparison with other species:* This larva resembles in shape the tellinids (superfamily Tellinacea) *Tellina fabula*, provisionally identified by Rees (1950), and *T. agilis*, described from laboratory culture by Chanley & Andrews (1971). It is also similar in shape to Unidentified Larva 2, but lacks the ridge line near the anterior shoulder.

*Distribution and seasonal abundance* (Table 1): This larva was observed only at the Bay of Islands and Wellington Harbour.

In the Bay of Islands, it occurred frequently during the spring of both years and summer 1970–71, and occasionally during the winter of both years. It was most often taken at the inner harbour stations.

In Wellington Harbour, the larva occurred abundantly or commonly during the summer, and

frequently or occasionally during the spring and winter of both years at all stations.

These observations suggest that the adults of this species spawn throughout most of the year.

#### UNIDENTIFIED LARVA 4

Fig. 12, Table 1

*Dimensions:* Late-stage larvae 200–250  $\mu\text{m}$  long, with average length to height ratio of 1:0.92, and ratio of length of larva to length of hinge line of 1:0.20.

*Shape* (Fig. 12): In the late-stage larva, the umbones are equal in size and angular. The anterior end is much longer and more pointed than the posterior end. The posterior shoulder is steeper and much shorter than the anterior shoulder. The ventral margin is broadly rounded.

*Other features:* There are widely separated, prominent concentric lines, particularly over the prodissoconch II shell. No obvious radial lines are visible, even under Nomarski DIC. There is no visible eyespot.

*Comparison with other species:* This larva resembles in shape the clam *Tagelus plebeius* (fam. Solecurtidae), described from laboratory culture by Chanley & Castagna (1971). The main difference in shape between this larva and Unidentified Larva 3 is the more rounded ventral margin of Unidentified Larva 4.

*Distribution and seasonal abundance* (Table 1): This larva was observed only at the Bay of Islands and Wellington Harbour.

At the Bay of Islands, it occurred at all stations, with peak densities occurring during summer 1970–71 and autumn 1971. It did not occur in autumn 1970.

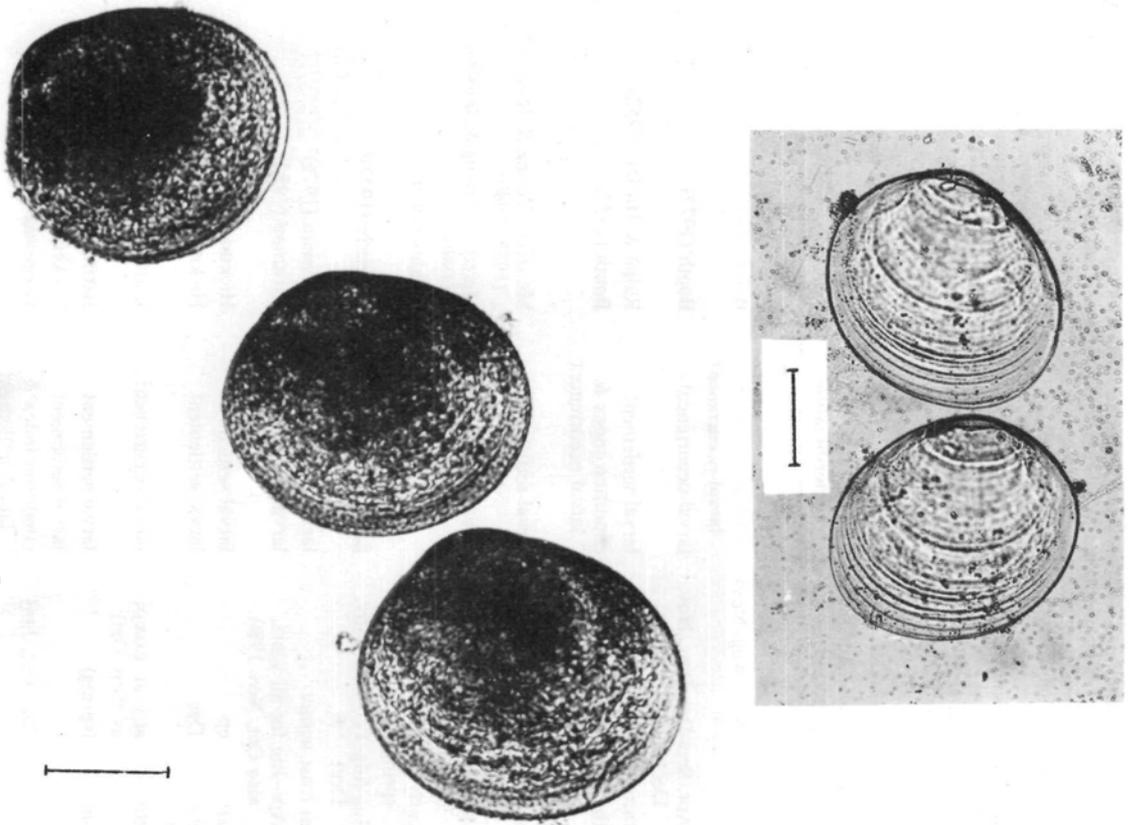


Fig. 12 Late stage larvae (left) and single valves (right) of Unidentified Larva 4; scale line, 100  $\mu$ m.

In Wellington Harbour, the larva occurred frequently at all stations during the summer and winter.

## DISCUSSION

Some distinguishing features useful in the separation of larvae observed in the plankton were the external shell morphology (described in each case), and, where applicable, the colour of the shell (e.g., the amber colour of *Hiatellid* 1). Recognition to superfamily level was most often on the basis of the hinge structure, following Rees (1950). Provisional identification to generic and specific level was usually made by comparing the larval features with those of the same genus from elsewhere, and relating to the most abundant adult species in the sampling localities. These methods make the following assumptions:

(a) The published larval descriptions are correct. However, although many bivalve species overseas

have been described, the identification of only a small proportion has been confirmed by laboratory culture. There have been cases of incorrect identification, e.g., Chanley & Castagna (1966) suggested that Rees's (1950) identifications of pandoracean larvae were in error.

(b) The larvae of the same genus, family, or superfamily have consistent features, including hinge structure. However, Rees (1950) has indicated that, for example, some superfamilies (Veneracea, Mactracea) have more than 1 basic hinge form.

(c) The most abundant bivalve species contributed to the larvae in the plankton during the sampling period. Instead it is possible that the adults in any 1 of the sampling localities were not spawning during 1970–72. For example, *Saccostrea glomerata* does not spawn consistently each year (P. Dinamani, Fisheries Research Division, M.A.F., pers. comm.). Also, the far greater densities of Pinnid 1 (provisionally identified as *Atrina pectinata zelandica*) observed in Wellington Harbour during 1971 than 1970, and the more prolonged occurrence

**Table 3** Inferred spawning periods of some bivalves from New Zealand, with sampling localities listed from the northern-most. (\*, larval identification is provisional only; †, although original larval identification was provisional, it has since been confirmed by laboratory culture; ‡, incubating species). For species in which larval occurrence or settlement is the determinant of the spawning season, no attempt has been made to take into account the larval brooding period (for incubatory species) or the larval development time. In such cases, it may be necessary to subtract 1–4 weeks to give the time of spawning. Particular behaviour such as secondary settlement of larvae may further obscure spawning times. 1, described as *M. planulatus*; 2, based on 'spawning gonads'; 3, 1 settlement examined; 4, an autumn settlement occurred in 1973; 5, intensity of spring settlement variable from year to year; 6, settlement usually sampled Oct–Apr; 7, variation in spawning months between areas noted; 8, described as *A. walteri*; 9, described as *Ostrea lutaria*; 10, described as *Ostrea* sp.; 11, described as rock oyster; 12, described as *Crassostrea glomerata*; 13, described as *Amphidesma ventricosum*, the provisional identification of *P. ventricosa* larvae has been questioned by Booth (1977); 14, described as *P. (Mesodesma) ventricosa*; 15, described as *B. australis*.

Family and species	Locality	Period of study	Inferred spawning periods (main periods)	Method of determination	Source
<b>MYTILIDAE</b>					
<i>Mytilus edulis aoteanus</i>	Bay of Islands	Apr 70–Feb 72	Feb, Apr–Nov (Aug–Nov)	condition index & larval occurrence†	Booth (1977)
	Raumati Beach	Jun 71–Jun 72	Apr, Sep–Dec (Apr, Nov, Dec)	larval occurrence†	Booth (1977)
	Wellington Hr	Apr 49–Apr 50	throughout year	larval settlement	Ralph & Hurley (1952) <sup>1</sup>
	Wellington Hr	May 70–Feb 72	throughout year, except Mar (May–Oct, Dec, Jan)	condition index & larval occurrence†	Booth (1977)
	Marlborough Sounds	Oct 75–Apr 76 + 2 other yrs	at least Oct–Apr (Oct–Jan)	larval settlement	Meredyth-Young & Jenkins (1978, 1980)
	Marlborough Sounds	Aug 78–Jun 79	Apr, May, Aug, Oct–Jan (Apr, May, Oct–Jan)	larval settlement	Meredyth-Young & Jenkins (1980)
	Marlborough Sounds	?	early winter & early spring	?	Jenkins (1979)
Taylor's Mistake	Jul 73–Jun 74	Jul/Aug–Feb/Mar (Nov, Dec)	gonad development & condition index	Kennedy (1977) <sup>2</sup>	
<i>Perna canaliculus</i>	Ninety Mile Beach	1974	at least winter	larval settlement	Hickman (1976) <sup>3</sup>
	Ninety Mile Beach	1979–81	Apr–Jun for all years, also Oct, Nov 1980	larval settlement	Hickman (1982)
	Whangaroa Hr	1972	at least Sep	larval settlement	Hickman (1979) <sup>3</sup>
	Ahipara	Dec 73–Dec 75	Jul, Oct, Dec (")	larval settlement	Hickman (1979) <sup>4</sup>
	Bay of Islands	Apr 70–Dec 71	throughout year, except Jan, May (Sep, Oct)	larval occurrence†	Booth (1977)
	Kaipara Hr	Oct 80–mid 81	unstated (spring)	larval settlement	Bartrom (1981)
Auckland	Jan 62–Dec 63	Jul–Oct	larval settlement	Luckens (1976)	
Coromandel Hr	Dec 70–Jan 73	Jul–Apr (Aug–Oct, Jan)	condition index & larval settlement	Greenway (1975)	

	Coromandel Hr	Oct 79–mid 81	late spring 1979, 1980, mid & late summer 1980–81 (spring)	larval settlement	Bartrom (1980, 1981)
	Te Kouma Hr	Jun 67–Jun 69	throughout year (Sep–Apr)	larval settlement	Greenway (1969b)
	Piha	Jan 62–Dec 63	throughout year (Jul–Dec)	larval settlement	Luckens (1976)
	Hauraki Gulf	at least 1968–70	much of year (?) (Feb, Mar, Sep, Oct)	larval settlement	Greenway (1972) <sup>5</sup>
	Raumati Beach	Jun 71–Jun 72	Mar–Dec (Mar–Sep)	larval occurrence†	Booth (1977)
	Te Kaha	?	unstated (Apr, Sep)	?	Waugh (1980)
	Te Kaha	1977–79	unstated (Mar–May, Sep–Nov)	larval settlement	Johns (1980)
	Tolaga Bay	?	unstated (Oct, May)	larval occurrence	Anon (1980b)
	Wellington Hr	May 70–Feb 72	throughout year except Apr, Nov (May, Jul–Oct, Dec–Mar)	larval occurrence†	Booth (1977)
	Marlborough Sounds	Oct 75–Apr 76 + 2 other yrs.	at least Oct–Apr (Feb–Apr)	larval settlement	Meredyth-Young & Jenkins (1978, 1980)
	Marlborough Sounds	Aug 77–May 78	Dec to at least Jun ( " )	} larval settlement	Meredyth-Young & Jenkins (1980)
	Marlborough Sounds	Aug 78–Jun 79	Sep to at least Jun (Nov to at least Jun)		
	Marlborough Sounds	Sep 80–Jun 81	Oct to at least Jun (Nov to at least Jun)	larval occurrence & settlement	Meredyth-Young (1981)
	Marlborough Sounds	?	early autumn & late spring	?	Jenkins (1979)
<i>Aulacomya ater</i> <i>maoriana</i>	Taylor's Mistake	July 73–Jun 74	Aug–Sep/Nov (Aug, Sep)	gonad development & condition index	Kennedy (1977) <sup>2</sup>
<i>Modiolus areolatus</i>	Bay of Islands	Apr 70–Dec 71	throughout year, except Jan, Mar (Feb, May– Sep, Nov, Dec)	larval occurrence*	Booth (1977)
	Raumati Beach	Jun 71–Jun 72	Feb–Jun, Nov (Feb–Jun)	larval occurrence*	Booth (1977)
<i>Xenostrobus pulex</i>	Bay of Islands	Apr 70–Dec 71	throughout year, except Mar (Aug–Oct)	larval occurrence†	Booth (1977)
	Mahurangi Hr	1972	at least Aug, Sep	larval settlement	Curtin (1973)
	Auckland	Jan 62–Dec 63	Jul–Jan (Jul–Oct)	larval settlement	Luckens (1976)
	Piha	Jan 62–Dec 63	throughout year	larval settlement	Luckens (1976)
	New Plymouth	Mar 73–at least Feb 74	throughout year	larval settlement	Luckens (1975)
	Raumati Beach	Jun 71–Jun 72	throughout year (Feb–Jun, Sep–Nov)	larval occurrence†	Booth (1977)

	Wellington Hr	May 70–Feb 72	Feb, May, Jul–Oct (Jul–Oct)	larval occurrence†	Booth (1977)
<i>Modiolarca impacta</i>	Bay of Islands	Apr 70–Dec 71	throughout year (Jan–Mar, Jun–Dec)	larval occurrence†	Booth (1977)
	Raumati Beach	Jun 71–Jun 72	Sep, Dec–Mar (Dec–Mar)	larval occurrence†	Booth (1977)
	Wellington Hr	May 70–Feb 72	throughout year, except Mar (Apr–Sep, Dec–Feb)	condition index & larval occurrence†	Booth (1977)
<b>PECTINIDAE</b>					
<i>Pecten novaezelandiae</i>	Mahurangi Hr	Oct 79–mid 80	autumn & spring	larval settlement	Bartrom (1980)
	Coromandel Hr	Oct 79–mid 80	late spring	larval settlement	Bartrom (1980)
	Golden Bay	Oct 77–Aug 79	Jan, Apr, May, Oct	larval settlement	Bull (1980)
	Marlborough Sounds	1971, 1973–1979	at least Oct–May (early summer)	larval settlement & gonad weight	Bull (1980) <sup>6</sup>
	Marlborough Sounds	at least 1973–74	at least Aug–Feb (Nov, Dec)	gonad development	Bull (1977)
	Marlborough Sounds	?	Mar–Jun	?	Anon (1974)
	Nelson Bays— Marlborough Sounds	?	Feb–May/Jun Nov–Jan (Feb–May/Jun)	?	Stead (1976) <sup>7</sup>
	Tasman Bay	Nov 59–Jan 60	Aug–Mar, or Mar, Aug, Sep (Mar)	general appearance of gonad	Choat (1960)
	Tasman Bay	at least Jun 63–Mar 65	Mar–Jun	gonad weight & appearance	Tunbridge (1968)
<i>Chlamys zelandiae</i>	Tasman Bay	Oct 78–May 79	at least Oct–Dec	larval settlement	Bull (1980)
	Bay of Islands	Apr 70–Dec 71	most of year (Jul–Aug/Oct)	larval occurrence*	present study
	Auckland	Jan 62–Dec 63	Sep–Dec	larval settlement	Luckens (1976)
	Raumati Beach	Jun 71–Jun 72	Mar, Jun, Jul ( " )	larval occurrence*	present study
	Wellington Hr	May 70–Feb 72	most of year (May– Dec/Jan)	larval occurrence*	present study
<b>PINNIDAE</b>					
<i>Atrina pectinata zelandica</i>	Bay of Islands	Apr 70–Dec 71	Jan, Feb, Apr–Oct ( " )	larval occurrence*	Booth (1979a)
	Raumati Beach	Jun 71–Jun 72	Jan ( " )	larval occurrence*	Booth (1979a)
	Wellington Hr	May 70–Feb 72	Jan–Mar, May–Jul (Jan, Feb, May–Jul)	larval occurrence*	Booth (1979a)

## ANOMIIDAE

*Anomia trigonopsis*

Bay of Islands	Apr 70–Dec 71	Dec–Mar/Apr (Dec–Feb/Apr)	larval occurrence*	Booth (1979a)
Auckland Hr	Feb 54–Jan 55	Nov–May (Nov, Dec, Apr, May)	larval settlement	Skerman (1959) <sup>8</sup>
Auckland	Jan 62–Dec 63	Mar, Apr, Oct	larval settlement	Luckens (1976)

## OSTREIDAE

*Tiostrea lutaria*‡

Auckland	Jan 62–Dec 63	Feb–Apr 1962, Jan, Apr, May 1963	larval settlement	Luckens (1976) <sup>9</sup>
Wellington Hr	at least Dec 60–Aug 61	at least Aug–Mar (Dec–Feb)	gonad appearance & larval brooding	Hollis (1963) <sup>9</sup>
Foveaux Strait	Nov 60–Sep 64	Aug–Mar (Nov–Feb)	larval brooding & larval settlement	Stead (1971) <sup>9</sup>
Foveaux Strait	Mar 65–Apr 67	Oct–Jul (Dec–Feb)	larval settlement	Cranfield (1968) <sup>9</sup>
Foveaux Strait	Sep 67–Apr 68	Nov–Feb (Nov–Jan)	condition index, larval brooding & settlement	Cranfield & Allen (1977) <sup>9</sup>

*Ostrea aupaouria*‡

Foveaux Strait	1970–71	spring–summer (Dec–Feb)	gonad development	Cranfield (1979) <sup>9</sup>
Bay of Islands	Apr 70–Dec 71	Oct/Dec–Apr/Jun (Dec–Apr)	larval occurrence†	Booth (1979a) <sup>10</sup>
Bay of Islands Mahurangi Hr	} ?	Nov–Apr/May (Jan, Feb)	larval brooding, occurrence & settlement	Dinamani (1981a)
Northland	?	Dec–Apr/May ( " )	larval brooding & settlement	Dinamani (1971) <sup>10</sup>

*Saccostrea glomerata*

Parengarenga Hr	Nov 71–Apr 72	at least Nov–Feb (Nov)	larval settlement	Curtin (1973) <sup>11</sup>
Bay of Islands	Apr 70–Dec 71	Dec–Mar/Apr (Dec–Feb/Apr)	larval occurrence†	Booth (1979a) <sup>12</sup>
Bay of Islands	Apr 70–Oct 72	Dec–Mar/Apr/May (Jan, Feb)	gonad development, larval occurrence, † & larval settlement	Dinamani (1974a) <sup>12</sup>
Whangateau Hr	Dec 71–Apr 72	at least Dec–Feb (Dec, Jan)	larval settlement	Curtin (1973) <sup>11</sup>
Mahurangi Hr	Dec 67–Jan 69	at least Dec–Mar/Apr (Jan–Mar)	larval settlement	Greenway (1969a) <sup>12</sup>
Mahurangi Hr	Sep 71–Apr 72	mid Dec–Mar (Dec, Jan)	larval settlement	Curtin (1973) <sup>11</sup>
Mahurangi Hr	Dec 73–May 74, at least Jan–Mar 78, Dec 79–Mar 80	late Dec–Apr (Jan–Mar)	larval occurrence & larval settlement	Dinamani & Lenz (1977); Dinamani (1978b); Anon (1980a)

<i>Crassostrea gigas</i>	Auckland	Jan 62–Dec 63	Jan–May	larval settlement	Luckens (1976) <sup>12</sup>
	Bay of Islands	1975	at least Feb, Apr ( " )	larval settlement	Dinamani (1975)
	Mahurangi Hr	1974–81	Dec/Jan—at least Apr (Feb, Mar)	larval occurrence & larval settlement	Dinamani (1975, 1978a, 1978b, 1981b); Anon (1980a)
<b>ERYCINIDAE</b>					
<i>Lasaea rubra hinemoa</i> ‡	Bay of Islands	Feb 71–May 72	most of year	larval brooding	Booth (1979b)
<i>Kellia cycladiformis</i> ‡	Bay of Islands	Apr 70–Dec 71	throughout year, except Mar (May–Feb)	larval occurrence	Booth (1979b)
	Raumati Beach	Jun 71–Jun 72	throughout year, except Sep–Nov (Dec–Jul)	larval occurrence	Booth (1979b)
	Wellington Hr	May 70–Feb 72	throughout year, except Oct (Apr–Jul, Dec, Jan)	larval occurrence	Booth (1979b)
<i>Borniola reniformis</i> ‡	Bay of Islands	Apr 70–Dec 71	throughout year (Oct–Feb)	larval occurrence*	present study
	Raumati Beach	Jun 71–Jun 72	Feb ( " )	larval occurrence*	present study
	Wellington Hr	May 70–Feb 72	throughout year (Dec, Jan, Apr–Jun)	larval occurrence*	present study
<i>Arthritica bifurca</i> ‡	Bay of Islands	Apr 70–Dec 71	throughout year ( " )	larval occurrence†	Booth (1979b)
	Raumati Beach	Jun 71–Jun 72	throughout year, except spring (Mar)	larval occurrence†	Booth (1979b)
	Wellington Hr	May 70–Oct 72	throughout year ( " )	larval brooding & larval occurrence†	Booth (1979b)
<b>VENERIDAE</b>					
<i>Chione (Austrovenus) stutchburyi</i>	Bay of Islands	Sep 70–Jan 72	at least Jan, Feb, Aug–Oct (Jan, Feb)	condition index	present study
	Wellington Hr	Sep 70–Jan 72	at least Sep, Oct, Dec, Jan (Dec, Jan)	condition index	present study
Venerid 1	Bay of Islands	Apr 70–Dec 71	throughout year (Sep–Nov)	larval occurrence	present study
	Wellington Hr	May 70–Feb 72	throughout year except late spring ( " )	larval occurrence	present study

MACTRIDAE					
<i>Spisula (Crassula) aequilateralis</i>	Raumati Beach	Jun 71–Jun 72	Dec–Apr ( " )	larval occurrence*	present study
MESODESMATIDAE					
<i>Paphies australis</i>	Bay of Islands	Apr 70–Dec 72	throughout year (Aug–Feb/May)	condition index & larval occurrence*	present study
	Raumati Beach	Jun 71–Jun 72	Feb, Mar, Sep, Dec (Feb, Mar)	larval occurrence*	present study
	Wellington Hr	May 70–Feb 72	throughout year (Aug–Apr)	larval occurrence*	present study
<i>Paphies ventricosa</i>	North Kaipara Beach (= Dargaville Beach)	Sep 38–Jun 39	at least Oct–Jun	gonad development, larval occurrence* & settlement	Rapson (1952) <sup>13</sup>
		at least Nov 39–Aug 40	Nov–Mar, Jun–Aug	"	Rapson (1952) <sup>13</sup>
	Dargaville Beach	Nov 68–Mar 71	May–Jul/Aug, Sep–Mar (Sep–Feb)	gonad development, condition index & larval settlement	Redfearn (1974) <sup>14</sup>
<i>Paphies subtriangulata</i>	Muriwai Beach	Nov 38	at least Nov	larval settlement	Rapson (1952) <sup>13</sup>
	Dargaville Beach	Mar 76–Feb 78	most of year (?) (Oct–Dec)	condition index	Greenway (1981)
HIATELLIDAE					
<i>Hiatella arctica</i>	Bay of Islands	Apr 70–Dec 71	most of year (May–Nov)	larval occurrence*	present study
	Raumati Beach	Jun 71–Jun 72	most of year (May–Feb)	larval occurrence*	present study
	Wellington Hr	May 70–Feb 72	May, Jul–Sep, Dec (Jul–Sep)	larval occurrence*	present study
PHOLADIDAE					
<i>Anchomasa similis</i>	Bay of Islands	Apr 70–Dec 71	Jul–Nov ( " )	larval occurrence†	present study
	Auckland	Jan 62–Dec 63	Jul, Aug 1962 May, Oct 1963	larval settlement	Luckens (1976)
	Raumati Beach	Jun 71–Jun 72	Jan, Mar, Jun, Jul, Dec ( " )	larval occurrence†	present study
	Wellington Hr	May 70–Feb 72	Jun–Sep, Dec ( " )	larval occurrence†	present study
<i>Pholadidea spathulata</i>	Auckland	Jan 62–Dec 63	Jul, Aug, 1962 May, Oct 1963	larval settlement	Luckens (1976)

## TEREDINIDAE

*Bankia australis*  
*B. neztalia*

Tauranga Hr	Apr 70-Oct 72	Jan-May (Feb-Apr)	larval settlement	McKoy (1981)
Tauranga Hr	Apr 70-Oct 72	most of year (Jan-Mar, Jul-Sep)	larval settlement	McKoy (1981)
Wellington Hr	Apr 49-Apr 50	most of year (Dec-Apr)	larval settlement	Ralph & Hurley (1952) <sup>15</sup>
Wellington Hr	Jul 70-Dec 72	most of year (May-Oct)	gonad development, larval occurrence* & larval settlement	McKoy (1980b, 1981)
Otago Hr	Oct 52-Dec 53	late Aug-Jun (Jan-Jun)	larval settlement	Hurley (1969) <sup>15</sup>
Tauranga Hr	Apr 70-Oct 72	Feb-Apr, Jun, Jul (Mar, Apr)	larval settlement	McKoy (1981)
Tauranga Hr	Apr 70-Oct 72	Nov-Apr/Jul (Jan-Apr/Jul)	larval settlement	McKoy (1981)
Tauranga Hr	Apr 70-Oct 72	Jan-May (Feb-Apr)	larval settlement	McKoy (1981)

*Lyrodus pedicellatus*†

*L. medilobatus*†

*Nototeredo edax*

of *Ostrea* sp. (= *O. aupaoria*) in the Bay of Islands during winter 1971 than in 1970 (see Booth 1979a) point to considerable variation from year to year in spawning success. Further confusion may stem from larvae originating from outside the sampling localities and being brought in by currents.

In addition, because of similarities in shape between larvae of species of the same genus, or between species of different genera at different stages of development, positive identifications are difficult. This is particularly so in field studies, when it is impossible to verify a character such as hinge structure in a large sample.

Because of these limitations, the identifications made in this study must be considered provisional until confirmed by laboratory culture.

### Seasonal patterns of larval occurrence

The frequency of sampling (approximately monthly intervals) makes it possible to determine only the broadest patterns of larval occurrence in the plankton. In addition, the patterns may be complicated by some larvae having a particularly prolonged pelagic period in which settlement and metamorphosis are delayed. This has been found to occur in some species overseas, e.g., *Mytilus edulis* (see Bayne 1965).

Bivalve larvae were abundant in the plankton during all months of 1970-72 in the study areas. This was also observed by Jillett (1971) to be the case in the Hauraki Gulf during 1963-65. However, in other parts of the world, very few larvae were observed in the plankton during several months of the year, particularly over winter (Jorgensen 1946; Sullivan 1948; Rees 1950; Chanley & Andrews 1971; Stromgren 1973). Lower sea temperatures in some areas compared with New Zealand may be the main reason for fewer larvae during winter.

There was considerable variation in the duration of specific larvae in the plankton (Table 1; Booth 1977, 1979a, 1979b). Some species occurred in the plankton for a short time (1-4 months), e.g., Unidentified Larva 1, *Anomia trigonopsis*, and *Saccostrea glomerata* in the Bay of Islands (present study; Dinamani 1974a; Booth 1979a). However, most species occurred throughout much of the year with 1-3 peaks of abundance, each lasting 1-4 months.

### Bivalve spawning seasons

The spawning seasons of some New Zealand bivalves, as inferred from this and other studies, are reviewed in Table 3. Several different methods have been used to assess the spawning season, and all have some limitations. For example, the use of gonad development may be misleading because although gonads are mature, environmental triggers

for spawning may not occur. Also the stage of gonad development may vary markedly between individuals within any particular sampling area. Condition index (or gonad condition) may fall rapidly for reasons other than spawning, and, in any case, changes in condition index caused by spawning are often difficult to detect. Furthermore, there is often a time lag between condition peaks and spawning peaks. Larval occurrence indicates spawning has occurred, but absence of larvae in a plankton survey does not necessarily mean that spawning has not taken place. Larval settlement cannot occur without suitable sea conditions for complete larval development, followed by the availability of suitable settlement substrates. The fouling of collectors by other organisms may obscure settlement.

Year to year variations in spawning success are a further source of error in estimating spawning season from published data, which are often based on studies of short duration (frequently little more than 1 year), and on infrequent or otherwise inadequate sampling. There may be large differences in the abundance of adults (and therefore in larval production) according to location. Delay between spawning and larval settlement and, for incubatory species, delay between spawning and release of larvae, are further sources of error. These and other limitations mean that only a general indication of the spawning period is available for most New Zealand species.

The following sections summarise available published data on bivalve spawning seasons for each family. Reference to unpublished theses has been omitted.

#### SUPERFAMILY MYTILACEA

##### MYTILIDAE

*Mytilus edulis aoteanus* has been studied at 5 localities between the Bay of Islands and Banks Peninsula. At all localities spawning occurred during spring as well as part of autumn or early winter, and in Wellington Harbour spawning occurred throughout the year. Furthermore, the peak spawning period included spring in all studies. However, there was some evidence for different spawning seasons at 'discrete' localities (localities separated by at least 20' of latitude, or which are hydrologically dissimilar) during the same years; spawning during 1970–72 appeared to be more prolonged in Wellington Harbour than at Raumati Beach or the Bay of Islands. At 2 localities (Wellington Harbour and Marlborough Sounds) studies covered more than 2 years, and the inferred spawning seasons were similar between years for each locality.

Studies on *Perna canaliculus* at 15 localities between Ninety Mile Beach and the Marlborough Sounds indicated spring spawning at all localities

(with the possible exception of some years off Ninety Mile Beach), but spawning also occurred during early autumn and/or throughout the year in many localities. In addition, the peak spawning period included spring in most of the studies.

Spawning periods at discrete localities during the same years were sometimes similar. Spawning was prolonged at the Bay of Islands, Coromandel Harbour, Raumati Beach, and Wellington Harbour during 1970–72, with early spring being a peak spawning time. However, spawning was more prolonged at Piha than at Auckland during 1962–63. Summer spawning which occurred during 1980–81 in the Marlborough Sounds was not evident at Ninety Mile Beach (1979–81) or in Coromandel Harbour (1979–80). Furthermore, Hickman & Illingworth (1980) suggested from condition index studies of *P. canaliculus* at 7 sites in central and northern New Zealand during 1973–75 that spawning was more prolonged at the northern compared with the southern localities. They concluded that 2 spawning peaks occurred, in spring/early summer and in autumn, with the autumn spawning being the heavier in central New Zealand and spring spawning heavier in the north.

Studies undertaken at 'contiguous' locations (localities separated by less than 20' latitude and which are hydrologically similar) in the Hauraki Gulf area (Auckland 1962–65; Coromandel Harbour 1970–73, 1979–80; Te Kouma Harbour 1967–69; Hauraki Gulf 1968–70) indicated spawning seasons of similar duration and timing, and with spawning peaks occurring at least during spring. The main exceptions were that no summer or autumn settlements were observed at Auckland during 1962–63 or in Coromandel Harbour during 1979–80.

Sampling extended for more than 2 years at 3 localities (Coromandel Harbour, Te Kaha, and the Marlborough Sounds), and some differences in the inferred spawning seasons between years were evident. The summer and autumn spawnings may not have occurred in Coromandel Harbour during 1979–80, and the spring spawning may have been very late in parts of the Marlborough Sounds during 1977. In addition, evidence from seaweed strandings point to spring settlement being variable from year to year off Ninety Mile Beach.

In summary, the data for *P. canaliculus* suggest that although spawning occurs at least during spring in northern and central New Zealand, there is some variation between discrete localities with respect to spawning at other times of the year. There is some evidence from condition index studies for a direct relationship between latitude and length of the spawning season. Contiguous localities usually had similar spawning seasons, but spawning seasons were not always entirely consistent between years for particular localities.

*Aulacomya ater maoriana* spawned during spring at 1 locality near Banks Peninsula during 1973–74.

*Modiolus areolatus* has been studied at 2 localities (Bay of Islands and Raumati Beach), and at least late summer, late autumn, and spring spawning seasons are indicated. Late summer and late autumn were the peak spawning periods in common between the 2 localities. Spawning at the more northern locality was much more prolonged than at the southern one during 1970–72.

At least late winter and spring spawning is indicated for *Xenostrobus pulex* at 7 localities between the Bay of Islands and Raumati Beach, with spring being part of the peak spawning period for all localities. However, spawning throughout the year seems likely for many North Island localities. In studies undertaken simultaneously at discrete localities, spawning was much more prolonged at Piha than at Auckland during 1962–63, and at the Bay of Islands and Raumati Beach compared with Wellington Harbour during 1970–72. In addition, the main spawning season was of much shorter duration at the Bay of Islands and Wellington Harbour compared with Raumati Beach.

*Modiolarca impacta* spawned at least during spring and summer at 3 localities (Bay of Islands, Raumati Beach, and Wellington Harbour), with summer being part of the peak spawning period for all localities. Although spawning appeared to be much less prolonged at Raumati Beach than at the Bay of Islands or Wellington Harbour during 1970–72, spawning throughout the year seems likely in many North Island localities.

#### SUPERFAMILY PECTINACEA

##### PECTINIDAE

*Pecten novaezelandiae* has been studied at 5 localities, 2 in the North Island (Mahurangi and Coromandel Harbours), and 3 in the north of the South Island. Further estimates of spawning times are available from Bull's (1980) growth back calculations for juveniles. These point to spawning in Fiordland and Takatu Peninsula at least during spring in 1971 and 1976 respectively; at least spring in 1976 at Whitianga; at least spring and early summer 1976–77 in Manukau Harbour; and at least summer and early autumn 1976–77 in Coromandel Harbour. Hence, spawning took place at least during spring and/or autumn in all studies. The peak spawning period varied with locality.

Spawning seasons at discrete localities during the same years were similar; spawning occurred during spring, summer, and probably autumn at each of 3 localities (Marlborough Sounds, Tasman and Golden Bays) during 1978–79. However, there appeared to be some variation in spawning season between years at both the Marlborough Sounds and

Tasman Bay, although different methods were used to assess the season in each of the years of study for Tasman Bay at least.

*Chlamys zelandiae* has been studied at 4 localities between the Bay of Islands and Wellington Harbour. Spawning seasons (and peaks in spawning) appeared to vary with locality, but spawning throughout the year is possible in many North Island localities. However, spawning was much more prolonged at the Bay of Islands and Wellington Harbour than at Raumati Beach during 1970–72.

#### SUPERFAMILY PTERIACEA

##### PINNIDAE

*Atrina pectinata zelandica* spawned at least over summer during 1970–72 at the Bay of Islands, Raumati Beach, and Wellington Harbour, and also during autumn and winter at the Bay of Islands and Wellington Harbour. The peak spawning period included summer for all localities.

#### SUPERFAMILY ANOMIACEA

##### ANOMIIDAE

*Anomia trigonopsis* spawned during summer and autumn at 2 northern localities (Bay of Islands and Auckland) and also during spring at Auckland. Settlement at Auckland during 2 separate periods (1954–55 and 1962–63) indicated similar spawning periods, except it was probably of shorter duration during 1962–63. Peak spawning months varied with locality.

#### SUPERFAMILY OSTREACEA

##### OSTREIDAE

*Tiostrea lutaria* has been studied at Auckland, Wellington Harbour, and Foveaux Strait, where spring and early autumn spawnings probably occur in addition to summer spawning. Studies made in Wellington Harbour during 1960–61 and Foveaux Strait during 1960–64 indicated similar length spawning seasons, with late spring and summer peaks, whereas a shorter season (and probably later peak) was observed at Auckland during 1962–63.

*Saccostrea glomerata* showed late spring, summer, and early autumn spawning at 5 localities in northern New Zealand, and Curtin (1973) provided evidence for similar spawning periods in several other areas of Northland. Several of the studies listed in Table 3 were made over the same years (1970–72), and at 2 localities (Bay of Islands, Mahurangi Harbour) the studies extended for more than 2 years, with consistent spawning patterns. Peak spawning months occurred between November and March.

Although studied at fewer localities, *Crassostrea gigas* and *Ostrea aupoiria* appear to have spawning periods similar to *S. glomerata*.

## SUPERFAMILY LEPTONACEA

## ERYCINIDAE

*Kellia cycladiformis* and *Arthritica bifurca* appeared to spawn throughout most of the year at northern (Bay of Islands) and southern (Raumati Beach and Wellington Harbour) locations during 1970–72, with summer being the peak spawning time in common. *Lasaea rubra hinemoa* and *Borniola reniformis* probably also spawn throughout the year in the North Island, with summer being the peak period in common for *B. reniformis*.

## SUPERFAMILY VENERACEA

## VENERIDAE

*Chione (Austrovenus) stutchburyi* probably spawned at least during spring and summer (peak spawning period) at both northern (Bay of Islands) and southern (Wellington Harbour) localities during 1970–72. Venerid I probably spawns throughout the year at these 2 localities, the peak varying with locality.

## SUPERFAMILY MACTRACEA

## MESODESMATIDAE

*Paphies australis* spawned throughout the year at both northern (Bay of Islands) and southern (Wellington Harbour) localities during 1970–72. However, it appeared to have a shorter spawning season at Raumati Beach where it is much less common. Summer was the peak spawning time in common between localities.

*P. ventricosa* studied at 2 contiguous localities on the west coast of Northland appeared to spawn at least during spring, but possibly throughout much of the year. However, at 1 of these localities (Dargaville Beach), different spawning seasons were indicated between years (1938–40, 1968–71). Based on the most detailed study, the peak spawning period in this area is probably September–February.

*P. subtriangulata* has been studied at a single northern locality, and at least spring and early summer spawning is indicated.

## SUPERFAMILY HIATELLACEA

## HIATELLIDAE

*Hiatella arctica* probably spawns throughout the year in the North Island, given the larval occurrences at the Bay of Islands, Raumati Beach, and Wellington Harbour during 1970–72. Winter and early spring were the peak spawning periods in common.

## SUPERFAMILY PHOLADACEA

## PHOLADIDAE

*Anchomasa similis* spawned at least during winter, and probably spring, at 2 northern (Bay of Islands and Auckland) and 2 southern (Raumati Beach and Wellington Harbour) localities.

Late autumn, winter, and spring spawning is indicated for *Pholadidea spathulata* at Auckland.

## TEREDINIDAE

Spawning of *Bankia australis*, *Lyrodus pedicellatus*, *L. medilobatus*, and *Nototeredo edax* occurred during summer and autumn (and early winter for the *Lyrodus* spp.) at Tauranga Harbour during 1970–72. *Bankia neztalia*, however, spawned throughout most of the year in Tauranga (peaks in summer and winter/early spring) and Wellington Harbours (winter and spring) during 1970–72. Although this species probably also spawned throughout the year in Wellington Harbour during 1949–50, peak spawning occurred at a different time (summer and early autumn). A similarly prolonged spawning season and summer/autumn peak occurred in Otago Harbour during 1952–53.

## SUMMARY

Although the observations cover only 1–2 years for most species at most localities, general indications of the spawning seasons are apparent. However, the inadequacy of some of the sampling methods used may partially obscure spawning patterns.

Spawning seasons, including peak periods, varied considerably between species, with several species spawning at any 1 time of the year. However, there were spawning seasons (and peaks) in common between localities and years for most species, even though they seldom exactly coincided.

Species studied at discrete localities (localities separated by at least 20' of latitude, or which are hydrologically dissimilar) during the same period sometimes showed considerable variation in inferred spawning season. However the peak spawning periods usually overlapped or coincided between localities. There was no clear evidence of any direct relationship between latitude and the length of the spawning season for any species, although the limited data do not preclude this possibility.

Species studied at contiguous localities (localities separated by less than 20' latitude and which are hydrologically similar) usually had similar spawning seasons and peaks. Inferred spawning seasons were often similar for species studied at the same locality over different years, and spawning peaks usually occurred at the same time of the year.

### Length of spawning season

The observations suggest that although some species have a relatively short (4 months or less), well-defined spawning season at some localities during some years, for most it is much more prolonged, perhaps with 'trickle' spawning through several months of the year. Generally it is unknown whether the extended spawning period is caused by some individuals spawning more than once during the year, or by lack of synchronised spawning.

### Spawning seasons and bivalve families

Of the families represented in these data by 3 or more species, the Mytilidae (with the possible exception of *Aulacomya ater maoriana*) and Erycinidae spawn over many months. Spring was the peak spawning period in common for the mytilids, all of which were studied at localities north of Banks Peninsula. Summer was the peak spawning period in common for the erycinids, studied as far south as Wellington Harbour. Members of family Ostreidae tend towards shorter spawning seasons, with peaks in late spring and summer (for *Saccostrea glomerata*, *Ostrea aupouria*, and *Crassostrea gigas* in Northland, and *Tiostrea lutaria* between Auckland and Foveaux Strait). The family Teredinidae contains species with both long and short spawning seasons, peaks varying with species and locality.

### Spawning season and sea temperatures

Sea temperature is recognised as a critical factor in the regulation of the breeding of marine animals (Orton 1920; Giese 1959). Latitudinal variation in sea temperature means that for some species in some localities spawning temperatures are seldom reached, and the species therefore occurs uncommonly (e.g., *Saccostrea glomerata* in southern localities).

Species with the most obvious link between sea temperature and spawning were usually those with short, well-defined seasonal occurrences in the plankton such as *Anomia trigonopsis* (larvae first seen in the Bay of Islands plankton when the sea surface temperature had risen to about 21°C), *Ostrea aupouria* (19°C), *Saccostrea glomerata* (21°C), and *Crassostrea gigas* (22°C) (Table 3; Dinamani 1974b; Booth 1979a). The main settlement of *Tiostrea lutaria* in Foveaux Strait begins in spring after the water temperature has reached 10–11°C (Cranfield 1979). Based on settlement times, McKoy (1981) suggested that the spawning of *Bankia australis*, *Lyrodus medilobatus*, *L. pedicellatus*, and *Nototeredo edax* in Tauranga Harbour occurred mainly at temperatures above 17–18°C.

A link between spawning and sea temperatures for most species with prolonged occurrences in the plankton was not obvious other than that spawning

occurred over a certain broad range of temperature. For these species, sudden and specific changes in temperature, possibly in conjunction with other environmental changes, may be important in controlling spawning.

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**APPENDIX 1: Adult condition index analysis**

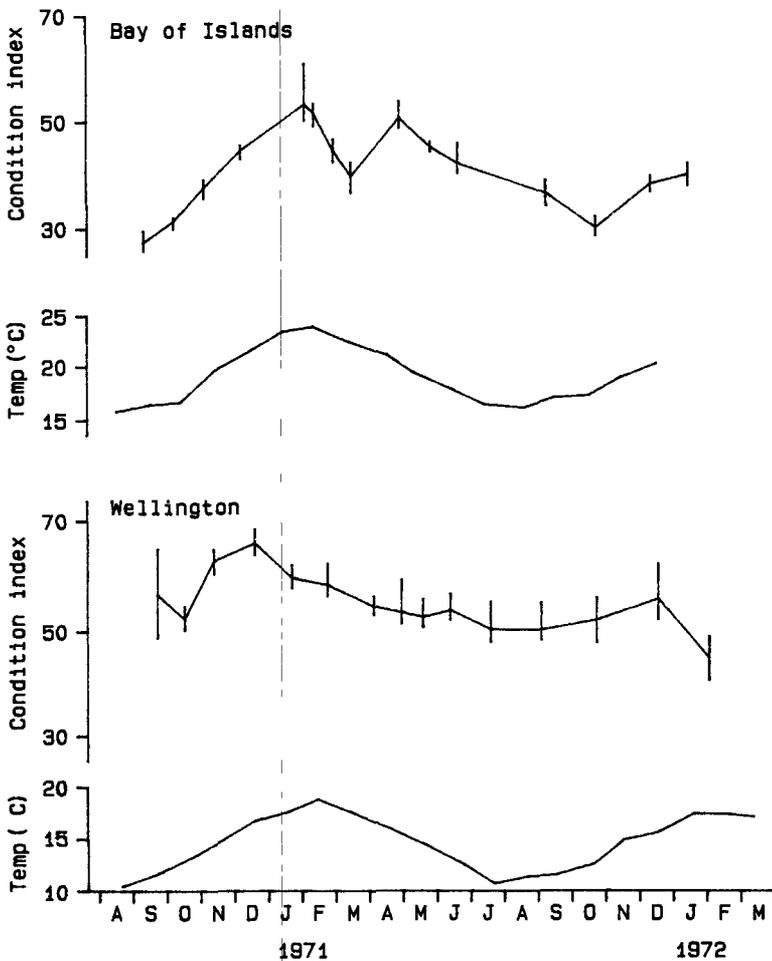
**METHODS**

The condition index of *Chione (Austrovenus) stutchburyi* from Wairoa Bay, Bay of Islands, and Petone Beach, Wellington Harbour, was studied from September 1970 to January 1972, and of *Paphies australis* from Shelly Bay, Kerikeri Inlet, Bay of Islands, from February 1971 to May 1972.

The condition index of 25 animals of similar size, taken from the same locality and tidal level, was measured, usually monthly, in 5 groups. The dry weight condition index of the firmly-closed *C.*

(*Austrovenus*) *stutchburyi* was determined by thoroughly cleaning all specimens and then placing the groups in a displacement jar similar to that described by Baird (1957) to record the volume of water displaced. The animals were then opened, and the volume of water displaced by the 5 pairs of valves alone was determined. The flesh of the 5 animals was then washed and dried at 60°C for 48 hours.

Condition index = (weight of dried flesh (g)/shell cavity volume (ml)) × 1000



**Fig. A1** Condition indices of *Chione (Austrovenus) stutchburyi* from the Bay of Islands (Wairoa Bay) and Wellington Harbour (Petone Beach), 1970-72. The vertical lines give the range of values for each group of 5 animals; mean values are joined. Monthly sea surface temperatures from Booth (1974, 1975).

A displacement method was not used for *P. australis*, because the animals were frequently found to be gaping before analysis. Condition index was determined by removing the flesh, draining the shell and flesh separately for a standard time (15 minutes) on filter paper, and then weighing.

Condition index = (weight of flesh (g)/weight of flesh + shell (g)) × 100

## Results

### *Chione (Austrovenus) stutchburyi* (Fig. A1)

BAY OF ISLANDS: The condition index cycle broadly followed that of the mean sea surface temperature, with peaks in water temperature and condition index occurring in February 1971. However, a rapid decline in condition, which may have followed spawning, occurred late in February and during March 1971. A rapid rise until mid-April was followed by a slow decline until October 1971. The condition index then slowly improved as the water temperature increased from October 1971 to January 1972.

WELLINGTON HARBOUR: There was less correlation between sea surface temperatures and condition index than in the Bay of Islands. The condition index peaked in December 1970 and December 1971. The most marked declines in condition index occurred during December-January 1970-71 and 1971-72. Otherwise, there was a steady decline in condition during most of the late summer, autumn, and winter of 1971.

The condition index of *C. (Austrovenus) stutchburyi* from Wellington Harbour was higher and showed less monthly variation than at the Bay of Islands. This may reflect a less abundant food source and/or a more prolonged spawning period in Wairoa Bay than at Petone Beach.

### *Paphies australis* (Fig. A2)

BAY OF ISLANDS: The condition index cycle broadly followed the pattern of sea surface temperature, but with a lag of about 2 months. High condition occurred in February-May 1971 and 1972. The rapid decline in condition occurring during May and June 1971 may possibly have been caused by spawning.

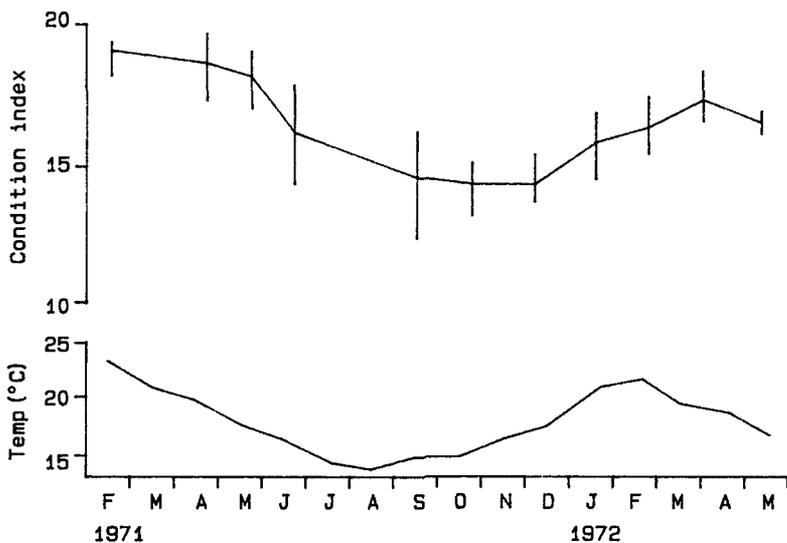


Fig. A2 Condition indices of *Paphies australis* from the Bay of Islands (Kerikeri Inlet), 171-72. The vertical lines give the range of values for each group of 5 animals; mean values are joined. Monthly sea surface temperatures from Booth (1974).